TO CHIRP OR NOT TO CHIRP: THE COSTS OF NON-BREEDING SEASON TERRITORIALITY IN *DENDROBATES PUMILIO*

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Abstract: The breeding season for strawberry poison dart frogs, (*Dendrobates pumilio*), peaks in the wet season in Costa Rica. However, males maintain breeding site territories throughout the year by vocalizing even though there are no immediate reproductive benefits. We investigated whether there are costs, such as reduced time spent foraging, associated with this behavior. We observed the behavior of *D. pumilio* males, and calculated time budgets for activities related to territoriality and foraging. In an experimental manipulation, we removed the nearest vocal neighbor from some frogs to determine whether their behavior would change when the pressure to maintain a territory was relieved. Males spent less time vocalizing in both control and when vocal neighbors were removed, with no variation between treatments. Their foraging behavior was also unaffected by frog removal. This suggests that there is a low cost to vocalizing in the non-breeding season, or that pressure from surrounding males is not a measure of that cost and predation may have a stronger effect.

Key words: strawberry poison dart frog, time budget, vocalization

INTRODUCTION

There are many benefits to being a territorial male, such as reduced competition for limited reproductive sites. There are also energetic costs and potential risks associated with acquiring and defending a territory. The poison dart frog, *Dendrobates pumilio*, maintains territories via vocalizations (bouts of quick, repetitive chirps) that result in males that are spaced evenly 2 - 3 m apart throughout their range in La Selva Biological Station (Robakiewicz 1989). *D. pumilio* maintain these territories from one month up to four years (Bunnel 1973; Robakiewicz 1989). These vocalizations also serve to attract females to ovipository sites. Territories allow for an elaborate courtship between male and female to take place undisturbed (Bunnel 1973). Donnelly (1989) reported seasonality in *D. pumilio* reproduction, with apparent peaks in female fertility at the onset of the rainy season. However, *D. pumilio* males maintain their territories with vocalizations throughout the non-breeding season.

We investigated the potential costs of maintaining territories in the non-breading season (e.g., time taken away from foraging). If vocalizing has a high cost, then individuals should reduce their time spent calling and increase their time spent foraging when pressure from nearby males is reduced. If vocalizing has a low cost, then we would expect to see calling behavior regardless of the presence of vocal neighbors.

Bunnell (1973) found that resident male vocalization peaked between 0600 and 1000 and Robakiewicz (1992) found that foraging behavior peaked later in the afternoon. If vocalization has a cost of reduced time foraging, then this pattern may be due to the limitations imposed by increased vocalization pressure in the morning.

METHODS

Between 0730 and 1630 on 15 - 17 February 2004, we located *D. pumilio* along the SUR, SOR, and STR trails and in the successional plots at La Selva Biological Station, Costa Rica. We identified 17 chirping frogs (with inflated throat pouches) as males and selected these for observation. We observed each focal frog from

~ 3 m away using binoculars, and noted the approximate distance to its nearest vocal neighbor and time of day. We recorded the length of time each frog spent vocalizing, walking, hopping, moving in place (foraging maneuvers), or sitting silently over a 10 min period or until the frog moved out of view. Foraging maneuvers and time spent walking were combined into one measure of foraging time (excluding instances when frogs were approaching other frogs). We calculated the percentage of time spent for each activity, and used correlation matrices to assess relationships between behaviors, distance to nearest neighbor.

For seven frogs that had not moved out of view after this first scan, we waited 20 minutes and repeated the 10 minute scan after an experimental manipulation. We removed the nearest vocal neighbor before repeating the scan for four frogs. To account for the effects of disturbance caused by the manipulation, we used three frogs as controls where we approached the neighboring frog but did not remove it. We assessed changes in behavior before and after the manipulation for both treatments and compared the amount of changes between treatments.

