

# CALL RATE VARIABILITY AND FEMALE CHOICE IN THE AFRICAN FROG, *HYPEROLIUS MARMORATUS*

by

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(With 1 Figure)  
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## Summary

1. Two-choice phonotaxis experiments were used to investigate female responses to short-term variation in call timing in the African painted reed frog, *Hyperolius marmoratus*. The number of calls produced per stimulus in each choice test were equalised over either 10 or 20 seconds.
2. All alternative stimuli were tested against a regular stimulus with an invariant inter-call interval (ICI = duration between the onset of successive calls). There were three categories of alternative call timing; bouts of rapid calling (short ICI) where the period of silence between bouts was shorter than the bouts of calling; bouts of rapid calling where the period of silence between bouts was longer than the bout of calling; and irregular calling (variable ICI) without prolonged periods of silence.
3. The only stimuli females discriminated against were rapid bouts of calling with prolonged periods of silence. Females showed significant differences in the number of responses when presented with two stimuli that differed in call timing over as short a period as 10 seconds.
4. We also calculated variability in the ICI of 25 males in the field. There was a significant negative relationship between mean call rate (calls/min) and variability in the ICI. Faster callers showed lower variability in ICI.
5. The phonotaxis experiments did not show a female preference for regular versus irregular call timing. So female mate choice of males with higher call rates in the field is not due to a preference for males with less variability in ICI.

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## Introduction

Directional female mating preferences for courtship signals produced at higher rates have been documented in numerous taxa (RYAN & KEDDY-HECTOR, 1992). Fewer studies, however, have investigated the effect on female mate choice of within-male variation in display rate. SULLIVAN (1990, 1994) noted that male characters used by females during mate choice may vary over the females' sampling period. Workers therefore need to determine both the duration of the female sampling period, and the corresponding variation in male characters over this time frame. This is particularly relevant for behavioural characters like display rate which may change rapidly over relatively short periods of time.

Even if the female sampling period is sufficiently long to result in two stimuli with different patterns of calling being perceived as having equal call rates (total number of calls per sampling period), mate choice may still occur based on females having preferences for different temporal patterns of calling. The most obvious example of variation in call rate over time is that of bout singing. In unison bout singing species of anuran amphibians and insects there is collective calling by groups of males, interspersed by periods of silence (GREENFIELD & SHAW, 1983; SCHWARTZ, 1991). In frogs, unison bout singing has been recorded in several species, for example, *Hyla microcephala* (SCHWARTZ, 1991), *Centronella granulosa* (IBÁÑEZ, 1993), *Pseudacris crucifer* (ROSEN & LEMON, 1974) and *Smilisca sila* (TUTTLE & RYAN, 1982). In addition, in several species, individual males also call in bouts, but these are not synchronised between neighbouring males (e.g. *Chiromantis xerampelina*, JENNIONS *et al.*, 1992). Bout singing provides an extreme example of short term variation in male call rate: males alternate between periods of rapid calling, and periods of total silence. At a lesser extreme males may show even shorter term variability in the temporal pattern of calling, for example, variability in the interval between successive calls. SIMMONS & ZUK (1992) have suggested that variability in syllable rate influences female choice in the field cricket, *Gryllus bimaculatus*, because it correlates with male mating success and females localise males on the basis of their calls.

Here we use two-choice phonotaxis experiments to examine female responses to conspecific calls in the African painted reed frog, *Hyperolius marmoratus*. In this species males call in a regular fashion, and periods of

silence are rare (see Methods). Females were offered a choice between a stimulus consisting of regularly spaced calls (1 call per second) and alternative stimuli in which calls were unevenly spaced through time. The total number of calls produced was the same for alternative and regularly stimuli. The alternative stimuli offered are *not* meant to mimic naturally observed phenotypic variation in male calling patterns. Instead they were chosen to address the issue of why male *H. marmoratus* call in an approximately regular fashion. Specifically, do females prefer a regular monorhythmic sequence of calls to a sequence in which there is variability in the interval between calls? Research investigating female mating preferences for unfamiliar, novel stimuli have also been conducted in a series of phonotaxis experiments by RYAN and colleagues (reviewed in RYAN & RAND, 1993). Although the alternative stimuli are novel, in most stimuli the minimum interval between successive calls fell within the natural observed range for *H. marmoratus*. We also present field data on within-male variability in call spacing in relation to mean call rate (call/min).

