

Alternative mating tactics in the strawberry poison frog (*Oophaga pumilio*)

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Alternative mating tactics are common in anuran amphibians. Calling males are sometimes parasitized by non-calling satellite males that adopt a conditional strategy associated with a lower reproductive success. In most dendrobatid species, males are highly territorial and use calls to attract females and deter competitors. In this study, a satellite tactic used by *Oophaga pumilio* males is reported for the first time. The satellite tactic was adopted both by territorial and non-territorial males, and was aimed at attracting females in the territory of calling males. This satellite behaviour seems to be facultative, depending on the ability of males to defend a territory, and on the distribution of receptive females.

Key words: Dendrobatidae, mating behaviour, poison-dart frog, satellite tactic

Mating behaviour can differ vastly between individuals within a species (Alcock, 2005), and Shuster & Wade (2003) demonstrated how males unable to compete for access to females using the primary mating tactic should adopt an alternative tactic as part of a conditional strategy. Alternative “satellite” tactics are common in anurans (Halliday & Tejedo, 1995; Gerhardt & Huber, 2002; Wells, 2007). Non-calling satellite males position themselves near calling conspecific males, and attempt to intercept females that are attracted to the calls. The adoption of the satellite tactic is mediated by various factors. When established males hold territories and attack other males that signal within them, adopting a satellite tactic may be the only possibility for small, young, or weak individuals to reproduce. Depletion of energetic reserves needed for calling or the risks posed by acoustically orienting predators and parasites might also promote satellite behaviour (Gerhardt & Huber, 2002; Wells, 2007).

Alternative mating tactics have been documented in the anuran families Bufonidae, Hylidae, Hyperolidae, Lepto- (or Eleuthero-) dactylidae, Myobatrachidae, Ranidae and Racophoridae (see Wells, 2007 for a review). This report describes the first observations on the alternative mating tactics used by a neotropical dendrobatid frog, the strawberry poison frog (*Oophaga pumilio*). The ecology and reproductive behaviour of males of this diurnal, toxic, aposematic and polygamous species are well known (Pröhl & Hödl, 1999; Meuche et al., 2011). This species has a prolonged breeding period throughout the

tropical rainy season (which lasts from approximately April to December) during which males defend their territories. Territories can remain stable for several months or years (Pröhl & Hödl, 1999). Males use advertisement calls to attract females, and advertisement calls, aggressive calls and physical combat to defend their territories against intruding males. Both calling sites and oviposition sites are located inside the territories of males. Oviposition normally takes place in the leaf litter, very often on dry leaves covered by other leaves (pers. obs.). The species has no amplexus. Males actively court females using advertisement calls, courtship calls and touching. If the female accepts the male, she follows it to an oviposition site. Females are morphologically indistinguishable from males, possess larger home ranges that cover several male territories, and perform most of the parental care (Weygoldt, 1987; Meuche et al., 2011).

Our study was conducted in a Caribbean lowland rainforest at Hitoy Cerere Biological Reserve in Costa Rica (9°40'N, 85°05'W), from April to December 1996 and 1997, and from August 2004 to August 2005. In 1996 and 1997, the study area was located in an old secondary forest with transition to primary forest. The vegetation consisted mostly of trees, palms, lianas and *Dieffenbachia* sp. (Araceae). In 2004 and 2005, two study areas were established in an old banana plantation with transition to a young secondary forest. The vegetation was mainly composed of perennial plants such as banana (*Musa* sp., Musaceae), *Heliconia* sp. (Heliconiaceae), or *Calathea* sp. (Maranthaceae), and caoutchouc trees (*Castilla elastica*). The study plots measured 884 m² (1996, 1997), 2400 m² (2004) and 505 m² (2005), and were divided by nylon strings into 1 m² quadrats to record the spatial distribution of all males for analysis of their territorial behaviour (Pröhl & Berke, 2001; Meuche et al., 2011). As calling behaviour was most intense from 0700 to 1000, and both mating and oviposition only occur in the morning (Pröhl, 1997), male behaviour was studied from 0600 to 1200. A territory was defined as the calling area of one male that was defended from male intruders (Pröhl & Berke, 2001; Meuche et al., 2011). Photos of each male and female were taken for re-identification using their individual patterns of black spots and short lines on the red dorsal ground colour. Because individual patterns change over time (Meuche, 2009), frogs were also toe-clipped.

