

Chorus dynamics of a neotropical amphibian assemblage: comparison of computer simulation and natural behaviour

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Abstract. The high population density of vocalizing males of the Puerto Rican treefrog *Eleutherodactylus coqui* in their natural habitat can lead to call overlap, which may interfere with the function of the call. Simulations of groups of calling males suggest that a given male can maximize the effectiveness of each call by actively avoiding acoustic overlap with at most two of its nearest neighbours. Analysis of vocal patterns of natural groups of frogs support this hypothesis: 14 of the 18 frogs tested actively avoided acoustic overlap with no more than two neighbours (one avoided acoustic overlap with three neighbours) while three frogs exhibited active call-jamming with one of their neighbours. Moreover, cross-correlograms of calling patterns between all pairs of frogs in a group were used to infer dynamic chorus structure. Overlap avoidance behaviour is discussed in terms of reproductive success and predator evasion.

While there has been a large body of experimental work on the nature of acoustic behaviour in insects (Alexander 1961; Jones 1966a, b; Bailey & Thiele 1983; Greenfield 1983; Brush et al. 1985) and in amphibians (see Littlejohn 1977 for review; Narins & Capranica 1976, 1977, 1978; Lemon & Struger 1980; Narins 1982a, b; Zelic & Narins 1982, 1983, 1985; Wells & Schwartz 1984), most of this work has dealt with the responses of an isolated individual to artificial stimuli. In fact, actual studies of group signalling behaviour are rare (see Hardy 1959 and Fox & Wilczynski 1986 for exceptions). This is due in part to the inherent difficulty of monitoring the behaviour of more than one individual at a time. Nevertheless, studies of the behaviour of individuals within groups must be undertaken in order to comprehend more fully the dynamics of the vocal interactions between members of such groups. Knowledge of the responses by one individual to the behaviour of its neighbours coupled with data regarding the behaviour of an isolated individual may lead to elucidation of the underlying mechanisms governing calling behaviour.

In organisms such as anurans and orthopterans, in which several individuals signal in close temporal and spatial proximity, 'chorusing' or non-random distributions of signals in space and time can occur (Anderson 1954; Hardy 1959; Foster 1967; Alexander 1975; Wells 1977a; Awbrey 1978;

Arak 1983b; Greenfield & Shaw 1983). Cases of asynchronous chorusing or call alternation have been observed in the acoustic signalling of orthopterans (Otte 1977; Greenfield 1983) and anurans (Whitney & Krebs 1975a; Wells 1977b). These non-random signal distributions can occur whether the species-specific features of the call are temporal (for example, chirp and pulse rates in many orthopteran mating calls, and pulse rates and amplitude modulation patterns in anuran calls) or spectral (such as frequency modulation patterns in anurans and birds).

Regardless of which aspects of their call are significant in species-specificity, male anurans are faced with the problem of placing their calls in such a way as to maximize their effectiveness, either in mate attraction or territorial defence (Arak 1983a). Central to the understanding of the phenomenon of chorusing is the elucidation of the underlying mechanisms of the behaviour (Wells & Schwartz 1984). In the present study, the problem can be posed as two questions, (1) Do frogs actively avoid temporal acoustic overlap with each other within the chorus? (2) How (in what patterns) do individual frogs call in order to maintain the group chorus structure? We have used both theoretical and experimental approaches to try to answer these questions as they apply to the Puerto Rican treefrog *Eleutherodactylus coqui*.

We chose *E. coqui* because it is, in many aspects, an ideal animal for field studies of acoustic behaviour. It is easily accessible and ubiquitous in its native habitat, its call is simple in structure and

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highly stereotyped, and it occurs in densities which indicate that acoustic interference with nearby calling males may be an important selective factor for these organisms (Narins & Capranica 1977; Stewart & Pough 1983; Narins & Smith 1986).

The species-specific 'co-qui' call consists of two notes, the frequencies of which vary with altitude (Narins & Smith 1986). The first, or 'co' note, is a constant frequency (approximately 1.5 kHz at 350 m) tone lasting ca. 80–110 ms separated from the second or 'qui' note (which sweeps up in frequency from ca. 2.2 to 2.6 kHz at 350 m and lasts from 140 to 170 ms) by an inter-note interval of 100–150 ms. Thus, the entire call has a duration of ca. 320–430 ms (Drewry 1970; Narins & Capranica 1977; Narins & Smith 1986).