## Methods

### Calling and mating behaviour of the study species.

*Hyperolius marmoratus* is a prolonged breeding frog, with males forming dense choruses on a nightly basis throughout spring and summer. There is no evidence for chorus organisation (*i.e.* call alternation, call synchrony or call triggering leading to leader-follower sequences). Playback experiments have shown that the calling rate of males is independent of that of neighbours (PASSMORE *et al.*, 1992). There is no unison bout calling. Male *H. marmoratus* have a steady call rate, and do not call in bouts. Using a minute by minute analysis, it has previously been shown that individual males are only silent for 3.3% of the time between the initial onset and final termination of calling over a night. Call rates (calls/min) of individual males are almost constant from approximately 2030 hours to 2130 hours. From 2130 hours onward there is a slow tapering off in calling, and call rate becomes more variable (see PASSMORE *et al.*, 1992, Fig. 5). Although the average call rate is around 60 calls/min, males are capable of calling at a rate of well over 100 call/min shortly before entering amplexus (DYSON, 1989). This corresponds to an inter-call interval (ICI = duration between onset of successive calls) of less than 600 ms.

Choruses begin to develop shortly after dusk, and the first 30 min after nightfall are characterised by aggressive interactions between males while call sites are established. By 2030 hours, male movement between suitable call sites has largely ceased and most males are calling. The majority of matings (90.4%) are initiated between 2020 and 2200 hours (N = 19 of 21). Females spend approximately 15 minutes in the chorus prior to mating.

### Phonotaxis studies of female responses to different stimuli.

Phonotaxis experiments were conducted between December 11, 1993 and January 26, 1994 in Mtnzini, South Africa (28°51' S, 31°46' E). To complete the second set of experiments, we also conducted trials using seven females at Vernon Crookes Nature Reserve (30°15' S, 30°45' E) between February 4-5, 1994. Gravid females were captured at

ponds and transported to the testing sites (less than 10 km away). All females were tested on the night of capture, and released the following night at the ponds. They were tested in an outdoor arena with a floor area of  $2.5 \times 2$  m and 0.5 m high cloth walls. The arena was illuminated by a dimmed 60 W red bulb suspended 1.8 m above the arena. Ambient temperature ranged from 18.7 to 24.9°C.

Stimuli were broadcast using two Nagra E tape recorders, a Klein & Hummel SB 280/II stereo amplifier and two Philips AD 50600 5-inch diameter loudspeakers. The loudspeakers were placed 2 m apart, facing each other and equidistant from the release container (a perforated plastic container). The observers sat on one side of the arena, equidistant from the speakers. Females were placed in the release container and stimuli broadcast for three minutes prior to the first trial, and for a minimum of two minutes between subsequent trials.

We tested individual females for several different stimulus pairs, presented as sequential tests on the night they were collected (e.g. WILCZYŃSKI *et al.*, 1995). However, no female was tested more than once with any one stimulus pair. The maximum number of tests performed by females was seven. The total number of females tested was 38. The order of stimuli pairs presented was randomised. We scored a positive response if the female touched the speaker or approached to within 10 cm of the speaker. Females were classified as unresponsive if they remained immobile for more than five minutes, or attempted to escape from the arena. Shout-vent-length of females was measured to the nearest 0.1 mm using dial callipers. Previous work has shown that female responses may be influenced by body size (JENNIONS *et al.*, 1995). We also measured the time between release and a positive response. Variation in response time among tests was analysed using a randomised block analysis of variance with females as the blocking factor. Only females that responded positively in all tests within a given set of experiments were used in the analysis so there were no missing cell values. Separate analyses were conducted for the two sets of experiments.

