Aggregation behaviour in a neotropical dendrobatid frog (*Allobates talamancae*) in western Panama

Gareth R. Hopkins[1,2,3] **& Peter N. Lahanas**[2]

([1] Department of Biology and the Ecology Center, Utah State University, Logan, UT, USA;
[2] Institute for Tropical Ecology and Conservation (ITEC), Gainesville, FL, USA)

Summary

Aggregation is a common behaviour in a number of animal taxa and is used for a variety of purposes. For example, aggregation may be a response to environmental resources, sexual reproductive behaviour or an antipredator response. Although commonly recognized in a variety of taxa, amongst amphibians aggregation has rarely been reported in adult poison dart frogs (family Dendrobatidae). The Talamanca striped rocket frog (*Allobates talamancae*) is a small, non-toxic leaf-litter dendrobatid frog found in the Bocas del Toro archipelago of western Panama. The purpose of our study was to describe the dispersion pattern of *Allobates talamancae* and elucidate a possible explanation for this pattern. Based on observations of grouping behaviour in captive frogs, we hypothesized that *A. talamancae* significantly aggregate in natural habitats. We conducted a series of field-based experiments that indicate that this species does significantly aggregate in the wild. Preliminary results suggest that aggregation may be an adaptive response to predation risk. We discuss this possibility, as well as critique other explanations for aggregation in this species, placing these results in the broader theoretical context of aggregation as an adaptive behaviour in animals.

Keywords: aggregation, antipredator, Dendrobatidae, Anura, frog, *Allobates*, *Colostethus*, neotropics.

1. Introduction

The aggregation of animals in multi-individual groups is a widespread behavioural phenomenon observed in a diversity of taxa. Perhaps most well-known are large congregations of migrating mammals (e.g., Fryxell, 1995),

flocks of birds (e.g., Miller, 1922; Heppner, 1974), or colonies of social insects (e.g., Holldobler & Wilson, 1990), but aggregation is also observed in many other invertebrate (e.g., Waters, 1959; Heip, 1975) and vertebrate (e.g., Graves & Duvall, 1995; Domeier & Colin, 1997) taxa. In the Class Amphibia, aggregation is well known in larvae (Brodie & Formanowicz, 1987; Glos et al., 2007; Smith & Awan, 2009) but is less recognized in adult animals. Amongst the poison dart frogs of the neotropics (family Dendrobatidae), aggregations of adult frogs have very rarely been reported.

Animals aggregate for a variety of ecological and behavioural reasons. Aggregation can occur as a result of shared resource use (i.e., light, water, or food concentrated in one area), as a result of sociality, aggression, direct competition, or as a byproduct of reproductive strategies (Wells, 1977; Graves & Duvall, 1995; Karvonen et al., 2000; Knopp et al., 2008). In addition, some animals aggregate to reduce parasite loads and/or risk of predation through dilution amongst group members (Hamilton, 1971; Arnold & Wassersug, 1978; Graves et al., 1993; Glos et al., 2007; Smith & Awan, 2009). In his classic paper 'Geometry for the Selfish Herd', W.D. Hamilton (1971) gives the hypothetical example of frogs jumping towards each other to avoid predation, diluting their individual risk until they 'quickly collect in heaps' (p. 296).

Hamilton's (1971) example was purely theoretical, but empirically, among anurans, tadpoles will often aggregate in response to predation risk (Brodie & Formanowicz, 1987; Glos et al., 2007; Smith & Awan, 2009), or for thermal benefits (Espinoza & Quinteros, 2008). Newly metamorphosed *Anaxyrus* species have also been reported to aggregate to reduce desiccation amongst individuals (Heinen, 1993), as well as reduce risk of individual predation (Arnold & Wassersug, 1978; Graves et al., 1993). Except for reproductive reasons (Lynch & Wilczynski, 2006; Swanson et al., 2007; Knopp et al., 2008; and reviewed in Wells, 1977), reports of aggregation behaviour in adult anurans are rare and, thus, to our knowledge, Hamilton's (1971) classic hypothetical example using adult frogs remains largely untested.

