Can we get a territory for the frog: Behavioral responses of *Dendrobates pumilio* to intraspecific territorial vocalizations

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Abstract: *Dendrobates pumilio* is a common inhabitant of Atlantic lowland rain forests Costa Rica. During the dry season (non-breeding season) males produce rapid, constant vocalizations believed to be a form of territorial maintenance. Territorial vocalizations and territorial displays of males could depend on distance to threat and be used as a means of avoiding potentially costly physical combat. I used playbacks of territorial calls to test the effects of distance to a perceived intruder on the behavior of a territorial male. Males employed both vocal and physical displays, responding more aggressively with decreasing distance to intruder. Males with greater body length responded more aggressively than smaller males. *D. pumilio* males have a repetoire of escalating behavioral responses to territorial intruders, presumably minimizing the risk of physical conflict.

Key Words: aggression, defense, digital recorder, territoriality

Introduction

Dendrobates pumilio, the "Strawberry" or "Blue Jeans" poison-dart frog, is a conspicuous inhabitant of tropical, wet lowland forests from northern Nicaragua to Panama (Silverstone 1975). *D. pumilio* produces a distinctive, rapid staccato vocalization throughout the dry season, which is presumed to be a form of territorial identification (Bunnell 1973). Although there is no significant correlation between habitat quality and intensity of vocalizations (Conte et al. 2000), males continue to vocally defend territories until the return of mating season (May to November). It has been postulated that *D. pumilio* maintains a territory through the dry season to increase its reproductive success at the onset of the wet season.

While Rabakiewicz (1992) showed that territory holders are occasionally displaced by intruders, these confrontations are almost always resolved without physical contact (Bizarro et al. 1992). When an intruder enters a territory, the occupant male has the option of either surrendering his territory or defending it, either vocally or physically. If physical contact is risky or energetically costly, most frogs should not respond to intruders with aggression unless they are directly threatened with losing their territory.

I hypothesized that male frogs would exhibit a defensive response to perceived intruders, but only when threatened at very close distance. If true, frogs should not respond aggressively to peripheral vocalizations. Furthermore, larger frogs would be expected to respond aggressively at greater distances as their size may confer to them superiority in combat and they should wish to advertise this to discourage encroachers. To test for behavioral changes in *D. pumilio* with respect to intruder distance, I used a recording of a territorial male vocalization to simulate a territorial threat.

Methods

Research was conducted on 13 - 16 February 2002 at La Selva Biological Station, Costa Rica. A SONY ICD-MS1 digital recorder was used to capture a 6 sec sound byte of a male territorial vocalization at a range of less than 2 m (rate = 266 chirps/min). This call was then played back to 39 individual subjects (28 male, 11 female) that were encountered in secondary forests within 4 km of the station on the STR, and within 1 km on both the SORA

and the CCC.

Once an individual frog was located by call or visual sighting, the sound byte was played at three distances relative to the frog: periphery (2 - 4 m), middle (1 - 2 m) and interior (<1 m). These ranges were selected based on the 2 – 3 m territory sizes reported by Rabakiewicz (1985). The resulting behavior of the frog was classified as vocalizing/chirping, silent, retreating (moving away) or aggressive (hopping towards recorder, circular hopping or chirping in response to recording). The recording was played no more than 3 times at each distance. If at any point, the frog appeared to alter its behavior as a result of my movement instead of the recording, the trial was aborted. After the final observation, each frog was captured, and its sex, mass and snout-vent-length (SVL) were recorded. I calculated the residuals from a regression of mass vs. SVL as a measure of condition (Conte et al. 2000). I also recorded whether or not a female was present within a male's territory, and vice versa.

A chi-square test was used to determine if distance to the playback instrument (3 categories) was related to *D. pumilio* behavior (aggression or chirping or silent). I used logistic regression to test whether the probability of aggressive behavior at the intermediate distance was related to SVL, mass or residual mass. Behavior at the intermediate distance was chosen because here about half of the males exhibited aggression. I used a chi-square to test whether the probability of aggressive behavior at the intermediate distance was related to the presence or absence of a female.

Results

The behavior of *D. pumilio* males changed with distance to recording ($\chi^2 = 18.62$, df = 4, P = 0.0009). A greater percentage of males exhibited aggressive behaviors with decreasing distance to recording, and fewer males chirped or were simply silent (Table 1). Of aggressive males, the most common behavior in the peripheral and middle zones was hopping, while the most common behavior in the interior was chirping combined with hopping (Fig. 1).