The first note of the call is important in male-male interactions (Narins & Capranica 1976, 1978). When an intruding male enters a resident male's territory and begins calling, the resident will respond by dropping the second note of his call and uttering only co notes. If the intruder does not leave at this point, he too may drop his second note, and the males engage in what is called a 'co bout', in which the two males exchange co notes. If the intruder does not retreat, the resident will eventually approach him and engage in a 'biting, butting attack' (Reyes Campos 1971).

The second (qui) note was shown to be important in female attraction in a series of experiments in which tape-recorded male calls were modified in various ways and then presented to females (Narins & Capranica 1978). In addition, neurophysiological evidence reveals a preponderance of auditory neurons in females with maximal sensitivities in the frequency range of the qui-note (Narins & Capranica 1976, 1980), lending further support to the importance of the qui-note to females.

Playback experiments involving artificial co notes have led to the discovery of two other important features of the call: the behavioural refractory period and the call activation phase. The behavioural refractory period (which lasts ca. 1130 ms on average) is the time period immediately following the vocal portion of a frog's call during which the animal is unable to give a vocal response to an acoustic stimulus (Narins 1982a). The call activation phase occurs just prior to the first note and is the period after neural initiation of the call but before actual sound production. In *Pseudacris streckeri* this period lasts from 5 to 30 ms (Loftus-Hills 1974), and is presumed to be 30–40 ms in *E.*

coqui (Narins 1982a). Thus, the minimum possible call period for a male is ca. 35 ms for the call activation phase plus 375 ms for the call itself and 1130 ms for the behavioural refractory period giving a total of 1540 ms. In nature, the observed call period is in the order of 2–3 s (Narins & Capranica 1977; Zelick & Narins 1985), which suggests that male *E. coqui* actively regulate their call timing, rather than maximize call rate.

E. coqui males typically begin calling around dusk, and continue until about midnight or 0100 hours, although a few individuals may continue to call throughout the night (Drewry 1970; personal observations). Individual males often alternate calls with their nearest neighbours, so that very few, if any, calls are overlapped with one another (personal observations), suggesting that male *E. coqui* in a given locality chorus or maintain some structure to the calling pattern within the group.

To study the behaviour patterns of groups of calling male *E. coqui*, we developed a model of individual behaviour based on computer network theory. Since the properties of the call notes themselves (and not the inter-call interval) are critical for female recognition (Narins & Capranica 1978), we chose an algorithm which will, from an individual male's point of view, minimize call overlap with his neighbours. Using computer simulations of our model, we generated expected behaviour patterns for comparison with those actually recorded during field observations.

METHODS

Simulations

In the field of computer network theory, there are numerous models for systems in which a large number of computers are interconnected in a network (see Tanenbaum 1981 for a review). These models typically deal with the partitioning of some shared resource (such as bandwidth, processor time, hardware, etc.) among a number of users. We have attempted to apply these models in slightly modified form to acoustic organisms, for which the shared resources include frequency bandwidth, transmission time, transmission sites and temporal coding patterns (Littlejohn 1977).

We chose a class of network models called carrier sense multiple access protocols (Tobagi 1974), in which computer terminals are assumed to emit information packets of constant length which are

periodically sent over a common communication or data line. Before sending its packet, a terminal first 'senses' the data line (i.e. checks to see if it is already in use). If another terminal is already transmitting, the terminal will defer transmission for some random period of time and then continue to sense the data line. If the data line is not in use, the terminal proceeds to transmit its information. In a version called P-persistent carrier sense multiple access (Kleinrock & Tobagi 1975), the information packet is not automatically transmitted when the resource is free, but is transmitted with a certain probability P , which is equivalent to deferring transmission with probability $1 - P$. The result of this reduced transmission probability is that the channel throughput (ratio of actual traffic to offered traffic) is increased (Tobagi & Kleinrock 1975). In our model, based on P-persistent carrier sense multiple access, the frogs represent terminals, their calls the information packets, and the shared resource is the frequency band of the call. To avoid undue confusion with statistical significance values, we shall hereinafter refer to the probabilistic parameter (P) of the P-persistent carrier sense multiple access models as the 'calling parameter', and represent it by π .

