REPRINT No. 19 from *Animal Behaviour*, 30, 2, May, 1982

Anim. Behav., 1982, **30**, 393–397

EVASIVE BEHAVIOUR OF A FROG IN RESPONSE TO BAT PREDATION

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Abstract. Chorusing frogs (*Physalaemus pustulosus*) visually detect hunting bats (*Trachops cirrhosus*) and models of *T. cirrhosus* on all but the darkest nights. Detection is apparently communicated rapidly, since all frogs in the area can quit calling withing less than a second of a *T. cirrhosus* arrival at the pond. *Physalaemus pustulosus* choruses remain silent longer following trials when a *T. cirrhosus* model is passed overhead than following normal shutdowns or those caused by a model of a small insectivorous bat. They often do not reduce calling in response to the normal activities of small bats.

The fringe-lipped bat (*Trachops cirrhosus*) acoustically locates and preys on a variety of frog species. Bat success varies according to frog calling behaviour, and few silent frogs are caught (Tuttle & Ryan 1981). Tuttle & Ryan suggested that frogs probably adjust calling behaviour to reduce predation. They noted that frogs could avoid predation by (1) stopping calling, (2) calling less frequently, (3) calling less loudly, (4) changing call characteristics to reduce locatability, or (5) calling from concealment.

Since most of these options probably reduce male success in attracting females (Ryan 1980), selection should favour frog detection of hunting bats, thereby permitting effective graded responses appropriate to threat intensity. In our investigation we addressed three questions: Does the frog *Physalaemus pustulosus* detect fringe-lipped bats? If so, does its response vary with the level of threat? Finally, can the frogs differentiate between *T. cirrhosus* and smaller insectivorous bats?

Methods

We conducted experiments at the Weir (approximately 11 m in circumference) and Kodak (1.5 × 2 m) Ponds on Barro Colorado Island (BCI), Panama, from 2 March to 26 May 1980. Both ponds were *P. pustulosus* breeding sites. *Physalaemus pustulosus* responses to *T. cirrhosus* were recorded on 12, 13, 28 and 30 March and on 2 and 17 April at Weir Pond, and responses to bat models were tested on 24 and 27 March; 4 and 14 April; 11, 18, 25, and 26 May at Kodak Pond.

Calls of *P. pustulosus* were recorded continuously at Weir Pond from 1830 to 2000 hours on each night of testing on a Nagra IV-D tape recorder and Sennheiser MKH 104 microphone. Observations of *T. cirrhosus* were made using a Javelin Model 221 night-vision scope. We recorded times of *T. cirrhosus* and other bat visits to the nearest second on a Pearlcorder model SD2 microcassette tape recorder. The temporal distribution of frog calls was later quantified, using a Type 1521 Graphic Level Recorder (General Radio Corp.), and times of bat visits to the pond were transcribed from the Pearlcorder tape to the paper chart on which numbers of calls/time were quantified (Fig. 1). We censused *P. pustulosus* at the beginning and end of each night's observations.

To determine the effect of bats on calling *P. pustulosus*, we counted the number of calls in the 15-s periods immediately before and after arrival of each bat. The maximum number of calls that could be detected in this analysis was 65. (If the bat had no effect, the number of calls in each period should be equal.) Bat visits were divided into two groups, one for *T. cirrhosus* and one for smaller insectivorous bats (mostly *Myotis*, *Rhogeesa*, and *Saccopteryx*), and the *T. cirrhosus* data were categorized by the following conditions: (1) full moon, clear; (2) full moon, cloudy; (3) no moon, clear; (4) no moon, cloudy. Incident light levels were measured with a Gossen Lunasix electronic exposure meter. We purposely selected nights that fit into these categories. We used a Wilcoxon signed-rank test to compare the number of calls before and after each *Trachops* or small bat visit and to test frog responsiveness among light categories.

Detailed observations of the responses of calling *P. pustulosus* to bat models were made at