A synthetic *Hyperolius marmoratus* advertisement call was used to prepare the stimulus tapes. It had a frequency excursion of 2850 to 3350 Hz and was 80 ms in duration, with a linear rise time of 10 ms and a fall time of 25 ms. These values approximate the means for these variables in the study population (see Dyson & Passmore, 1988). The sound pressure level of broadcast stimuli was set at 104 dB (peak) at 50 cm, which is the mean intensity of a natural call at this distance. Sound measurements were made using a Bruel and Kjaer 2230 sound level meter with a Bruel and Kjaer type 4165 microphone.

Thirteen stimulus tapes were made for 12 two-choice tests. In each test we investigated female response to a stimulus with a regular call rate *versus* one with an alternative temporal pattern of calling. The regular call rate stimulus (REGULAR) consisted of evenly spaced calls, with an ICI of 1000 ms (60 calls/min). Details of call timing for the alternative stimuli are provided in Tables 1 and 2. The alternative stimuli can be placed in one of three categories:

1. Bouts of calling with a short ICI followed by a period of silence where the period of silence is longer than the bout of calling (SHORT BOUTS).
  2. Bouts of calling with a short ICI followed by periods of silence where the period of silence is shorter than the bout of calling (LONG BOUTS).
  3. Calling without periods of silence, but with variable ICI (IRREGULAR).
- Bout length is defined as the duration between the onset of the first and last call. These stimuli allowed us to investigate the effect of three factors on mating preferences: (1) the presence of periods of silence; (2) the importance of bout length relative to that of the inter-bout silence; (3) variability in call rate within a bout of calling.

The study was divided into two sets of experiments. In the first set, the alternative stimuli were such that the call rate was equalised over 10 seconds and was identical to that of REGULAR (10 calls/10 seconds). In the second set of experiments, the time period over which the call rate was equalised was 20 seconds (20 calls/20 seconds). It was not possible

to ensure a consistent temporal relationship between the stimuli due to differences in ICI. We therefore randomised this relationship in each trial by simply switching on the REGULAR stimulus without reference to the alternative stimulus. Because REGULAR was used in every trial, we also switched the end from which it was broadcast between successive trials. The proportion of responses to each stimulus in each two-choice test was analysed using exact binomial probabilities. There was no end bias. Because of the potential risk of Type I error due to 12 sets of experiments involving the REGULAR stimulus we combined data from similar categories of alternative stimuli and then use the Bonferroni correction to obtain table-wide probabilities. We have thus grouped these data into the three categories listed above (IRREGULAR, SHORT BOUT and LONG BOUT). This pooling of data treats responses from the same female as being statistically independent (Table 3). However, we also performed analyses in which only one response per female per category was used. We used the response to the first stimulus pair in the category of interest with which the individual female was tested.

#### Variability in male call rate.

In an earlier field study we collected data on male call rate at a natural breeding site in Muzuni. Small microphones (Acoustica M31 dynamic, hyper-cardioid) were positioned on adjustable monopods within 10 cm of calling males and the microphones then hooked up to an eight channel event recorder. The event recorder logged the relative onset time of each call to the nearest 10 ms (for further details see Passmore *et al.*, 1992). We used this data to calculate ICI for 25 males ( $N = 22$  ICI per male). Call rate varies with time of night, and we therefore analysed calls produced between 2030 and 2100 hours when call rate per minute showed the least variability (Passmore *et al.*, 1992, Fig. 5). For each male we then calculated the coefficient of variation for ICI over the period in which it gave the 23 calls.

## Results

### Female responses.

In the first set of experiments with call rate equalised over 10 seconds, females responded significantly more often to REGULAR than SHORT BOUT A which had an inter-bout silence of 5.4 s. There was no significant difference in the number of responses to REGULAR and LONG BOUT A, which had an inter-bout silence of 3.4 s. In the second set of experiments where call rate was equalised over 20 seconds, females also responded significantly more often to REGULAR than SHORT BOUT B, which had an inter-bout silence of 10.4 s, but showed no difference in the number of responses to REGULAR and LONG BOUT D, which had an inter-bout silence of 6.0 s. None of the other tests revealed a significant difference in the number of female responses to REGULAR and alternative stimuli (Tables 1 and 2).