To be compatible with the analytical requirements of carrier sense multiple access models, the call structure of any anuran we choose to model must satisfy several criteria, as follows. (1) The length of the signal must be relatively constant; that is, the calls must have a fixed duration. (2) Inter-call intervals must exhibit a well-defined mean and standard deviation. (3) Individuals must call preferentially during relatively quiet periods, but must also be able to call occasionally during noisy periods (that is, during periods when neighbours are also calling) so that even under acoustically crowded conditions a male will not remain completely silent, thus retaining some chance of attracting a mate. All three of these conditions are met by the call of the male *E. coqui*. In addition, to simplify the analysis, each frog in a simulated assemblage follows identical calling rules.

In our model, the calling behaviour of an individual consists of a relatively small number of specific states, which are executed sequentially and automatically. Each of these states represents one aspect of the proposed calling behaviour of *E. coqui*. In the first state, the animal is silent, ready to call, and monitoring the environment. If the animal does not detect a call from any of its neighbours, it

will transmit its own call with probability π (and remain silent with probability $1 - \pi$). Otherwise, the animal remains silent (and stays in state 1). Transmitting a call encompasses two states: the call activation phase (state 2, set to 40 ms in the simulations) and the call itself (state 3). In state 2, the animal is presumed to be able to detect sounds in its environment, and to sense whether or not another individual begins calling, which will result in jamming of his signal. Following the call activation phase is the call itself, simplified to a single note with a fixed duration of 400 ms. After the acoustic portion of the call is complete, there is a behavioural refractory period during which the animal is incapable of initiating another call sequence (state 4, set at 1140 ms). If, during the call activation phase or the behavioural refractory period, the individual detects an ongoing call from any of its neighbours, it exhibits a jamming avoidance behaviour: the individual attempts to minimize its chances of being interrupted again by delaying its next call by some random time (state 5). This random delay was uniformly distributed between 0 and 800 ms (i.e. up to twice the call duration, see Kleinrock & Tobagi 1975). If no call is detected during the call activation phase or behavioural refractory period, the animal returns to state 1 again.

This model is implemented for computer simulation by setting up the parameters and letting time pass in discrete, 5-ms increments. During each time increment, each individual in the specified chorus performs one 'state operation', that is, executes one of the above steps. After all of the individuals have been updated, the program checks to see which individuals, if any, are calling and maintains a record of the calling pattern. The user of the routine specifies the length of the various states, the calling probability π , the number of individuals, and the number of time increments to be executed. Written in machine language, the program can iterate five individuals 1000 times per s, or 20 individuals about 200 times per s.

In this study, computer simulations were used for two purposes. First, our version of the P-persistent carrier sense multiple access model was used to simulate various size groups of frogs. From these simulations, optimal group sizes and calling strategies were explored. Second, randomly generated sequences of calls fitting a specified distribution were compared with actually observed call sequences of natural frog choruses (see below).

Field Studies

Behavioural experiments were conducted from 25 August to 10 September 1985, at the field station (elevation 350 m) of the Center for Energy and Environmental Research (CEER), near El Verde, Puerto Rico. A custom-built encoder which permitted simultaneous recordings of the vocalizations of up to eight individuals was used in the field experiments. Groups of from two to five calling male *E. coqui* were isolated acoustically from other males by removing calling males from around the periphery of the group. A directional microphone (Radio Shack Highball-7) was mounted within 30 cm of each male in the group to record his vocalizations. Each microphone was connected to a separate channel of the encoder, with its own threshold adjustment. Whenever the signal level on one of the input channels exceeded the threshold, the pulse-tone output of an oscillator was sent to a single channel of a cassette tape-recorder (Sony TC-D5M). The oscillator frequency was unique for each channel. With this technique, the spectral information in the signals is sacrificed, but the temporal information is retained, facilitating analysis of call sequence and overlap among the members of the group. All recordings were made using high bias metal tape (Denon). After marking the locations of each calling frog on a map of the study site, the natural calling behaviour of the isolated groups was recorded for 3 min or until one of the frogs moved.

Field data were transferred from the cassette recorder through a custom-built decoder to an IBM AT personal computer for analysis. The decoder consists of eight sets of tunable bandpass filters (arranged in parallel), each tuned to one of the frequencies used in the encoder, and one output line for each set of filters. When a signal of the appropriate frequency and of sufficient amplitude is detected by one of these sets of filters, the voltage on the corresponding output line is set to +5 V. When the signal ceases, the voltage returns to +0 V. The eight data output lines were sent to a parallel port on the computer, where they were sampled at 1 kHz and saved to fixed media storage. After decoding, the data were filtered to remove any noise introduced in the encoding-recording-decoding process. Details of this process will appear in a subsequent paper (Brush & Narins, unpublished data). Filtered data were used in all subsequent analyses.