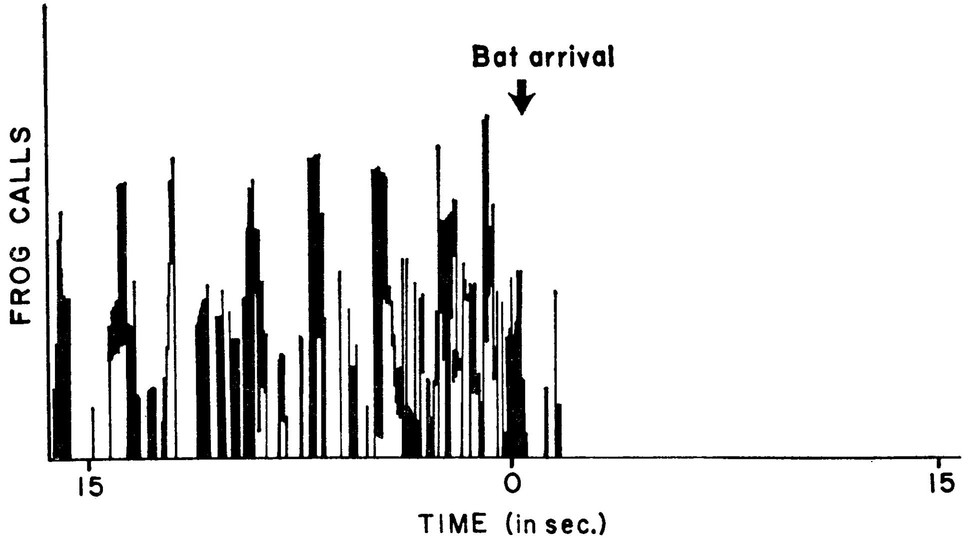

Fig. 1. Chart recording made at Weir Pond showing typical full moon night response of chorusing *P. pustulosus* to the arrival of hunting *T. cirrhosus*. Vertical lines represent frog calls; the height represents the amplitude of the call, i.e. the distance of the frog from the microphone, and is not used in our analysis.

Kodak Pond under varied light conditions. Models of *T. cirrhosus* and a small insectivorous species (*Micronycteris megalotis*) were made by tracing an outline of an individual of each species with wings spread. The outline was then cut out of heavy cardboard, stained to approximately the bat's colour, weighted below, and rigged above with a small roller. The models were passed diagonally across the pond on a taut, inclined, monofilament line. Speed was adjusted to approximately normal *T. cirrhosus* flight speed by adjusting the incline of the fish line. A control model, mechanically identical to the *T. cirrhosus* model but lacking wings and most of the body, was used to test for possible sound detection by the frogs. (Barely detectable sounds were produced by the line passing over the roller on the models.)

In these tests the models were passed over the pond beginning at 1.0 m and ending at 0.2 m. The observer was 4 m from the pond and out of the frog's view. We recorded the following times during trial and control runs: (1) time for model or control model to reach near side and middle of pond; (2) time to chorus shutdown (if shutdown occurred) following model release; (3) time until chorus restarted (at least three frogs calling simultaneously and continuously); (4) time until full chorus began (most males calling continuously).

Because *P. pustulosus* choruses occasionally shut down in the absence of any apparent threat, we recorded data during a 15-min control period prior to each experimental trial. The time from cessation of calling by the frogs to resumption of full chorusing was noted for each 15-min period. We ran each test after a full chorus had been in progress for 30 s following the 15-min control period. If the frogs ceased calling within the time required for the model to traverse the pond, the model was considered to have caused the cessation. We compared the duration of the silent interval following the shutdown and the average duration of normal shutdowns during the preceding 15-min control period with a Wilcoxon signed-rank test.

At least five experimental trials and an equal number of controls were conducted during each night of experimentation. We performed the following tests between 1930 and 2400 hours: (1) *T. cirrhosus* model at intermediate light intensities (incident light approximately 0.17 to 0.35 lx) and in 'total' darkness (incident light $\ll 0.17$ lx, no moon, heavy overcast); (2) wingless model at intermediate light intensity; (3) *T. cirrhosus* model versus small bat model at incident light intensity of 0.52 to 1.40 lx. In the third comparison, we ran the two models separately for each trial, and alternated models between trials. Thus the *T. cirrhosus* model was run first one time and second the next. The second model was run as soon as the frogs had restarted a full chorus for 30 s, but 15-min control periods were run between pairs of trials. We compared duration of chorus shutdown in control and experimental situations with a Wilcoxon two-sample test.

We tested the responses of individual frogs to varied heights (1.00 to 0.13 m) of the *T. cirrhosus* model. As the model passed along the downward sloping monofilament line, height decreased from one side of the pond to the other. The model was run along both the east and west sides of the pond, nine times headed north and nine times headed south. Model runs were made at approximately 10-min intervals from 2000 to 2230 hours.

Both east and west sides of the pond were marked every 30 cm, and just prior to each run, we noted the position and posture of each calling male on a pond diagram. The model was passed over the calling *P. pustulosus* as soon after a 10-min interval ended as three consecutive counts under a dim headlight consistently showed the same numbers and positions of calling frogs in each marked section.

Immediately after the model passed over the frogs (model was remotely released), a dim headlight was used to note changes in body posture and degree of inflation of each frog. Missing frogs were assumed to have dived (verified by night-vision scope observations during several model passes). Frog responses to model height were categorized as follows: (1) continued calling, (2) stopped calling but remained inflated, (3) stopped calling and deflated, (4) deflated and lowered body till only top of head protruded above water (*P. pustulosus* calls only from the water), (5) dived.

