this species.

Table 1 Sightings of Ameiva festiva festiva in the young and old successional plots at La Selva Biological Reserve, Costa Rica, on February 10, 1991.

Time	Age of Lizard	Age of Successional Plot	Primary Activity	Food Items
0956	Juvenile	Young	foraging*	Small Lepidopteran
1021	Juvenile	Old	sunning	—
1021	Juvenile	Young	sunning	—
1024	Juvenile	Young	foraging	Avoided bullet ant
1033	Juvenile	Young	moving	—
1040	Adult	Old	sunning	—
1048	Juvenile	Young	nothing	—
1108	Juvenile	Young	moving	—
1118	Adult	Young	nothing	—
1135	Juvenile	Old	sunning	—
1149	Juvenile	Old	nothing	—
1201	Juvenile	Young	foraging	Lepidop./Orthop.
1201	Juvenile	Young	foraging	Lepidop./Orthop.
1201	Juvenile	Young	foraging	Lepidop./Orthop.

*In all cases, foraging occurred on the ground.

Literature Cited

Janzen, Daniel. Costa Rican Natural History. Chicago: University of Chicago Press 1983.

COMMUNICATION SYSTEMS OF DENDROBATES PUMILIO: AGGRESSIVE RESPONSES TO VARIOUS STIMULI

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Abstract

I studied communication systems of Dendrobates pumilio by examining aggressive responses to various stimuli. I found that D. pumilio responded to auditory, chemical, and visual cues more significantly than to controls, but was unable to distinguish the relative importance of these three types of cases in D. pumilio communication. I also found that D. pumilio responded significantly more to conspecific cues than heterospecific cues, indicating that they utilize species-specific communication. Finally, I found that D. pumilio responded to foreign males significantly more than familiar males. This suggests that they also utilize individual-specific communication.

Introduction

Poison Arrow Frogs' (Dendrobates pumilio) social system relies on communication for establishing and maintaining territories and for finding mates (Sanchez, 1985). If communication is important to the social organization, then, the communication system that would develop might help develop to maintain the population by increasing individual fitness.

I studied several factors to examine whether the D. pumilio communication system is important for D. pumilio fitness. Auditory cues are known to be used for communication (Bartz, 1980), and I wanted to learn if chemical and visual cues are also used. I hypothesized that auditory stimuli would be the most important cues,but that chemical stimuli also would be used as a secondary cue. I further hypothesized that visual stimuli would play a role but be less important than chemical stimuli because it is probably more difficult to see than to smell in the litter substrate they inhabit. However, I expected it to be a factor because it might become important when the frogs are in view of one another.

I next wanted to know if these cues were limited by distance. It could be possible that the cues only would be effective over a limited distance. It is also possible that frogs would respond only to cues within their territory because other frogs are not a threat until they invade a territory. I hypothesized that aggressive responses to a stimulus would increase as distance between the frog and the stimulus decreases.

The final two questions I addressed dealt with recognition. Do D. pumilio recognize the cues of their own species? If so, are they able to recognize conspecific individuals? I hypothesized that aggressive responses would be greater for conspecific males than heterospecific males and that aggressive responses would be greater for unknown, or foreign conspecific males then local, or familiar conspecific males.

Methods

I studied D. pumilio from 10-12 February, 1991 at La Selva, Costa Rica. I collected nineteen D. pumilio individuals: fifteen from the old cacao plantation, 20 meters beyond the clearing on the SOC trail and four from Rafael's house, which lies 20 meters off the SOR trail. I chose adult males and females from the SOC trail and only males from the SOR trail. I collected litter from each of these sites. I also obtained two other frogs of different unidentified species.

I placed five SOC males in a 75 x 35 x 30 cm tank. I set up five other holding containers: flower pots lined with litter and covered with insect nets. I placed the extra SOC males in one pot, the females in a second, the SOR males in a third, and the two other frog species separately in the fourth and fifth. I kept the SOR males in a separate room from the rest of the frogs.

The five tank individuals were used in very trial. I introduced a stimulus into the tank and measured the tank males' aggressive responses. I classified responses into six categories, ranking them from zero to five on a scale of aggression as follows:

0	No Response	no aggressive behavior directed toward stimulus
1	Alert	a change in erect posture oriented toward stimulus
2	Approach	movement directed toward stimulus
3	Chirp	any vocalization directed toward stimulus
4	Grapple	ventral/ventral combat between frogs
5	Mount	one frog climbs on the back of another

I did not record feeding, grooming, or haphazard movement because these activities did not seem to represent aggressive behaviors.

