Bat Predation and the Evolution of Frog Vocalizations in the Neotropics

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diminished during hypothyroidism in adult rats. The spontaneous discharge rate of Purkinje neurons is determined to a large extent by the tonic inhibitory noradrenergic afferents originating in the nucleus locus coeruleus (13). Thus, an increased spontaneous discharge in the Purkinje neurons of hypothyroid rats is consistent with the diminished responsiveness of such neurons to norepinephrine. A hypoactive afferent projection from the locus coeruleus is ruled out by several studies on the peripheral and central nervous systems (5, 14, 15) demonstrating an increased amount of norepinephrine discharged at the sympathetic nerve endings during hypothyroidism. Thus, alterations in postsynaptic function could conceivably lead to the electrophysiological changes reported here (6, 15). β-Receptors might be altered in number or in their affinity or functional coupling with adenylate cyclase. In fact, diminished β-receptor binding (with no change in affinity) during hypothyroidism has been demonstrated (3, 15). In peripheral tissues, parallel changes in adenylate cyclase activity have been reported (16). Our electrophysiological studies agree well with previous observations (3, 6, 15, 16). In another study (2), the activity of cyclic AMP phosphodiesterase (E.C. 3.1.4.17) did not change in the cortices of hypothyroid rats. The studies we report here suggest that the subsensitivity occurring during hypothyroidism resides in the β-receptor–adenylate cyclase complex. Furthermore, our results and those of others (3, 6, 15) suggest that T_3 may decrease the number of β-receptors which might thus account for the subsensitivity of Purkinje neurons to norepinephrine.

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Bat Predation and the Evolution of Frog Vocalizations in the Neotropics

Abstract. Bat predation has probably had an important influence on the evolution of frog vocalizations in the Neotropics. The rate at which fringe-lipped bats capture frogs is significantly higher when the frogs are calling. These bats respond to a wide variety of calls from edible frogs, and, when simultaneously presented with a choice, choose the recorded call of a palatable species over that of a poisonous species and the call of a small species over that of one too large to capture. Thus the selective advantages of loud, rapid mating calls in anurans are balanced by an increased risk of predation.

Many animals use conspicuous vocalization to attract mates. The benefits are obvious, but biologists have long suspected that this also leads to increased vulnerability to sound-responsive predators (1, 2). Although such counterselection is believed to influence the evolution of vocal advertisement (3), documentation is rare (2) and is entirely lacking for vertebrates. In this report we show that the fringe-lipped bat (Trachops cirrhosus) uses acoustic cues to capture calling frogs, and we consider the possible role of call-responsive predators in the evolution of anuran calling and courtship behavior.

On 35 nights from January to June 1980 we visited 14 frog breeding sites on Barro Colorado Island, Panama (4). Trachops cirrhosus was observed hunting on each night. Seven of the nights were spent at a breeding pond of the frog

Table 1. Responses of T. cirrhosus to playbacks of the advertisement calls of four anuran species.

Species	In cage		In field	
	Bats tested	Responses	Sites visited	Responses
Hyla boulengeri	5	35	6	66
Bufo typhonius	5	5	6	3
χ^2	42.81 (10), $P < .005$		70.63 (12), $P < .005$	
Physalaemus pustulosus	5	36	3	26
Leptodactylus pentadactylus	5	1	3	2
χ^2	47.15 (10), $P < .005$		31.52 (6), $P < .005$	

Table 2. Responses of T. cirrhosus to the recorded advertisement calls of two anuran species played at different repetition rates and volumes.

Species "calling"	Bats tested	Responses
Physalaemus pustulosus		
1.6-second interval between calls	3	22
3.2-second interval between calls	3	2
χ^2		22.62 (6), $P < .005$
Centrolenella fleischmanni		
1.6-second interval between calls	3	18
6.4-second interval between calls	3	1
χ^2		22.19 (6), $P < .005$
Physalaemus pustulosus		
78 dB SPL	2	13
74 dB SPL	2	2
χ^2		14.14 (4), $P < .01$

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Physalaemus pustulosus, where the bats were seen hunting during 10 percent of the observation time (5). They caught a total of 95 frogs. Hourly catches averaged 6.3 frogs but ranged from 2.5 to 12.1, depending on the frogs' calling behavior. We divided the choruses of *P. pustulosus* into four categories and counted the number of bat visits per capture for each category: (i) full chorus, 1.8 (68 total visits); (ii) partial chorus, 2.3 (61); (iii) few calling, 3.4 (81); and (iv) none calling, 42.7 (128). The bats were least successful when no frogs were calling [χ^2 (2) = 46.32, $P < .005$].

Captive *T. cirrhosus* responded to recorded advertisement calls from a variety of edible leptodactylid and hylid frogs. To test the hypothesis that fringe-lipped bats do not merely respond to any sound but discriminate among frog calls, we simultaneously presented the advertisement calls of an edible frog, *Hyla boulengeri*, and a poisonous toad of similar size, *Bufo typhonius*. Five bats were tested in a flight cage, with eight trials per individual (6). As shown in Table 1, the bats preferred the call of *H. boulengeri*. In field tests at six widely distributed sites on Barro Colorado Island, bats again preferred the *H. boulengeri* call over that of *B. typhonius* (7).