RESULTS

D. pumilio spent the majority of its time sitting silently or vocalizing (Table 1). The percent of time spent sitting was therefore strongly negatively correlated with percent of time spent vocalizing (Table 2). Other less common behaviors included hopping and foraging (Table 1). There was a significant correlation between foraging and time of day, with more foraging in the afternoon (Table 2). Vocalizing was more common in the morning, but this was not significant (Table 2). There was no correlation between the distance of a frog to its nearest vocal neighbor and any observed behavior, even in a model that also included time of day (t = 0.52, df = 15, P = 0.61; Table 2).

Table 1. Means ± SE of time budgets for 17 focal *D. pumilio*.

% time spent:	Mean ± SE
Sitting	73.73 ± 6.06
Vocalizing	22.10 ± 5.87
Hopping	0.44 ± 0.14
Foraging	3.58 ± 0.92
Total observation time (s)	540 ± 26
Distance to nearest vocal neighbor (m)	3.25 ± 0.33

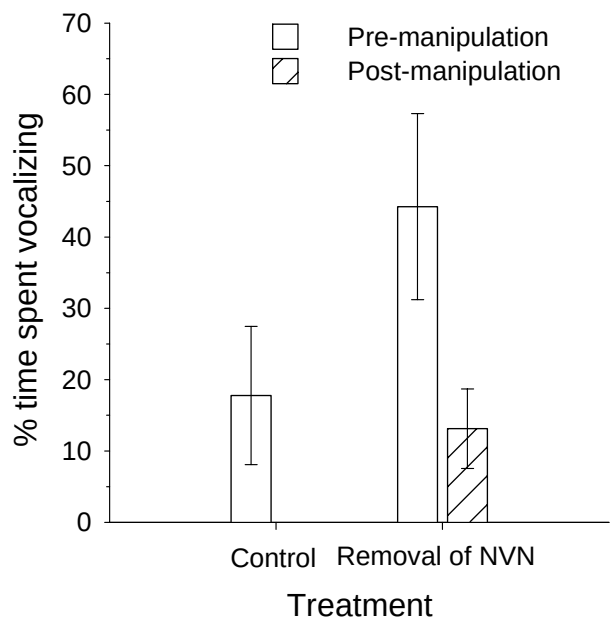

Figure 1. Percent of time spent vocalizing by *D. pumilio* before and after experimental manipulation. The nearest vocal neighbor (NVN) was removed from four experimental frogs, but not from three control frogs. Standard error bars are shown. The decrease in vocalizing time is significant for experimental frogs, but not control frogs, although post-manipulation yielded 0% time spent vocalizing. The magnitude of the decrease in vocalizing time did not differ significantly between treatments.

Frogs spent significantly less time vocalizing when their nearest vocal neighbor was removed (paired-t = 3.99, df = 2, P = 0.03; Fig. 1, 2). There was an insignificant decrease in vocaliza-

Table 2: Correlation matrix for *Dendrobates pumilio* behaviors, time of day, and distance to the nearest vocal neighbor (NVN) for 17 focal frogs observed for up to 10 minutes each. Only 16 focal frogs are included in analyses of distance to NVN. Foraging behaviors include walking and foraging maneuvers in place.

	Distance to NVN (m)	% time sitting	% time vocalizing	% time hopping	% time foraging
% time sitting	0.16				
% time vocalizing	-0.18	-0.99*			
% time hopping	0.33	-0.22	0.17		
% time foraging	0.04	-0.22	0.06	0.20	
Time of day	0.35	0.28	-0.39+	0.19	0.65*

* P < 0.05, + P = 0.12

tion in control frogs (paired-t = 1.83, df = 2, P = 0.21; Fig. 1). However, the change in vocalization behavior as a result of manipulation treatment did not differ between experimental and control frogs (t = 1.09, df = 5, P = 0.33; Fig. 1). In a model that encapsulated all these variables, there was a definite effect of disturbance caused by the experiment on vocalization ($F_{1,3}$ = 15.8, P = 0.01).