When the number of responses from the two SHORT BOUT *versus* REGULAR experiments were pooled, there were significantly more responses to REGULAR. If only one response per female is used (to

TABLE 1. Responses in two-choice phonotaxis when call rate is equalised over 10 seconds

Alternative stimulus	N	Responses to		Binomial probability
		Alternative	Regular	
SHORT BOUT A Bout of 10 calls with ICI of 506 ms + 5446 ms silence	20	5	15	0.041
LONG BOUT A Bout of 10 calls with ICI of 737 ms + 3418 ms silence	20	10	10	1.00
LONG BOUT B Bout of 5 calls with ICI of 737 ms + 2094 ms silence	20	10	10	1.00
LONG BOUT C Bout of 10 calls (5 pairs) with ICI within a pair of 506 ms and ICI between pairs* of 1000 ms, + 2470 ms silence	20	11	9	0.824
IRREGULAR A Paired calls with ICI within a pair of 506 ms and ICI between pairs of 1494ms	20	12	8	0.503
IRREGULAR B 5 calls with ICI of 506 ms + 5 calls with ICI of 1507 ms	20	8	12	0.503
IRREGULAR C (ICIs of 1000, 743, 2987, 600, 350, 300, 512, 1187, 800, 1494)	20	13	7	0.263

The regular stimulus has an ICI of 1000 ms. N = number of females tested for a given stimulus pair. The total number of females tested for these stimulus pairs was 24. \* ICI between pairs is the duration between the onset of the first call of successive paired calls

TABLE 2. Responses in two-choice phonotaxis when call rate is equalised over 20 seconds

Alternative stimulus	N	Responses to		Binomial probability
		Alternative	Regular	
SHORT BOUT B 20 calls with ICI of 506 ms + 10386 ms silence	16	3	13	0.021
LONG BOUT D Bout of 20 calls with ICI of 737 ms + 5997 ms silence	16	8	8	1.000
LONG BOUT E Bout of 20 calls with ICI within a pair of 506 ms and ICI between pairs of 1000 ms + 4940 ms silence	16	7	9	0.804
IRREGULAR D 10 calls with ICI of 506 ms + 10 calls with ICI of 1500 ms	16	5	11	0.210
IRREGULAR E 10 calls with ICI of 400 ms + 10 calls with ICI of 1600 ms	16	9	7	0.804

The regular stimulus has an ICI of 1000 ms. N = number of females tested for a given stimulus pair. Total number of females tested = 16.

guarantee statistical independence), the number of females responding to REGULAR *versus* SHORT BOUT stimuli are 27 and 8 respectively (Binomial exact,  $p < 0.001$ ). There was no significant difference in the number of responses to REGULAR or alternative stimuli in the LONG BOUT *versus* REGULAR, or IRREGULAR *versus* REGULAR experiments (Table 3). An analysis based on only one response per female yielded the same conclusion (Binomial exacts, both  $p < 0.5$ ).

The size of females responding to REGULAR *versus* alternative stimuli did not differ significantly in any of the 12 tests (Mann-Whitney U-test, all  $p > 0.10$ ; but see JENNIONS *et al.*, 1995). There was also no significant difference in response time among two-choice tests in either the 10 calls/10 second (ANOVA,  $df = 6, 78, F = 1.07, p = 0.39$ ), or 20 calls/20 second experiments (ANOVA,  $df = 4, 52, F = 0.72, p = 0.58$ ).

#### Male call rate.

The average inter-call interval for the 25 males was  $1215 \pm 222$  ms (mean  $\pm$  SD) (Fig. 1). The median coefficient of variation (CV = standard deviation/mean) for male ICI over the 23 calls was 12.7%. There was a strong positive relationship between a male's mean ICI and the CV for ICI (Spearman,  $r_s = 0.58, N = 25, p < 0.005$ ). This relationship held even when two outliers (CV  $> 40\%$ ) were excluded ( $r_s = 0.58, N = 23, p < 0.01$ ). Although both variables contain the same component (mean ICI), the CV contains the reciprocal of mean ICI. This should bias the correlation towards a negative relationship, hence the significant positive correlation is unlikely to be a statistical artefact (JACKSON & SOMERS, 1991). In sum,

TABLE 3. Results of two-choice phonotaxis for the 3 classes of alternative stimuli

Alternative stimulus type	N	Responses to		Binomial probability
		Alternative	Regular	
SHORT BOUT	36	8	28	0.0012*
LONG BOUT	92	46	46	1.00
IRREGULAR	92	47	45	0.916

N = number of trials.