The Talamanca striped rocket frog (*Allobates talamancae* Cope) is a small (male SVL = 17–24 mm, female SVL = 16–24 mm), non-toxic member of the family Dendrobatidae which feeds on small arthropods in the leaf-litter of primary and secondary lowland wet forests in Central America (Savage, 2002). Aggregation behaviour in this frog, like most other dendrobatids, has

Figure 1. Photograph of four grouped captive *A. talamancae* sitting centimetres apart from each other in a terrarium.

not been described before. We observed in the laboratory that captive *A. talamancae* individuals will tend to aggregate in multi-individual groups (Figure 1), and are not evenly distributed in a terrarium. This observation led us to the purpose of this study, which was to determine if *A. talamancae* significantly aggregates in its natural habitat and to elucidate a possible explanation for aggregation in this understudied species of dendrobatid frog.

2. Materials and methods

2.1. Study area

This study took place at the Institute for Tropical Ecology and Conservation's Bocas del Toro Biological Station, and in the tropical lowland wet forests in the surrounding area of Boca del Drago on Isla Colon in the Bocas del Toro archipelago in western Panama (lat. 9°20′40.7″N, long. 82°30′54.1″W).

2.2. Experiment 1: Dispersion of frogs along a 20 m transect in a lowland forest habitat

In the morning of July 6, 2009, five 20-m transects were laid out in a lowland forest habitat with fairly homogeneous leaf litter that had been cleared of the majority of under-story vegetation. Non-overlapping transects were laid out at randomly chosen angles of 110, 340, 224, 88 and 148° by placing a metre

tape on the ground. Each transect was then walked and the location of every *A. talamancae* within a 1.0 m distance from either side of the transect was noted by placing a small piece of flagging tape at its location. Twenty random numbers between the values of 0.0 and 20.0 were then chosen along each transect using a random number table, and the distance from these points to the location of each frog was measured, as prescribed by the point-quarter distance method (Krebs, 1989). The point-quarter distance method was used to determine the dispersion pattern of frogs along each transect. A ratio of variance/mean < 1 indicated a uniformly distributed population, a ratio equal to 1 indicated a randomly distributed population, and a variance/mean ratio > 1 indicated a clumped or aggregated population.

2.3. Experiment 2: Dispersion and nearest neighbour analysis of frogs in a 500 m² plot in a lowland forest habitat

On July 8, 2009, a 50×10 m plot was laid out in the same forest as Experiment 1, by placing metre tape along the ground to mark out the plot boundaries. Two observers, evenly spaced along the 10 m, walked the length of the plot, and dropped a small flag at every location where a frog was observed. The distance from each flag to both its neighbour flag, and its second nearest neighbour was then measured to be used in a nearest neighbour analysis of patterns of dispersion in this plot, where the mean distance to nearest neighbour and the mean distance to second nearest neighbour was calculated and compared using a paired t-test ($\alpha = 0.05$). In addition, across this 50×10 m plot, 125 4.0 m² quadrants were placed and the number of frogs found in each quadrant was counted to be used to calculate indices of dispersion in the plot. The variance/mean ratio of number of frogs was calculated, as well as Morisita's Index of Dispersion (Morisita, 1962; Graves et al., 1993), which was compared against an index value indicating randomness, using a Chi-Squared test, with $\alpha = 0.05$.

2.4. Experiment 3: Directional response of frogs to 'predation risk' in a terrarium habitat

Eight *A. talamancae* ($N_{\male} = 2$, $N_{\female} = 6$) were collected through manual search efforts, July 1–2, 2009, in a lowland tropical wet forest. These animals were placed in a 113.6 l terrarium with approximately 2 cm of dried leaf litter collected from the same forest habitat from which the frogs were collected.