To ascertain the effect of prey size, we simultaneously presented the advertisement calls of *P. pustulosus* (maximum snout-to-vent length, 35 mm) and *Leptodactylus pentadactylus* (200 mm). The latter is too large to be captured by *T. cirrhosus*. The advertisement calls of these two species have approximately the same frequency range (200 to 1000 Hz). The calls were presented at the same intensity, even though *L. pentadactylus* produces a louder call. Five caged bats preferred the call of *P. pustulosus*, and bat responses in the field were similar (Table 1) (7).

We also sought to determine whether *T. cirrhosus* predation is affected by call repetition rate and volume (Table 2). When three fringe-lipped bats in the flight cage were simultaneously presented with *P. pustulosus* advertisement calls played at 1.6-second intervals (about normal) and 3.2-second intervals, the bats preferred the faster call rate. Three additional *T. cirrhosus* preferred *Centrolenella fleischmanni* calls played at rates of 1.6- versus 6.4-second intervals (about normal). When simultaneously presented with *P. pustulosus* advertisement calls at intensities of 74 and 78 dB SPL at 1 m, two bats both preferred the louder call.

In the absence of counterselection forces, one would expect male anurans to make themselves as conspicuous and locatable as possible when attempting to attract mates (8). Nevertheless, with the exception of poisonous or unusually large species such as *B. typhonius* and *L. pentadactylus*, few neotropical anurans do so. Clearly the selective advantages of sexual advertisement are balanced by the increased risk of predation. Thus we suggest that predation has had an important influence on the evolution of frog vocalizations in the Neotropics.

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4. *Trachops cirrhosus* were mist-netted at 11 sites and observed with a Javelin model 221 night vision scope as they responded to recorded frog calls at three sites.
5. These observations, made at Weir Pond on Lutz Stream between 1845 and 2400 hours on 17, 18, 20, 22, 23, and 27 April, totaled 14.3 hours. The average number of *P. pustulosus* in the nightly breeding chorus was 242 (range, 44 to 425). Of the 95 capture attempts believed successful, in 42 cases bats were actually seen carrying frogs; characteristic departure behavior was used to determine the result of the remaining 53 attempts. Chorus categories were defined as follows: full chorus, sustained use of complex calls (whine plus one to six chucks per call) by a majority of males in the pond, partial chorus, sustained use of complex calls by less than half of the males; few calling, sustained use of simple calls (whine only) with or without sporadic complex calls; none calling, mostly silent with no more than an occasional simple call. When fewer than 50 frogs were present, the maximum call category used was "partial chorus."
6. Calls were recorded on a Nagra IV-D tape recorder and played to the bats at 38 cm/sec on Stellavox recorders with small extension speakers. Speaker intensities were balanced at 75 dB SPL at 1 m. The flight cage was 4.5 m square and 2.3 m high and was illuminated by a single red 25-W bulb in the center. The observer sat in one corner and the bat perched in the opposite corner. One speaker was located in each of the remaining corners, about 4 m from the bat. A response was recorded if the bat passed within 1 m of a speaker within 60 seconds of call presentation. (Most responding bats flew within 30 cm of a speaker, and often landed on it.) There were no rewards for a correct choice. Speaker inputs were switched after each trial to reverse call location, and trials were repeated at intervals of 5 to 15 minutes. Bats were tested in only one set of trials per night and never twice in the same experiment. None was used in more than two experiments. The null hypothesis of no preference was tested by comparing $-2 \Sigma \ln p$ to a χ^2 distribution, d.f. = $2n$ (9).
7. All trials were made between 1840 and 2020 hours from 18 to 25 February and 2 to 18 April. Calls were played simultaneously at an intensity of 74 dB SPL at 1 m on Pearlcorder model D 120 microcassette tape recorders at 2.4 cm/sec. The call interval was 1.6 seconds. Speakers were placed 4 m apart and were simultaneously observed with a Javelin model 221 night vision scope from a distance of 12 m. *Trachops cirrhosus* can be identified in flight. Responses were recorded when a *T. cirrhosus* passed within 1 m of a speaker (most responding bats flew closer than 30 cm). Data were analyzed as in (6).
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Thyrotropin-Releasing Hormone Effects in the Central Nervous System: Dependence on Arousal State

Abstract. *Thyrotropin-releasing hormone was microinjected into the dorsal hippocampus of ground squirrels (Citellus lateralis) when they were at different levels of arousal, as assessed by electrophysiological and behavioral criteria. When administered to the awake animal, thyrotropin-releasing hormone produced dose-dependent decreases in body temperature accompanied by behavioral quieting and reductions in metabolic rate and electromyographic activity. The magnitude of these effects was greater when the peptide was microinjected during a period of behavioral activation. In contrast, administration of the peptide during slow wave sleep produced increased thermogenesis, an increase in electromyographic activity, and an increase in the amount of electroencephalographic desynchronization.*

Thyrotropin-releasing hormone (TRH), traditionally recognized for its ability to release thyrotropin from the pituitary gland, is now known to be widely distributed throughout the brain (1), and to affect several physiological and behavioral processes independent of its action on the pituitary (2). For example, changes occur in body temperature, respiration, blood pressure, electroencephalogram (EEG), and motor activity after central nervous system (CNS) administration of TRH in conscious animals (3). In addition, TRH reverses the hypother-