Discussion (SLS)

We could not reject the null hypothesis that a male will return to his last mate as often as he will mate with another receptive female in a two male, two female system. Therefore, we have no support for our theory that there is fidelity in males in order to protect their investment of sperm. We believe that the riding posture is most likely an instinctive behavior at any encounter with another millipede. We observed several occasions in which a male rode another male and ones in which a male would ride a female without copulating. There also appears to be no recognition of previous mates by the male since we observed some males copulating with a female with which he had just mated.

Because of the small number of matings that actually occurred in our second experiment, we could not conclude that a male will actually mate with more females in the absence of male competition. We did, however, notice (although not significantly) that there is a decrease in the total number of matings when another male is present. We believe that in both of these cases, limited time may have been a factor in the low number of observed copulations. Further studies should include many more replicates for longer periods of observation.

Captivity conditions (artificial habitat, time of day and reuse of experimental subjects) may have altered the activity of the millipedes in this experiment. Future students may wish to conduct similar research in natural settings. The results of these experiments apply to laboratory settings only and one should be cautious when extrapolating the results to natural conditions.

Literature Cited

Heisler, I. L. 1983. *Nyssodesmus python*. In *Costa Rican Natural History*, ed. D. H. Janzen, 747-49. Chicago: University of Chicago Press.

RESIDENT-WIN THEORY AND FORAGING BEHAVIOR IN *DENDROBATES PUMILIO*

Joseph J. Bizzarro, Jeffry L. Dudycha and Alan B. Shabel

Abstract. Male *Dendrobates pumilio* (poison dart frogs) establish territories to have access to mates and food resources (ants and termites). In other territorial organisms, it has been shown that the territory holder often has an advantage in aggressive encounters. We demonstrated this in *D. pumilio*. Territory size is, in part, affected by food preferences and ability to forage on different substrates. Our data suggest that *D. pumilio* forages equally well in leaf litter and over bare dirt, and may prefer termites to ants. (JLD)

Introduction (ABS)

Dendrobates pumilio is a territorial species of poison dart frog that is found in lowland forests from northern Nicaragua to Panama (Silverstone 1975). Males advertise their territories with repeated chirps (Levey, et al. 1980) and during a territorial dispute, two males stage chirping bouts that occasionally escalate to grappling.

It is well documented in many species that a territory holder has an advantage over a challenger in a territorial dispute: resident-win theory. Residents have a greater stake in a confrontation since they already have an investment in the established territory. They should, therefore, be prepared to risk a higher level of conflict than interlopers. Furthermore, an interloper should only involve himself in a battle that he is likely to win since he has no investment in the territory. We predicted that male *D. Pumilio* individuals would successfully defend their territories against interlopers. Resident-win theory had not previously been tested for this species (Rabakiewicz 1987).

Crump (1983) states that most Dendrobatids feed on ants and termites. We predicted that *D. pumilio* individuals would show a consistent preference for either ants or termites when offered both, and that, as visual predators, they would capture more prey items on a bare dirt substrate than on a dirt substrate with a layer of leaf litter.

Methods (JLD)

We conducted our study at Finca La Selva, Costa Rica from 7-9 February 1992. We tested resident-win theory by introducing an interloper into a male frog's territory. We located a male via sound, captured him and measured his snout-vent length (SVL). He was then placed within 10cm of another chirping male. Interactions were observed until one frog left the area. We conducted these observations in the Old Cacao Plantation, near the Sendero Occidental.

For the foraging study, we collected *D. pumilio* in the Arboretum and kept them in 12 specially constructed cells next to the lab. We built the 35cm x 35cm cells out of cinder blocks. Cells were covered with heavy clear plastic held down by a second layer of cinder blocks. A hole (6cm x 6cm) was cut in the center of the plastic over each cell. All cells were lined with 2cm packed dirt, sealed with mud, and included a petri dish of water. Leaf litter and moss were added to 6 cells to cover ~75% of the floor. A frog was placed in each of

10 cells, the remaining 2 cells (one dirt, one leaf litter) were controls.

We compared food preference and foraging ability on different substrates by offering prey to the 10 frogs. We introduced 5 adult termites (all from the same nest) and 5 leaf-cutter ants (all of the minima worker class) to all 12 cells simultaneously, then counted the insects remaining after 2hr. The controls served to determine the escape rate for each insect on each substrate. Four 2hr trials were conducted.