\*  $p < 0.01$  with Bonferroni correction.

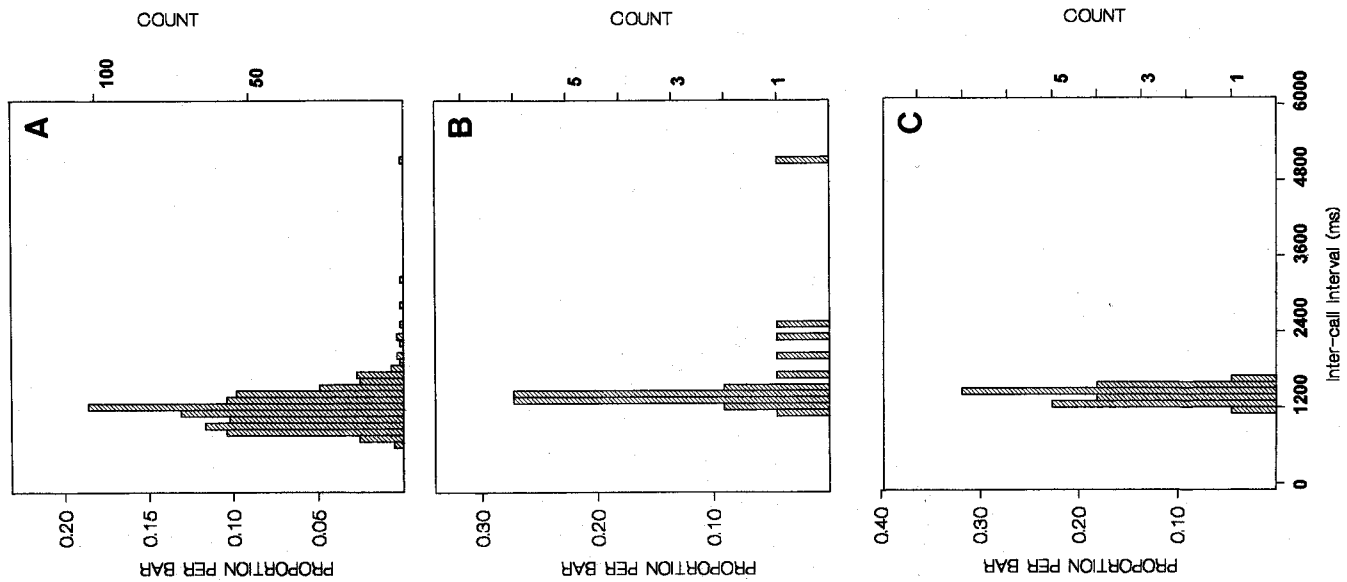


Fig. 1. Frequency distributions of male inter-call intervals (ICI). (a) pooled data from 25 males ( $N = 22$  ICI per male); (b) data from a male with a high coefficient of variation in ICI; (c) data from a male with a low coefficient of variation in ICI.

males with faster average call rates (calls/min) showed less variability in ICI.