The leaf litter was homogenously distributed so as to provide a similar habitat throughout the terrarium. A small plate with a quarter of a ripe banana was placed in the centre of the terrarium to attract frugiverous insects to provide a food source for the anurans. A mesh screen was then placed over the terrarium to prevent the frogs from escaping, and the habitat was evenly misted with water for moisture. Prior to experimentation, the animals were given a week to habituate in the terrarium.

For the experiment, a misted, empty 38 l terrarium was placed in a separate area that provided homogenous environmental characteristics (i.e., light level) throughout the enclosure. Two randomly chosen frogs were placed on one side of the terrarium, while the other side of the terrarium was left bare. A third frog (focal frog) was then placed directly in the centre of the terrarium, facing neither the other two frogs nor the bare side of the terrarium. After approximately 15 s of acclimatization, an observer then brought his hand directly down on top of the middle frog as if to catch the animal. This action was repeated up to five times until the focal frog initiated a flight response. The direction of flight, either towards the other two frogs or the bare side of the terrarium, was recorded. This procedure was repeated for each of the eight captive frogs. In all cases, only the focal frog exhibited a flight response, with the other two frogs not moving during the simulated 'attack'. To determine if there was an effect of what side of the terrarium the two frogs were placed, the whole experiment was repeated with the two frogs placed on the opposite side of the terrarium (rotate from 'position 1' to 'position 2'). The number of frogs that fled to either direction was summed and compared using logistic regression ($\alpha = 0.05$), with the binomial response variable being presence or absence of focal frog on side of terrarium, after 'predation' threat.

3. Results

3.1. *Experiment 1: Dispersion of frogs along 20 m transects in a lowland forest habitat*

A total of eighteen *A. talamancae* (adult females, males, and subadults) were counted in this experiment. No frogs were located along transect 5. As such, this transect was excluded from any further analysis, and only results for transects 1–4 are presented in Figure 2. The number of frogs
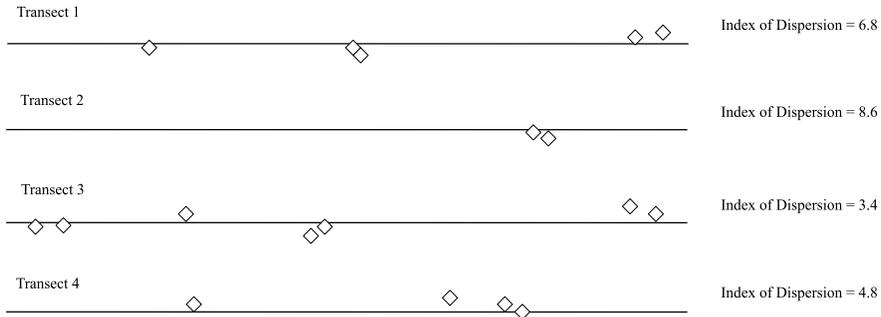
Transect 1   Index of Dispersion = 6.8

Transect 2   Index of Dispersion = 8.6

Transect 3   Index of Dispersion = 3.4

Transect 4   Index of Dispersion = 4.8

Figure 2. The locations of *A. talamancae* on 20 m line transects in a lowland forest in Bocas del Toro, Panama (diamonds represent *A. talamancae* individuals). Variance: mean ratios are presented for each transect, showing a significantly clumped population distribution in each case (index of dispersion > 1.0).

found along each transect varied between 2–7 individuals. In each case, the variance/mean ratio > 1.0, indicating their distributions were significantly clumped, and that the frogs were aggregating in the wild (Figure 2).

3.2. Experiment 2: Dispersion and nearest neighbour analysis of frogs in a 500 m^2 plot in a lowland forest habitat

The mean distance from one individual *A. talamancae* to another in the 500 m^2 plot was 1.02 ± 0.10 m, which was significantly less than the mean distance to its second nearest neighbour, 2.69 ± 0.14 m (paired $t_{102} = 9.37$, $p < 0.0001$), indicating that frogs were not uniformly distributed throughout the plot (Figure 3). When the number of frogs within quadrants was calculated, frogs were found to be in a significantly clumped or aggregated distribution throughout the plot (Figure 4), with a variance/mean ratio of 1.33, and a Morisita's Index of Dispersion of 1.80, which was significantly different from random ($\chi^2_{124} = 165.75$, $p < 0.01$).