One male in 1996 (population size N=15), none in 1997 (N=12, of which five males were also present in 1996), three males in 2004 (N=29) and one male in 2005 (N=13) adopted a satellite tactic. These five satellite males intruded into the territories of calling males and either did not call (behaving like a female) or called using a very low volume. They either remained undetected by the territory owner or the territory owner tried to court them.

All males seemed to adopt the satellite tactic facultatively as part of a conditional strategy. In 1996, the satellite male (S1, Table 1) was a non-territorial male that visited the territories of two other males and attempted to solicit females to move to an oviposition site by calling softly.

Table 1. Evidence of satellite behaviour in five strawberry poison frog males. Numbers refer to the frequency with which specific behaviours occurred.

Satellite male	Defence of territory	Observed in territories of other males	Calling in territories of other males	Courted by territorial males	Courting females in territories of other males	Courting females outside territories of other males	Successful matings inside territories of other males	Successful matings outside territories of other males
S1 (1996)	No	6	No: 4 Yes: 2 (very low)	3	2	5	0	0
S2 (2004)	Unknown	1	No	1	1	Unknown	1? ¹	Unknown
S3 (2004)	Unknown	1	1 (very low, only few notes)	1	1	Unknown	0	Unknown
S4 (2004)	Yes	1	No	1	1 ²	13	0	1
S5 (2005)	Yes	4	No: 2 Yes: 2	2	2	11	2	3

¹Satellite male and female followed the territory owner to oviposition site. It is unknown whether the satellite male fertilized some of the eggs.

²Male started courtship inside its own territory and then led the female into the territory of a second male.

The (non-territorial) male also attempted to attract females by calling in areas that were not defended by other males; no successful mating attempts were observed. In 2004 and 2005, at least two of the males observed adopting a satellite tactic also defended their own territories. Both entered the territory of a neighbouring male where they courted the females present (S4 and S5, Table 1). Male S5 successfully mated with two females. Occasionally non-calling satellite males were courted by the resident male, and followed it together with a female to an oviposition site (Table 1). In one case, the satellite male (S2) spent considerable time with the pair where the eggs were laid. Unfortunately, it was not possible to observe whether the satellite male, which left the oviposition site after the territory holder, was able to fertilize the laid eggs.

The present observations show that both territorial and non-territorial strawberry poison frog males may behave as satellite males, and that there are two possible ways whereby satellites can fertilize female eggs. Firstly, females may follow courting satellite males and oviposition may successfully occur inside or outside the territory of the resident male. Secondly, satellite males may behave like females, moving to the oviposition site together with a mated pair. However, molecular paternity analyses would be required to determine the extent to which satellite behaviour results in reproductive success (Queller et al., 1993; Hauswaldt et al., 2009). The use of satellite tactics was only observed for five out of 77 males. Because non-calling satellite males can easily be confused with females, the present data at best reflect the minimum frequency with which satellite behaviours are adopted. Because of the small sample size, it was not possible to determine whether satellite males differ from non-satellite males in size, age or call parameters. Our observations

provide, however, the first evidence that male dendrobatid frogs can adopt a satellite strategy. Such behaviour may result from a low ability to attract females to given territories (see Arak, 1988; Humfeld, 2008; Castellano et al., 2009). In some cases (e.g. S1), satellite behaviour might also be temporary: when males are trying to establish territories after most other males have already established their territories, satellite behaviour can be part of a conditional strategy. Such males might abandon the satellite role later in the breeding season to occupy territories deserted by other males.

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