### Discussion

We found that *Hyperolius marmoratus* females do not discriminate between stimuli with irregular and regular call timing. However, depending on the ratio of bout duration to inter-bout silence, they prefer regular to bout calling. In *H. marmoratus* the duration of the interval between male advertisement calls in a sequence of calls had a relatively low coefficient of variation of 12.7% (which is still much higher than that for call features such as dominant frequency, see GERHARDT, 1991). Although *H. marmoratus* has a fairly steady call rate, other empirical work suggests that an investigation of call rate variability is relevant. First, work on the field cricket *Gryllus bimaculatus* have shown that females may use variability in syllable rate to discriminate between young and old males (SIMMONS & ZUK, 1992). Second, in *H. marmoratus* males are capable of dramatically increasing their call rate for short periods of time. When males detect a female they produce a so-called 'courtship' call which is basically the advertisement call produced at a faster rate (increasing from 60 calls/min to over 100 calls/min, DYSON, 1989). Female *H. marmoratus* prefer faster call rates (PASSMORE *et al.*, 1992) and it might therefore benefit males to call rapidly in bouts even if energetic constraints on total call production leads to these call bouts being followed by periods of silence (see SCHWARTZ, 1991). There is thus no obvious physiological constraint on males that limits their ability to call in rapid bouts (in 'courtship' calling, ICI < 600 ms). Third, SCHWARTZ (1991) in a phonotaxis study of the neotropical frog *Hyla microcephala* equalised the number of calls produced over 30 seconds. He found that females did not show a mating preference when offered a choice between a bout of 30 calls with an ICI of 0.5 s (2 call per second) followed by 15 seconds of silence, and steady calling at the rate of 1 call per second.

Here we show that female mating preferences are influenced by the temporal pattern of calling. Females discriminated against bouts of rapid calling followed by a period of silence longer than the calling bout. Although females often oriented, and even moved, towards a speaker broadcasting a bout of rapid calling, during the inter-bout silence they reoriented and moved towards the regular call. Thus, in spite of repeated

reorientation, they eventually choose the stimulus with the constant call rate. There also appears to be an interaction between bout length and the duration of the inter-bout silence, as shown by the different results for Short Bout A and Long Bout D which both had inter-bout silences of around 6 seconds but calling bouts of different duration. SCHWARTZ (1991) found no female discrimination between regular and bout calling in *Hyla microcephala* and suggested that female preferences are not responsive for bout calling in this species. However, in *H. marmoratus* there is active discrimination against calling in bouts. This raises the possibility that female preferences may influence the evolution of bout calling if the ancestral preference discriminates *against* bout callers.

A strategy of regular calling by male *H. marmoratus* is as effective as any of the alternatives tested. Of course, given a sufficiently long period of time for equalisation of call rate, the duration of a bout of rapid calling will be sufficiently long for females to perceive that stimuli as being produced by a male with a consistently higher call rate. However, given constraints on total call production (WELLS & TAIGEN, 1989; SCHWARTZ, 1991) and the unpredictable arrival of females, males may benefit more by calling at a slower rate and spending an increased amount of time 'on air'. FORESTER *et al.* (1988) performed a phonotaxis experiment in which they varied the amount of time over which speakers broadcast calls. When the choice was between speakers emitting calls for 20, 40, 60 and 80% of successive 10 minute periods, females preferentially responded to the speakers that spent more time 'on air'. Unfortunately, call rate was constant in all four stimuli, therefore the total energy emitted varied between speakers. None the less, this result does suggest that a more regular pattern of calling is beneficial. Finally, several studies suggest that localisation of males is an important factor in anuran calling (see BAILEY, 1991 for localisation in insects). A continuous sequence of calls is probably more easily localised by females than a series of short calling bouts interspersed by silence.

In our field study of male calling we found a significant positive relationship between call rate and ICI variability. Faster callers showed less variability in ICI. However, this does not appear to explain the mating advantage of males with higher call rates seen in the field (see PASSMORE *et al.*, 1992). There was no evidence that females discriminated

against stimuli with greater variability in ICI when calling was more or less continuous (see Table 3).

Numerous phonotaxis experiments show that female frogs prefer stimuli with higher call rates. These experimental results are supported by fieldwork documenting a positive relationship between call rate and mating success in anurans (reviewed in PASSMORE *et al.*, 1992). Similar female preferences for higher call rates have also been reported in birds and insects (RYAN & KEDDY-HECTOR, 1992). Less attention, however, has been given to the possible existence of female preferences based on short-term variation in call rate. In general, it has been assumed that 'calls per minute' is a sufficiently accurate description of the temporal pattern of calling to fully account for female mate choice. Our results suggest that it may be worthwhile to pay greater attention to these short-term fluctuations in male calling rate or, in a similar vein, temporal variation in display rate in visually signalling animals.