3.3. Experiment 3: Directional response of frogs to 'predation risk' in a terrarium habitat

When *A. talamancae* were 'threatened' by a simulated predation event, 7 out of 8 frogs jumped to the side of the terrarium where two other frogs were located, versus the bare side of the terrarium (Figure 5). When the two frogs were placed on the other side of the terrarium, and the experiment was repeated, 6 out of 8 frogs jumped to the group of frogs present in the
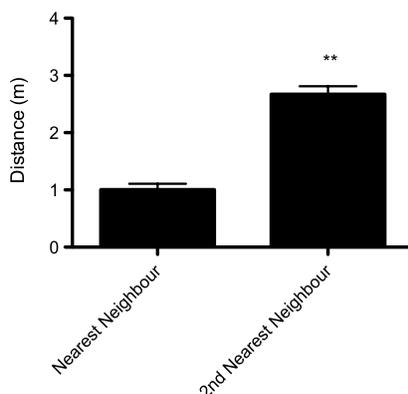
Figure 3. Mean ± SE distances from each *A. talamancae* to its nearest neighbour and second nearest neighbour in a 500 m² plot in lowland forest habitat in Bocas del Toro, Panama. Asterisks indicate significant differences between means (paired $t_{102} = 9.37$, $p < 0.0001$).

terrarium (Figure 5). In both cases, significantly more frogs chose to flee to the side of the terrarium where conspecifics were present, versus the side of the terrarium without frogs (position 1: $\chi^2_{14} = 10.12$, $p < 0.001$; position 2: $\chi^2_{14} = 4.19$, $p < 0.05$).

4. Discussion

Allobates talamancae were observed to significantly aggregate in natural habitats. Our preliminary observations in captivity revealed that frogs were found in mixed-sex groups of 2–5 individuals (Figure 1), and in our experiments in nature we found mostly groups of two or three individuals. Our observation of aggregation behaviour in this dendrobatid contrasts with results by Summers (2000) that indicate encounters between *A. talamancae* individuals in the wild are relatively rare. Aggregation in post-metamorphic *Anaxyrus cognatus* in both captivity and the wild has been reported (Graves et al., 1993), but other than reports of breeding aggregations (Wells, 1977; Lynch & Wilczynski, 2006; Swanson et al., 2007) there are very few published cases of aggregation by adult anurans in either captivity or the wild. Tinbergen (1963) famously asked the question: How does the behaviour of an animal promote its ability to survive and reproduce? Here, we discuss and critique possible answers to this question of adaptivity in regards to our observations of aggregation behaviour in *A. talamancae*.
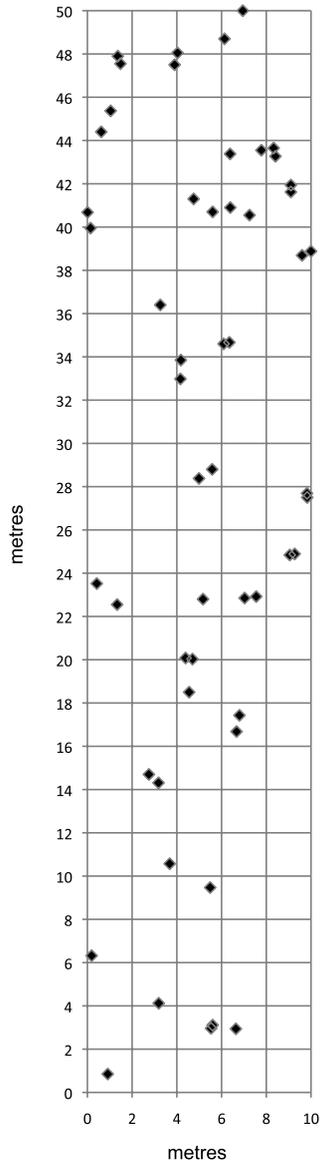
Figure 4. Map of 500 m² plot in a lowland forest habitat in Bocas del Toro, Panama, with dots showing the location of each *A. talamancae* frog found ($N = 53$) (*x*- and *y*-axes are in m). The 4.0 m² grid shown indicates the location of each of the 125 4.0 m² quadrants used in dispersion analyses (grid lines added after for visual effect). Frogs were significantly aggregated in the plot (variance/mean ratio = 1.33; Morisita's Index of Dispersion = 1.80, $\chi^2_{124} = 165.75$, $p < 0.01$).
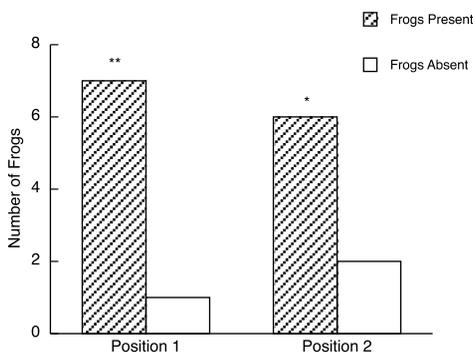
Figure 5. The directional movement of *A. talamancae* frogs (*y*-axis) when threatened by a 'predator' in experimental terrarium trials. Significantly more frogs moved towards conspecifics ('frogs present' vs. 'frogs absent') when threatened. (**position 1: $\chi^2_{14} = 10.12$, $p < 0.001$; *position 2: $\chi^2_{14} = 4.19$, $p < 0.05$). Position 2 differs from position 1 by the location of frogs in the terrarium moving 180°.