To test the first hypothesis I presented the tank frogs with six stimuli, comprised of three treatments and three controls.

To test the level of aggressive response to an auditory stimulus I played a one-minute recording of D. pumilio vocalization that I recorded near the laboratory compound. I replicated this treatment eight times. I also presented a one-minute recording of background noise similar to that on the vocalization recording as a control. I completed

three of these control trials.

To test the response to a chemical stimulus, I placed an extra SOC male in a dark mesh bag and placed the bag in the tank for five, five-minute trials. This allowed the tank males to smell the frog but not to see it; I threw out any trials in which the stimulus frog chirped. As a control, I ran two trials where I placed the bag in the tank without the frog in it.

To test the response to a visual stimulus I placed one of the extra SOC males in a glass jar and placed the jar in the tank. This way, the males could see the stimulus male but not smell him. Again, I did not count any trials in which the male chirped, leaving a total of five five-minute trials. Two control trials were run with an empty jar.

I used data collected during the first three treatments to test my second hypothesis. I recorded the distance from each frog to the stimulus and the aggressive response of each frog. By testing the relationship between these two parameters I was able to measure whether aggressive response was affected by stimulus distance.

While testing the first and second hypotheses I noticed that all five tank males were at the same end of the tank, indicating that they probably had not established territories. Before testing the last two hypotheses, I changed the litter and rotated the tank, but they still stayed close together. I then added to females and the males immediately responded by displaying and distributing themselves throughout the cage. I ran the remaining trials with the females in the tank.

I introduced the heterospecific frogs into the tank to test my third hypothesis. I ran two five-minute trials with each frog, for a total of four trials.

I introduced conspecific males into the tank to test my fourth hypothesis. I ran twelve five-minute trials all together. For six trials I presented other SOC males (as familiar males) and for six trials I presented SOR males (as foreign males).

Results

Using a Kruskal-Wallis test I determined that there was no significant difference between the responses to auditory, chemical, or visual cues ($H=5.76$, $n = 18$, $p > 0.05$). There was no response to any of the controls of these three treatments. The response to the auditory stimulus was significantly greater than its control ($U_s = 24$, $n = 8$, $n_2 = 3$, $p < 0.05$). The chemical and visual stimuli, however, were not significantly greater than their controls ($U_s = 7$, $n = 5$, n_2, $p > 0.05$; $U_s = 7$, $n = 5$, $n_2 = 2$, $p > 0.05$).

Using a regression, I found that each male frog's response was not significantly related to its distance from the stimulus ($r = -0.157$, $r^2 = 0.025$, $n = 29$, $p > 0.05$; $r = -0.207$, $r^2 = 0.043$, $n = 17$, $p > 0.05$; $r = -0.310$, $r^2 = 0.096$, $n = 14$, $p > 0.05$).

I found that the response to conspecific frogs was greater than heterospecific frogs ($U_s = 24$, $n = 6$, $n_2 = 4$, $p < 0.05$), and that the response to foreign frogs was significantly greater than familiar frogs ($U_s = 33$, $n = 6$, $n_2 = 6$, $p < 0.05$).

See Table 1 for a summary of the raw data, and Table 2 for a synthesis of hypotheses, treatments, and results.

Discussion

Though I found that there was no significant difference between the responses to auditory, chemical and visual stimuli, the data presents a strong trend. I should also note that there was one outlying raw data point that overlapped the distribution of auditory data. The rest of the chemical data was much lower than this one point. With an increased sample size, then, the data might have shown a significant difference. The response to auditory cues was significantly greater than its control, suggesting that auditory stimuli are important in D. pumilio communication. A nonsignificant difference between the chemical and visual cues and their controls indicates that these two cues might not be very important for D. pumilio communication. These data make sense in light of their habitat, moist areas covered by litter. Because of this, it is likely that they rely on auditory cues to find one another. It is probably easier to hear than smell or see through leaf litter.

Because D. pumilio are territorial, I had expected that a frog would respond more strongly if the stimulus was closer. I did not find this, however. The nonsignificant relationship that I found could have occurred if the tank had been too small support five full-sized territories; in this case the territories might overlap. Thus, no matter where I put the stimulus it would be in one or more territories, and rule out distance as a factor.