Results (ABS)

Territoriality. We were able to initiate 9 territorial disputes between male frogs. Resident males successfully defended their territories significantly more times (8) than they were displaced ($\chi^2 = 6.34$, $p<0.025$; Table 1).

Foraging. Our control plots allowed us to approximate the escape rates of ants and termites from cells with different substrates. We subtracted these values from the number of individuals missing from out treatments to estimate how many prey items were eaten per trial (Table 2). *D. pumilio* appears to prefer termites over ants, although the difference was only marginally significant ($t=1.62$, $0.1>p>0.05$). There was no significant difference in the number of prey captured on the different substrates.

Discussion (JJB)

Territoriality. As hypothesized, our results demonstrate that male *D. pumilio* territory holders usually prevail in encounters with interlopers. Confrontations were usually settled by chirping bouts with the interloper leaving the territory (7 of 9 trials). In the only instance in which a resident was displaced, a long, physical struggle occurred. It seems that a resident will not abandon its territory unless it is physically displaced.

Also, in observed encounters, size did not seem to be a factor determining a resident's ability to drive off an interloper (Table 1). However, the only interloper that succeeded in displacing a resident was the larger of the two.

Foraging. Termites and ants, the primary food sources for *D. pumilio*, are plentiful in Finca La Selva. However, within this general diet, we might expect some preferences. Small termites, with a soft body and fewer defensive capabilities, would seem to be easier to capture and assimilate than leaf-cutter ants. If both insects are available, we hypothesized that termites would be preferred. Our findings were marginally significant in establishing a feeding preference for termites (only termites were actually observed being eaten). Further testing is necessary to more conclusively determine a preference for termites and to expose the proximate cause for this preference.

In relating foraging ability to substrate composition, we hypothesized that bare ground would provide a better foraging medium than leaf litter due to higher visibility of prey items. However, *D. pumilio* seemed to forage with equal success in both substrates. These findings imply that the territories of *D. pumilio* are not restricted to areas of low litter. Territories, therefore, are likely to be established based upon the availability of resources.

Our findings on foraging behavior may, however, have been affected by the ability of insects to escape the holding cells. Although average values for escape rates in both bare and littered cells were low, there were isolated cases where a majority of each insect escaped. It is, therefore, possible that foraging results were at least partially skewed by escaping insects.

Table 1. Aggressive male encounters.

Encounter #	Resident SVL (mm)	Interloper SVL (mm)	Comments
1	21.5	18.5	Chirped at one another, interloper fled.
2	21.5	21.5	4min grappling bout; resident male in control throughout; interloper fled.
3	20.0	21.5	Resident chirped sporadically; after 12min the interloper left.
4	21.5	21.0	Resident chirped loudly; interloper remained within 25cm for 38min, after 42min he was 2m away.
5	18.0	18.5	Resident chirped and interloper attacked; 12min of grappling, pushing, flipping and then a chirping bout that lasted over one minute; battle recommenced and after 52min the resident male fled his territory.
6	20.5	21.5	After 10min within 20cm of one another, resident chirped and interloper fled
7	20.0	20.5	Resident chirped soon after interloper was introduced, interloper fled.
8	19.5	20.0	Resident chirped three times, then interloper chirped, resident chirped again and interloper fled.
9	20.5	19.0	Resident chirped and interloper fled.

Table 2. Consumption of insects by *D. pumilio* on two different substrates.

	Termites		Ants	
Substrate Type	Litter	Dirt	Litter	Dirt
Escape rate (ind/hr)	0.89	0.56	0.22	0.33
Mean # ind eaten/hr	1.2±1.3	1.6±1.2	0.5±0.9	1.1±1.1

Literature Cited

Crump, M. L. 1983. *Dendrobates granuliferus* and *Dendrobates*

pumilio. In *Costa Rican Natural History*, D. H. Janzen, ed. Univ. of Chicago Press: Chicago, pp. 396-8.

Levey, D., et al. 1980. Territoriality and courtship behavior in *Dendrobates pumilio*. OTS80-3: 72-75.

Rabakiewicz, P., et al. 1987. Resident-win effects and morphological correlates of territoriality in *Dendrobates pumilio*. OTS 87-3: 350-352.

Silverstone, P. A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates*. Wagler. Natural History Mus. Los Angeles County Sci. Bull. 21: 1-55.