#### References

- BAILEY, W.J. (1991). Mate finding: selection on sensory cues. — In: Reproductive behaviour of insects (W.J. BAILEY & J. RUDSILL-SMITH, eds). Chapman & Hall, London, p. 42-74.
- DYSON, M.L. (1989). Aspects of social behaviour and mate choice in a caged population of painted reed frogs, *Hyperolius marmoratus*. — PhD thesis, University of the Witwatersrand.
- & PASSMORE, N.I. (1988). Two-choice phonotaxis in *Hyperolius marmoratus* (Anura: Hyperoliidae): the effect of temporal variation in presented stimuli. — Anim. Behav. 36, p. 648-652.
- FORESTER, D.C., LYKENS, D.V. & HARRISON, W.K. (1988). The significance of persistent vocalisation by the spring peeper, *Pseudacris crucifer* (Anura: Hylidae). — Behaviour 108, p. 197-208.
- GERHARDT, H.C. (1991). Female mate choice in treefrogs: static and dynamic acoustic criteria. — Anim. Behav. 42, p. 615-635.
- GREENFIELD, M.D. & SHAW, K.C. (1983). Adaptive significance of chorusing with special reference to the orthoptera. — In: Orthopteran mating systems: Sexual competition in a diverse group of insects (G.K. MORRIS & D.T. GWYNN, eds). Westview Press, Boulder, Colorado, p. 1-27.
- IBÁÑEZ R.D. (1993). Female phonotaxis and call overlap in the neotropical glassfrog *Centronella granulosa*. — Copeia 1993, p. 846-850.
- JACKSON, D.A. & SOMERS, K.M. (1991). The spectre of 'spurious' correlations. — Oecologia 86, p. 147-151.
- JENNIONS, M.D., BACKWELL, P.R.Y. & PASSMORE, N.I. (1992). Breeding behaviour of the African frog, *Chiromantis xerampelina*: multiple mating and polyandry. — Anim. Behav. 49, p. 181-186.
- , — & — (1995). Repeatability of mate choice: the effect of size in the African frog, *Hyperolius marmoratus*. — Anim. Behav. 49, p. 181-186.
- PASSMORE, N.I., BISHOP, P.J. & CARRNESS, N. (1992). Calling behaviour influences mating success in male painted reed frogs, *Hyperolius marmoratus*. — Ethology 92, p. 227-241.

- ROSEN, M. & LEMON, R.E. (1974). The vocal behaviour of spring peepers, *Hyla crucifer*. — *Copeia* 1974, 940-950.
- RYAN, M.J. & KEDDY-HECTOR, A. (1992). Directional patterns of female mate choice and the role of sensory biases. — *Amer. Nat.* 139, p. S4-S35.
- & RAND, A.S. (1993). Sexual selection and signal evolution: the ghost of biases past. — *Phil. Trans. Roy. Soc. B* 340, p. 187-195.
- SCHWARTZ, J.J. (1991). Why stop calling? Unison bout singing in a Neotropical treefrog. — *Anim. Behav.* 42, p. 565-577.
- SIMMONS, L.W. & ZUK, M. (1992). Variability in call structure and pairing success of male field crickets, *Gryllus bimaculatus*: the effects of age, size and parasite load. — *Anim. Behav.* 44, p. 1145-1152.
- SULLIVAN, M.S. (1990). Assessing female choice for mates when the males' characters vary during the sampling period. — *Anim. Behav.* 40, p. 780-782.
- (1994). Mate choice as an information gathering process under time constraints: implications for behaviour and signal design. — *Anim. Behav.* 47, p. 141-151.
- TUTTLE, M.D. & RYAN, M.J. (1982). The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. — *Behav. Ecol. Sociobiol.* 11, p. 125-131.
- WELLS, K.D. & TAIGEN, T. L. (1989). Calling energetics of the neotropical frog *Hyla microcephala*. — *Behav. Ecol. Sociobiol.* 25, p. 13-22.
- WILCZYNSKI, W., RAND, A.S. & RYAN, M.J. (1995). The processing of spectral cues by the call analysis system of the tungara frog, *Physalaemus pustulosus*. — *Anim. Behav.* 49, p. 911-929.