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BAT PREDATION AND SEXUAL ADVERTISEMENT
IN A NEOTROPICAL ANURAN

Many mating systems are characterized by conspicuous male sexual displays (Emlen and Oring 1977; Wells 1977). Predation and parasitism are thought to be important counter-selection forces in the evolution of acoustic sexual displays (Marler 1955; Moynihan 1970). However, only studies of crickets have shown that acoustically advertising males have a higher probability of attracting predators (Bell 1979; Walker 1964) or parasites (Cade 1975), and Cade (1979) showed that parasitism influences whether a male adopts a calling or a noncalling mating strategy. Recently we reported that the bat *Trachops cirrhosus* eats frogs and uses the frogs' advertisement calls for locational cues (Tuttle and Ryan 1981). Here, we investigate the role of predation in the evolution of the vocal repertoire of the frog *Physalaemus pustulosus*.

Male *P. pustulosus* produce calls of varying complexity (1 whine + 0–6 chucks; Rand and Ryan 1981) and chucks contain information about male body size (Ryan 1980). Soloing males produce the simple call (whine only) and only increase call complexity (i.e., the number of chucks) in response to other males (Rand and Ryan 1981). But females prefer calls that contain chucks (Rand and Ryan 1981). This creates a paradox: Why is it that males do not maximize their mate attraction ability by always producing calls more attractive to females? Rand and Ryan (1981) suggested that more complex calls might also be more attractive to acoustically foraging predators.

We conducted a series of experiments in a flight cage and in the field to test the hypothesis that male *P. pustulosus* that produce calls more attractive to females (i.e., more complex calls) are also more prone to predation by *T. cirrhosus*. These experiments were conducted on Barro Colorado Island, Panama, from January to May, 1980.

In the flight cage a *T. cirrhosus* was presented with a simple (whine only) and a complex (whine + 3 chucks) advertisement call. Calls were presented at a rate of one call/1.6 s. (about the normal *P. pustulosus* calling rate) and at an intensity of 75 dB SPL at 1 m from the speaker. The flight cage was 20 m² and 2.1 m high. The observer was in one corner and the bat perched in the opposite corner. One speaker was located in each of the remaining corners. At the beginning of each trial the bat was about 4 m from each speaker. The stimuli were presented only when the bat was perched in the appropriate corner, and the stimuli were discontinued as soon as the bat flew from the perch to avoid habituation of the bat to the stimuli. (In other studies, bats almost invariably landed on speakers that continued to broadcast frog calls; Tuttle and Ryan 1981.) A response was recorded if a bat flew within 1 m of a speaker. In all responses the bat flew directly toward a speaker. The bats landed on a speaker in 44% of the responses and passed within 4

TABLE 1

SUMMARY OF DISTANCES WITHIN WHICH BATS APPROACHED THE SPEAKER FOR ALL RESPONSES

	LANDED ON SPEAKER	APPROACHED WITHIN			
		0-4 inches	4-8 inches	8-12 inches	> 12 inches
Responses	14	15	11	1	3

inches of a speaker in 66% of the responses (table 1). When the bats did not land on the speaker they usually either landed on the wall and perched near the speaker or returned to the perch on which they began the trial. This is similar to the behavior of *T. cirrhosus* hunting at frog choruses (Ryan et al. 1981).

In the field, simple and complex advertisement calls were played at five sites of known *T. cirrhosus* activity. Calls were played simultaneously from two speakers at a rate of one call/1.6 sec. Speakers were placed 4 m apart and were observed simultaneously with a Javelin model 221 night vision scope from about 12 m. *Trachops cirrhosus* can be identified on the wing and a response was recorded if a bat passed within 1 m of a speaker. Calls were played 1.3 h each night.

Because sample sizes of trials were not equal, data were analyzed by computing the exact binomial probability of a random choice by each bat (flight cage) or on each night (field tests). The null hypothesis of no preference was tested by comparing $-2\sum \ln P$ to a χ^2 distribution (Sokal and Rohlf 1969).

Table 2 shows that in the flight cage bats were preferentially attracted to the complex call ($\chi^2 = 40.1, P < .005$). In the field experiments we did not know how many individual bats made passes at the speakers, but there were significantly more passes at the speaker producing the complex calls ($\chi^2 = 51.2, P < .005$, table 3).

Complex calls are of longer duration and contain more total energy and a larger range of frequencies than simple calls. Although we do not know which qualities of the complex calls made them more attractive to bats, we have demonstrated that by increasing the attractiveness of their calls to females, male *P. pustulosus* also increase predation risk from the bat *T. cirrhosus*. Previous studies have

TABLE 2

RESPONSES OF INDIVIDUAL *T. cirrhosus* IN THE FLIGHT CAGE TO SIMPLE (whine only) AND COMPLEX (whine + three chucks) *P. pustulosus* ADVERTISEMENT CALLS

Bat	Complex	Simple	P
f 7	8	0	.0039
m 9	4	2	.3437
m 12	9	3	.0730
f 13	8	0	.0039
f 14	10	0	.0001

TABLE 3

NUMBER OF PASSES MADE BY *T. cirrhosus* IN THE FIELD OVER SPEAKERS BROADCASTING SIMPLE (whine only) AND COMPLEX (whine + three chucks) *P. pustulosus* ADVERTISEMENT CALLS

Date	Site	Complex	Simple	<i>P</i>
2/11/80	Nemesia	56	37	.0307
2/13/80	Barbour	15	8	.1050
2/14/80	Shannon	52	22	.0003
2/15/80	Standley	37	13	.0004
2/17/80	Chapman	8	1	.0195

shown that predation can increase the cost of sexual advertisement (Ryan et al. 1981) or influence when a male calls (Cade 1979). Our results show that predation can also have an important, and perhaps subtle, role in the evolution of the types of signals involved in a sexual display. These results also support the suggestion of Rand and Ryan (1981) that the complexity series of the *P. pustulosus* advertisement call has evolved to allow males to effect a compromise between maximizing mate attraction ability and minimizing predation risk.

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