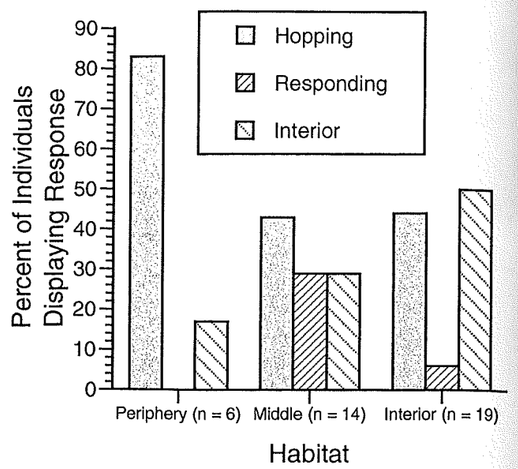

FIG. 1. Distriubtion of aggressive behavioral responses for male *D. pumilio* with resepct to distance.

Several individuals responded to the sound byte with a behavior that involved hopping rapidly in a circle (completing a circle of radius 5 cm in less than 5 sec). All hopping males remained visible during their displays. One individual hopped around a tight circular while always facing outwards from the circle's center. Another hopped up and down repeatedly on his vertical perch. Despite variations in individual hopping patterns, overall displacement for each male was less than 5 cm. The behavior was clearly not a typical predator avoidance maneuver, as the frogs did not hop away or take shelter. Instead, it appeared to be a stereotypical territorial display. Responding males would always cease vocalizations during the recording and immediately re-initiate chirping upon completion of the sound byte. This response was qualitatively different from regular vocalizations as the responsively chirping males consistently faced the recorder and directed their calls at the "intruder".

Males with greater SVLs tended to display aggression more frequently in response

TABLE 1. Number of *D. pumilio* males that were calling, silent or aggressive in response to playbacks of a territorial male at periphery (2 – 4 m), middle (1 – 2 m) or interior (<1 m) or their territories. Initial behaviors were before any playbacks. Expected values for the null hypothesis or row x column independence are in parentheses.

Behavior	Initial	Periphery	Middle	Interior
Calling (5.3)	24	11	4	1
Silent (10)	4	12	10	8
Aggressive (12.6)	0	5	14	19

TABLE 2. Number of *D. pumilio* females that were calling, silent, aggressive or retreating in response to playbacks of a territorial male at periphery (2 – 4 m), middle (1 – 2 m) or interior (<1 m). Initial behaviors were before any playbacks.

Behavior	Initial	Periphery	Middle	Interior
Calling	4	0	0	0
Silent	7	8	9	10
Aggressive	0	3	1	1
Retreating	0	0	1	0

to the recording (χ^2 for logistic regression = 2.77, P = 0.096, n = 28 frogs). There was no relationship between probability of aggression and frog mass or residual mass (P > 0.37 for both logistic regressions). Male aggression was unrelated to the presence or absence of females; of 6 males with females, 3 displayed aggression at the intermediate distance and 3 did not, and of 22 males without females, 11 displayed aggression and 11 did not.

Female *D. pumilio* showed different responses than those exhibited by the males. Most females were initially silent. Several individuals responded to the recording by moving away or beginning a short series of weak chirps that were observed to be qualitatively softer and less frequent than the vocalizations produced by the males (Table 2).

Discussion

Most *D. pumilio* males exhibited unmistakable changes in behavior in response to a territorial vocalization presented within their territory. Patterns of male responses changed, becoming increasingly aggressive as the "intruder" penetrated more deeply into their territory. This supports the hypothesis that males respond more aggressively with decreased distance to intruder. It also indicates that males wait until interlopers are well inside their territory before focusing their attention on them.

Larger males (higher SVLs) tended to initiate aggressive behaviors at greater distances. Surprisingly, there was no relation between aggression and residual mass, which should be a good indicator of present physical condition. If SVL (a measure of skeletal size determined at maturation) is a surrogate for male dominance, then results support the hypothesis that frogs employ displays to avoid combat. Apparently larger males are more assertive in advertising their claim to the territory, which is logical if they would be the likely victor of a confrontation. Especially in the non-mating season, the costs of chirping may be offset by the potential gains of avoiding physical contact.

Although my sample size was small, data indicate that female presence has little or no affect on male aggression. Limerick (1980, *in* Donnelly 1994) proposed that male vocalizations may attract females, but I found no evidence of this, as in all 3 distances most females remained silent. If females are not

truly responding to male vocalizations, there must be an alternative purpose for male chirping during the dry season.

Future research should quantify how habitat refuge influences the territorial displays of male frogs. Additionally, it would be informative to investigate variations between call types to further understand the role of vocalizations in how *D. pumilio* establishes and maintains territories. Studies of responses to playbacks during the breeding season would indicate if male behavior is more strongly territorial, which might help resolve the puzzle of why *D. pumilio* maintain territories during the non-breeding season.

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