Aggregation as an antipredator behaviour is likely adaptive, and it is well documented in a variety of taxa, ranging from insects, birds and fish to bats and ungulates (reviewed in Hamilton, 1971; Vulinec, 1990). According to Hamilton (1971), animals will selfishly move closer to conspecifics when threatened by predation, so as to minimize their individual potential contact with predators, which is more likely when one is alone or on the margins of a group. Although Hamilton (1971) initially outlined his theory with adult frogs, aggregation as an antipredator behaviour has primarily been empirically demonstrated only in larval anurans (Brodie & Formanowicz, 1987; Spieler & Linsenmair, 1999; Glos et al., 2007; Smith & Awan, 2009). Arnold & Wassersug (1978) do, however, hypothesize that aggregation behaviour in post-metamorphic *Anaxyrus boreas* is an antipredator strategy, in which the 'selfish herd' (Hamilton, 1971) effect applies. This was also found to be true with post-metamorphic *Anaxyrus cognatus*, which aggregated in response to conspecific chemical cues and appeared to flee predators faster when in groups than alone (Graves et al., 1993). Our result that the vast majority (75–87.5%) of *Allobates talamancae* tested will significantly move to an aggregation of conspecifics when threatened by a 'predator' suggests a similar antipredator function may exist in this leaf litter frog; thus, it provides some of the first preliminary empirical evidence of the 'selfish herd' effect that Hamilton (1971) theoretically described in adult frogs. Aggregation may seem to be a counter-intuitive antipredator strategy, as predators may be able

to see larger groups more easily. However, aggregation as an antipredator response is selfishly selected for by the individual, not the group or species (Williams, 1966; Hamilton, 1971) and, thus, the individual benefits of risk dilution indicate that aggregation may still be selected for as an antipredator response.

There is also a possibility that aggregation by frogs may not be a 'selfish herd' effect (Hamilton, 1971), but rather function to confuse a predator (Miller, 1922), as has been shown for aggregations of marine insects (Treherne & Foster, 1981) and *Daphnia* (Milinski, 1979). Large groups of prey items all moving together make it more difficult for a predator to chose which prey item to attack (Miller, 1922), and as such, predator latency to attack is increased, and attacks are generally reduced in number (Milinski, 1979). The effectiveness of aggregations in producing a predator confusion effect is dependent on the size of the aggregation (Miller, 1922; Milinski, 1979), and without actual predation data, we do not know what that effective size might be for *A. talamancae*. Poulin et al. (2001) however found no *Allobates* species present in an avian predator's diet (that readily ate other neotropical frog and lizard species) and while this could be due to a number of reasons, it might be suggestive of an effective predator-mediated aggregation in *A. talamancae*.