Auto- and cross-correlation techniques (modified from Heiligenberg 1973) were used to determine chorus structures. Correlograms were constructed for each pair of frogs in the groups with four and five frogs, with time on the abscissa and the Pearson product-moment correlation coefficient r on the ordinate. In row i and column j of the correlogram, the height of the curve at any point x on the time axis represents the correlation between calls initiated by frog i at time t and those initiated by frog j at time $t+x$. The autocorrelation of a periodic calling function is characterized by a sequence of regularly spaced peaks, where the spacing between peaks corresponds to the call period. The degree to which the frog call deviates from periodicity is reflected in unequally spaced peaks in its autocorrelation function. Since the heights of the correlogram peaks represent the degree of correlation of two calls separated by a particular time interval, a frog which regularly calls some fixed interval after the call of some other frog will have a peak in the cross-correlation function at that time interval. With the number of observation periods used (3–5 min with a 400 ms bin width = 450–750 periods), any peak with a magnitude greater than ca. 0.1 is significant at the 0.05 level (Chapman & Schaufele 1970). Any frog for which the correlogram exhibited a significant peak within the call period of a given frog was said to be a follower of that frog. The frog which followed with the shortest delay from the onset of a given frog's call was taken as its primary follower for the chorus diagrams. Chorus structure was then represented on maps of the study site by an arrow from each frog to its primary follower.

Comparison of Simulations with Field Data

To determine whether active avoidance of acoustic overlap by the frogs was underlying the observed call interval distribution, we compared the call overlap observed between individuals in each group with that observed in simulated 'random' choruses of the same frogs. To accomplish this, we compiled records of the actual call and inter-call interval lengths for each animal. These events were then rearranged randomly to yield a new sequence of calls for each member of the group (essentially, we created a 'random' chorus with the same distribution of call lengths and inter-call intervals as the original, thus facilitating statistical

comparison between the two), and the degree of overlap between each pair of frogs was determined.

In these comparisons, the degree of call overlap of frog i by frog j was defined to be the proportion of frog j 's calls that were initiated during a call of frog i . The degree of call overlap between individuals of several groups was compared with that observed in 100 different 'random' choruses using the Z-score (Sokal & Rohlf 1981).

Data analysis and statistical tests were performed by hand, using tables from Sokal & Rohlf (1981), and on an Apple Macintosh personal computer, using the StatWorks (1985) statistical analysis package.

ANALYSIS AND RESULTS

Graphical results from simulations of the modified carrier sense multiple access model are presented in Fig. 1, which shows the average (over 10 trials) number of calls generated in 2 min that were not interrupted by any other calls (such calls will be referred to as non-overlapped calls), as a function of group size and the 'calling parameter', π . The highest point in Fig. 1 (the overall maximum number of non-overlapped calls observed) occurs at a group size of five frogs, and a value of π of ca. 0.4.

In general, for a given group size, the number of non-overlapped calls generated by the group increases with π to some maximum, and then decreases. For group sizes of five and 20 frogs, the maximum number of non-overlapped calls was achieved at π values of 0.35 and 0.01, respectively (Fig. 2a). Similarly, for a fixed value of π , increasing the group size increases the number of non-overlapped calls per group per unit time (this number was used as a measure of group performance) to a maximum, after which enlarging group size is detrimental to group performance. For π values of 0.20 and 0.05, the group sizes that yielded maximum group performance were five and seven frogs, respectively (Fig. 2b). The magnitude of the value of π that yielded the best group performance at a particular group size decreased with increasing group size (Kendall's $T = -0.901$, $P < 0.005$).

Let π_{\max} represent the value of π at a particular group size at which the maximum number of non-overlapped calls (represented by C_{\max}) is generated, and let π_{+95} and π_{-95} represent the values of π above and below π_{\max} , respectively, that yield 95% of C_{\max} .