After behavioural and postural changes were noted, the bat model was slowly passed back along the monofilament line, and a metre stick was used to measure model height above each frog. A Spearman rank correlation was used to test dependence of mean frog response to model height.

Results

Table I shows that under most light conditions *P. pustulosus* significantly reduced calling following *T. cirrhosus* arrivals at Weir Pond. However, frogs failed to respond on cloudy moonless nights. Figure 1 illustrates a typical full-moon night response of *P. pustulosus* to the arrival of a hunting *T. cirrhosus*. Following 11 of 19 visits by small insectivorous bats, *P. pustulosus* produced at least the maximum countable number of calls (see Methods). However, in the remaining eight cases there were significantly ($Z = -1.75$, $P = 0.04$) fewer calls after small bat arrivals than during the control periods.

In the 20 trials in which the model *T. cirrhosus* was passed over chorusing *P. pustulosus* at intermediate light intensities, all frogs stopped calling within 0.4 to 1.8 s (mean = 1.0, SE = 0.079) of the time the model first reached the pond edge. Also, average chorus shutdown times following these trials were significantly longer than controls (Table IIA). In contrast, in the five trials made in nearly total darkness, the frogs, did not stop calling, and lengths of the next normal shutdowns did not differ from controls (Table IIB).

When presented with alternating passes of small bat versus *T. cirrhosus* models, *P. pustulosus* choruses shut down in 8 of 10 versus 10 of 10 trials respectively. Times of chorus shutdowns were longer following both small bat and *T.*

Table I. Effect of *T. cirrhosus* on *P. pustulosus* Calling under Varied Light Conditions*

Light condition	*N*	*Z* statistic	*P*	$\bar{X}$ number of calls emitted	
				Before	After
Full moon, clear	3	—	—	38.0	1.3
Full moon, cloudy	11	-2.93	0.002	27.9	2.5
No moon, clear	17	-3.39	< 0.001	31.1	9.2
No moon, cloudy	59	-0.98	0.164	53.2	50.8
All conditions combined	90	-4.36	< 0.001	45.4	35.4

*A Wilcoxon signed-rank test was used to compare the number of calls 15 s before and after a bat pass.

Table II. Frog Responses to *T. cirrhosus* and Wingless Control Models at Kodak Pond*
A. Control versus *T. cirrhosus* model (incident light approximately 0.17 to 0.35 lx)

Night	Number of frogs present (beginning–end)	$\bar{X}$ Control (N)	$\bar{X}$ *T.* cirrhosus model (N)	$t_{\rm s}$†	P
24 Mar.	24–22	25.5 (52)	112.0 (5)	1.674	< 0.005
27 Mar.	30–32	33.7 (29)	353.6 (5)	3.525	< 0.005
4 Apr.	29–26	25.5 (47)	193.2 (5)	3.647	< 0.005
14 Apr.	17–23	27.7 (50)	201.6 (5)	3.660	< 0.005

B. Control versus *T. cirrhosus* model in 'total' darkness (incident light $\leqslant$ 0.17 lx)‡

Night	Number of frogs present (beginning–end)	$\bar{X}$ Control (N)	$\bar{X}$ *T. cirrhosus* model (N)	$t_{\rm s}$†	P
18 May	30–18	23.4 (19)	27.6 (5)§	$U = 52$	NS

C. Control versus wingless model (incident light approximately 0.35 lx)

Night	Number of frogs present (beginning–end)	$\bar{X}$ Control (N)	$\bar{X}$ *T. cirrhosus* model (N)	$t_{\rm s}$†	P
11 May	39–22	33.4 (19)	52.6 (5)	1.384	NS

*Times (in seconds) till resumption of calling following natural versus experimentally induced chorus shutdowns are presented.

†Wilcoxon two-sample test.

‡For one additional pass, the illumination was artificially increased to approximately 0.35 lx. The frogs stopped chorusing during the model's run and did not resume calling for 124 seconds.

§Frog choruses were uninterrupted by passage of these models over the pond. Times used in calculations are duration of next normal shutdown following passage of the model.

cirrhosus model runs compared with controls ($\bar{X}$ control $= 29.4$ s, $N = 42$; $\bar{X}$ small bat model $= 54.9$ s, $N = 10$; $\bar{X}$ *T. cirrhosus* model $=$ 189.4 s, $N = 10$; small bat model versus control, $t_{\rm s} = 2.855$, $P < 0.005$), but shutdowns caused by the *T. cirrhosus* model averaged longer than those caused by the small bat model ($U_{\rm S} = 89.5$, $P < 0.005$). For the two trials when frog choruses were uninterrupted by passage of the small bat model, duration of the next normal shutdown was used in the calculations. On the two nights of testing, frog numbers varied from 16 to 5 and 12 to 9 respectively.