Regardless of the specific reason for antipredator aggregation (i.e., dilution, Hamilton, 1971; or confusion, Miller, 1922), the development of this behaviour would likely be especially beneficial for *A. talamancae*, as unlike its more colourful dendrobatid cousins, this species has no known protective skin toxins (Savage, 2002) and, thus, selection should favour development of alternative predator avoidance and antipredator measures.

Aggressive and competitive behaviours, often tied with reproductive strategies, can sometimes result in multiple individuals of a species coming into contact with each other. This is well documented in a variety of vertebrate taxa, including mammals (Fryxell, 1987), birds (Karvonen et al., 2000), fish (Domeier & Colin, 1997) reptiles (Graves & Duvall, 1995) and amphibians (Wells, 1977). Aggressive behaviours between individual *A. talamancae* frogs in our study were never observed in either captive or natural environments, and this is in concurrence with the observation that neither male nor female *A. talamancae* appear to show aggressive behaviour (such as fighting) to each other (unlike many closely related *Dendrobates* and *Phyllobates* species) (Summers, 2000). *A. talamancae* males have been shown to not be

subject to mate guarding, nor is there evidence of female preference for a particular male (Summers, 2000). This tolerance of multiple individuals around mates suggests a reproductive strategy in *A. talamancae* that could be conducive to aggregation, though Summers (2000) did not note the occurrence of this phenomenon in his study. Breeding aggregations and lekking behaviour are common in anurans that are explosive breeders (Wells, 1977; Swanson et al., 2007; Knopp et al., 2008; Smith & Awan, 2009), but have not been reported to such a degree in prolonged breeders that reproduce throughout the year (Knopp et al., 2008). While *A. talamancae* is a prolonged breeder, it is possible that some modified form of lekking or reproductive aggregation could still occur, and this hypothesis is consistent with our observations of multiple females and males in the same group in captivity. We were unable to readily identify males and females in the field without catching them, and so information on the sexual make-up of individual groups of frogs found in the forest is not available. A possible inconsistency with reproductive behaviour being a driving force behind observed aggregations in our study is the fact that while being overall prolonged breeders, most related *Allobates* species reportedly mate more regularly in the rainy season, generally between November and May (Juncá et al., 1994; Juncá, 1998; Lima et al., 2002). This study was conducted in early July, past that period of increased reproductive activity, and we observed no mating occurring during the study (G.R.H., personal observation).

Animals will often aggregate around a particular environmental resource, such as food or water. Classic examples of this phenomenon include the aggregation of birds and mammals around watering holes in east Africa (Ayeni, 1975), and the annual congregation of bear (*Ursus arctos*) predators to streams of spawning salmon and trout prey in North America (Mattson & Reinhart, 1995). Among amphibians, however, predator attraction to prey in frogs does not appear to be a significant determinant in predicting overall spatial patterns of predatory frogs in the wild (Hammond et al., 2007). In addition, reported aggregations of post-metamorphic *Anaxyrus cognatus* did not occur as a response to environmental conditions, but rather as a result of attractions to conspecifics (Graves et al., 1993). It is unlikely that attraction to resources was a significant influencing factor in the aggregation of *A. talamancae* in this study. Although we cannot rule out environmental differences within microhabitats definitively, we made every effort to ensure a homogenous environment in the wild and aggregation towards any one part of the natural habitat was not observed.

We have here presented evidence of aggregation behaviour occurring in a wild adult neotropical dendrobatid leaf-litter frog. Quantitative observations of this sort for the family Dendrobatidae are extremely rare, and our results that aggregation may be an antipredator response for *A. talamancae* suggest a significant adaptive value for this under-reported behaviour in adult frogs.

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