The amount of time a frog spent foraging was unaffected by the removal of its nearest vocal neighbor (paired-t = 0.17, df = 2, P = 0.88; Fig. 3). Control frogs also showed no change in foraging time before and after manipulation (paired-t = 0.46, df = 2, P = 0.69; Fig. 2). There were no differences in foraging time between control frogs and frogs with neighbors removed (t = 0.35, df = 5, P = 0.77; Fig. 2).

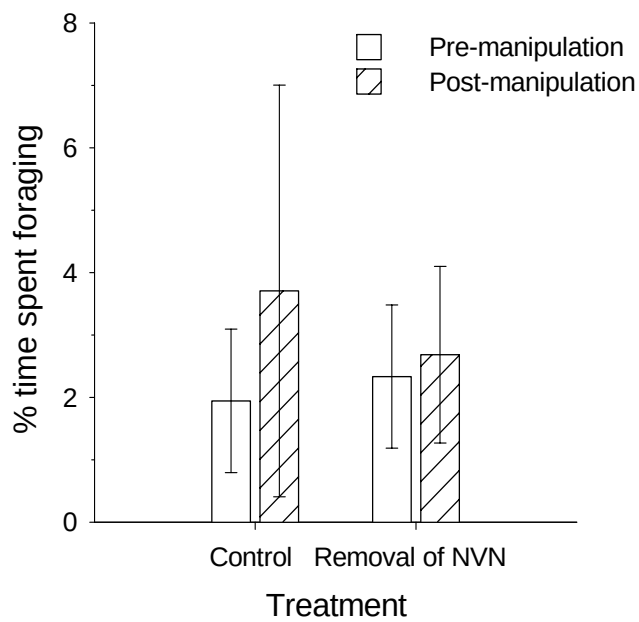

Figure 2. Percent of time spent foraging by *D. pumilio* before and after experimental manipulation. The nearest vocal neighbor (NVN) was removed from four experimental frogs, but not from three control frogs. Standard error bars are shown. There were no significant changes in time spent foraging before and after manipulation in either treatment, and no differences between treatments.

Discussion

The lack of a significant difference between treatments and the lack of correlations in behavior to nearest vocal neighbor distance suggests that there is a low cost to vocalizing, and that *D. pumilio* calls regardless of pressure to maintain territories. If we had found that vocalization was a costly behavior, this would imply that frogs already having claimed a territory when the breeding season begins would incur greater fitness through increased reproductive success early in the breeding season. However, since we found little cost to vocalization, the delayed benefits in the breeding season do not necessarily have to be large to offset these low costs. Even so, if there are large benefits, then to fail to maintain a territory by vocalizing may have

high fitness cost.

Regardless of the cost, *D. pumilio* does partition time between foraging and vocalizing. Foraging activity peaks in the afternoon, while vocalizing is more common in the morning. If the species is constrained to specific foraging hours, perhaps by food availability, then during the hours they do not forage their default behavior may be chirping, which is not costly.

Although our study suggests that there is no cost to vocalizing in the non-breeding season, frogs often stopped vocalizing in response to a slight disturbance. Also we lost sight of ten out of the 17 frogs we observed when they moved under the leaf litter. This suggests that *D. pumilio* exhibits predation avoidance behavior. Although *D. pumilio* is a Dendrobatid frog, its toxins are not as potent as other members of the poison dart frog family (Crump 1983). This suggests that it may still be vulnerable to predation, although little is known about its potential predators. Vocalizing calls attention to the frogs, leading to an increase in exposure. Therefore vocalizing may have a cost of increased predation risk. Future studies could investigate predation rates on these frogs and how they relate to male vocalization.

There were some limitations to our study. Our low sample size made it difficult to compare treatments in our manipulative study, and the effect of experimental disturbance confounded these results. Future studies should give more time after manipulation to allow frogs to habituate to experimental conditions. Furthermore, *D. pumilio* spent the majority of observation time sitting still, and we were unable to determine whether this behavior was related to foraging or territoriality. Robakiewicz (1992) defined sitting behavior as characteristic of an alert foraging stance, while Donnelly (1987) defined it as an alert territorial posture. Further investigation of the differences between these two stances is needed.

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