There was a significant correlation between average *P. pustulosus* response to the *T. cirrhosus* model, and model height above the frogs ($r_{\rm s} = -0.96$, $P < 0.01$) (Table III). At heights below 0.20 m most frogs dived. At heights of 0.21 to 0.60 m most stopped calling but remained inflated, and at heights of greater than 0.60 m this was the only response.

The wingless control model of *T. cirrhosus* (Table IIC) did not cause *P. pustulosus* to stop calling or otherwise noticeably respond.

Discussion

Field observations and tests with model *T. cirrhosus* demonstrate that *P. pustulosus* detects approaching fringe-lipped bats and stops calling.

Table III *P. pustulosus* Responses to Varied Height of the *T. cirrhosus* Model*

Model height (m)	Response categories 1	2	3	4	5	N	Mean
0.11–0.20	0	7	1	6	22	36	4.2
0.21–0.30	0	5	1	1	3	10	3.2
0.31–0.40	0	6	3	2	1	12	2.8
0.41–0.50	0	26	2	2	2	32	2.4
0.51–0.60	0	23	1	1	0	25	2.1
0.61–0.70	0	13	0	0	0	13	2.0
0.71–0.80	0	17	0	0	0	17	2.0
0.81–0.90	0	3	0	0	0	3	2.0
0.91–1.00	0	2	0	0	0	2	2.0

*Response categories are: (1) continued calling; (2) stopped calling but remained inflated; (3) stopped calling and deflated; (4) deflated and lowered body till only top of head protruded above water; (5) dived. Incident light was approximately 1.4 lx.

Detection is immediate and apparently rapidly communicated, since entire choruses can shut down within a second of the time that a fringe-lipped bat or fringe-lipped bat model arrives at the edge of their pond.

Calling frogs are inflated, floating on the water's surface. They remain inflated during a calling bout and pass air over the vocal chords by shuttling the air back and forth between the lungs and the gular sac. Bucher et al. (1982) showed that the energetic cost per call decreases with calling rate. They suggested that this is due to the cost of the initial inflation before a calling bout. Frogs not directly threatened remained inflated and ready to resume calling quickly. When the *T. cirrhosus* model approached to within less than 0.60 m, the type of frog response was correlated with the distances between model and frog. Such graded responses to bat threat are probably selectively advantageous in avoidance of predation, and in minimizing the energetic costs of calling and overall bat disruption of frog breeding.

Discrimination between *T. cirrhosus* and numerous smaller bats that are harmless to frogs additionally minimizes unnecessary disruption. The fact that frogs seldom responded to small bats at Weir Pond but did respond to small bat models at Kodak Pond is not surprising. At Weir Pond small bats frequently swooped to within 30 cm or less of the water but mostly did so over the open water and only in brief passes. Low passes at the edge tended to be at right angles to the shoreline and were also brief. In contrast, hunting *T. cirrhosus* remained constantly within 30 cm or less and usually followed the shoreline, where they quickly disturbed many more frogs.

In our tests at Kodak Pond, both *T. cirrhosus* and small bat models were run along identical courses, most of them similar to those naturally traversed by hunting *T. cirrhosus*. Even so, the frogs responded less frequently and resumed calling more quickly following passage of the small bat model.

The fact that *P. pustulosus* failed to detect both bats and models on exceptionally dark nights suggests dependence upon visual detection. *Physalaemus pustulosus* also may change its calling behaviour or select certain calling times or locations to take advantage of lunar cycles or other factors that may affect visual detection. Ryan et al. (1982) have shown that when frogs produce call types of greater attractiveness to females, they also attract more bats. Detection of hunting bats by frogs is probably not limited to *P. pustulosus*. Numerous detection and avoidance strategies probably exist, and knowledge of frog responses to acoustically-orienting predators, such as the fring-lipped bat, is essential to an understanding of anuran behaviour and communication.

Acknowledgments

We thank A. S. Rand for his suggestions and K. Adler and A. S. Rand for critically reading an early draft of the manuscript. This research was supported by a grant from the National Geographic Society to M.D.T. M.J.R. was supported by a Smithsonian Institution Predoctoral Fellowship and a grant from the National Science Foundation (DEB-7908893). We also are grateful to the Smithsonian Tropical Research Institute for the opportunity to work on Barro Colorado Island.

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(*Received* 20 *April* 1981; *revised* 3 *August* 1981;
MS. number: A2644)