The frogs did respond significantly greater to the presence of a conspecific frog than a heterospecific frog. This indicates that D. pumilio can recognize conspecific individuals so that they don't waste energy in unnecessary interactions, such as engaging in aggressive behavior with a heterospecific frog. Breeding and territory establishment and defense depend on intraspecific communication. Because D. pumilio breeds all year round, increased exposure to each other could lead to increased mating and therefore an increase in fitness of the individual frogs.

In addition to supporting the idea that D. pumilio can recognize species-specific cues, my data also suggest that D. pumilio can recognize individual: they showed a significantly greater response to the foreign frogs than the familiar frogs. This can be explained in terms of the male dominance hierarchy that D. pumilio create. Males establish and maintain this hierarchy via aggressive interactions. It would seem too great an energy

cost to reestablish this dominance each time males interact. If they recognize each other, they know their relative dominance positions and don't need to escalate aggression levels. If they come in contact with a male they haven't seen before, this new male must be incorporated into the dominance hierarchy. Both may have a chance of winning and the initial energy cost could be outweighed by benefits associated with a higher dominance position. If D. pumilio can recognize individuals, then, one would expect a greater response to a foreign male than a familiar male. My data supported this expectation and thus suggest that D. pumilio can differentiate between conspecific individuals.

The results I obtained in this experiment suggest that D. pumilio uses an effective and efficient communication system. The system is effective in that they rely most heavily on a cue that is best suited to their environment. The system is efficient because they (1) recognize species - specific cues, and (2) can differentiate between conspecific individuals.

Though this experiment revealed significant trends, there is much more that can be studied. Marking individuals would aid in answering many questions: Are male dominance hierarchies static or fluid? What determines dominance? Is there a female dominance hierarchy? How do females influence male aggression levels? How is substrate divided between males and females? Is substrate partitioned according to dominance? Do aggression levels vary according to external (weather, disturbance) factors?

In further study I would change a few aspects to my experiment. I would (1) test only one frog at a time, (2) allow more habituation time, (3) wait longer between each trial, (4) replicate trials more, and (5) use more frogs.

Table 1 Mean average aggressive responses and standard deviations for stimuli presented to D. pumilio in experiment conducted 10-12 February, 1991.

Stimulus	Mean Average Aggressive Response	Standard Deviation
Auditory	0.79	0.46
Auditory Control	0.00	0.00
Chemical	0.43	0.66
Chemical Control	0.00	0.00
Visual	0.17	0.24
Visual Control	0.00	0.00
Conspecific	2.00	1.01
Heterospecific	0.00	0.00
Familiar	0.58	0.61

Table 2 Hypotheses, treatments, and results of D. pumilio experiment conducted at La Selva, Costa Rica 10-12 February, 1991.

Hypothesis	Treatment	Result
Response to auditory cues >	auditory response vs. chemical response	auditory > chemical $U_s=33$, $n_1=8$, $n_2=5$, $p<0.05$
chemical cues > visual cues	auditory response vs. visual response	auditory > visual $U_s=35.5$, $n_1=8$, $n_2=5$, $p<0.05$
	chemical response vs. visual response	chemical = visual $U_s=14.5$, $n_1=5$, $n_2=5$, $p>0.05$
	auditory response vs. control response	auditory > control $U_s=24$, $n_1=8$, $n_2=3$, $p< 0.05$
	visual response vs. control response	visual = control $U_s=7$, $n_1=5$, $n_2=2$, $p>0.05$
Response to stimulus	auditory response vs. distance	$r=-0.157$, $r^2=0.025$, $n=29$, $p>0.05$
increases as distance from	chemical response vs. distance	$r=-0.207$, $r^2=0.043$, $n=17$, $p>0.05$
stimulus decreases	visual response vs. distance	$r=-0.310$, $r^2=0.096$, $n=14$, $p>0.05$
Response to conspecific individuals > response to heterospecific individuals	D. pumilio vs. two other species	D. pumilio > two other species $U_s=24$, $n_1=6$, $n_2=4$, $p<0.05$
Response to foreign males > response to familiar males	foreign response vs. familiar response	foreign > familiar $U=33$, $n_1=6$, $n_2=6$, $p<0.05$

Literature Cited

Bartz, S., "Population characteristics of D. pumilio, " OTS 80-3: 52-56.

Janzen, Daniel, Costa Rican Natural History, Chicago University Press: Chicago, 1983.

Sanchez, Miguel, "Territorialidad en machos de D. pumilio con algunas anotaciones del comportamiento reproductivo," OTS 85-2: 517-528.