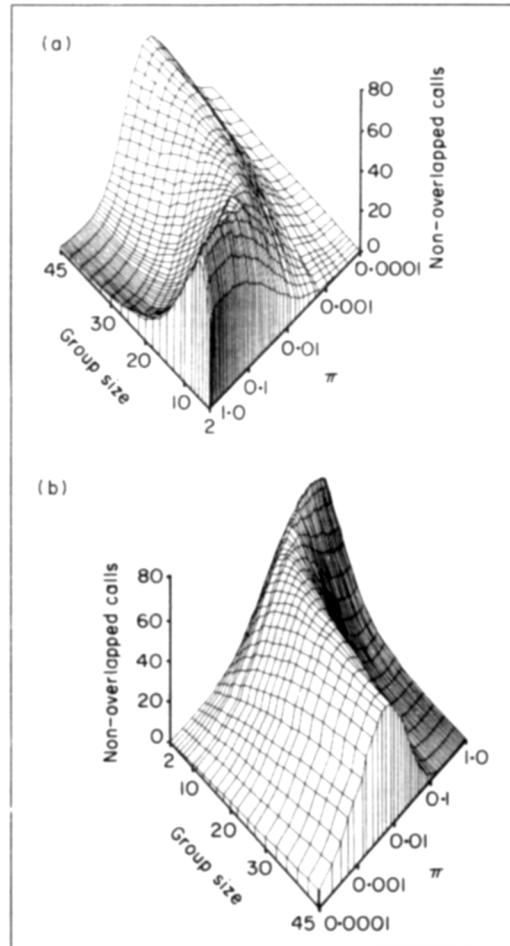


Figure 1. The entire simulation data set: the number of non-overlapped calls generated by a group of simulated frogs in a 2-min period is shown as a function of 22 different group sizes (from two to 45) and 53 values of π (from 0.0001 to 1.0). The points in this figure represent the average of 10 trials, and the entire simulation took 9 h to run on a 6502-based microcomputer. (b) Same as (a) but rotated by 180°.

Then, the difference between π_{+95} and π_{-95} can be thought of as a measure of the 'leeway' individuals in groups of various sizes have in choosing a value of π that results in a maximal number of non-overlapped calls. The size of this range decreases with increasing group size (Kendall's $T = -0.943$, $P < 0.005$). Thus, individuals in small groups of frogs have more flexibility in their choice of the calling parameter than do those in large groups (this corresponds to the narrowing of the 'ridge' of Fig. 1 with increasing group size).

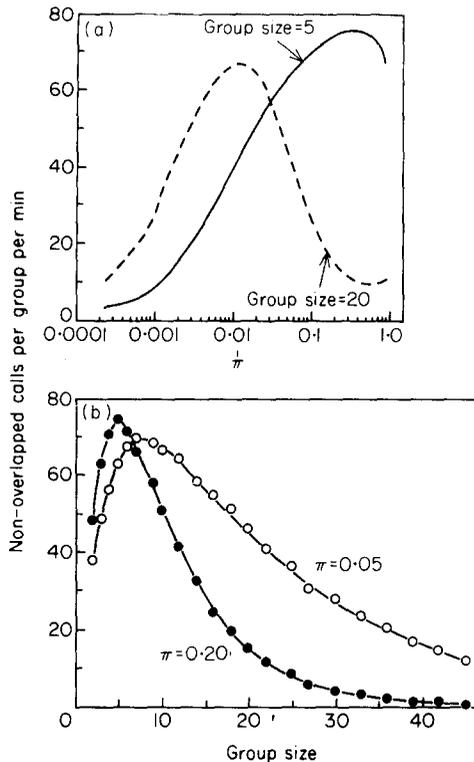


Figure 2. The number of non-overlapped calls per group per min as a function of calling parameter π , for groups with five and 20 frogs (simulation results). These curves represent cross-sections through Fig. 1, parallel to the π axis, at group sizes of five and 20. The highest point on each curve occurs at the best value of π for that group size. (b) Non-overlapped calls per group per min as a function of group size, for two arbitrary calling parameters $\pi = 0.20$ and 0.05 . These curves represent cross-sections through Fig. 1, parallel to the group size axis, at π values of 0.20 and 0.05 .

There are several ways to determine an optimum group size and calling parameter from the simulation data. One method is to choose the combination of parameters that yields the highest overall number of non-overlapping calls per group per unit time. This corresponds to the highest point in Fig. 1, which occurs at a group size of five frogs, with a value of π between 0.25 and 0.7 . Instead of emphasizing overall group performance, one might instead look at the number of non-overlapped calls per frog. In this case, the interpretation of group size is that number of frogs (including himself) with which a particular male will actively avoid call overlap. The 'best' performance with respect to this criterion occurs when the group size is one (that is,

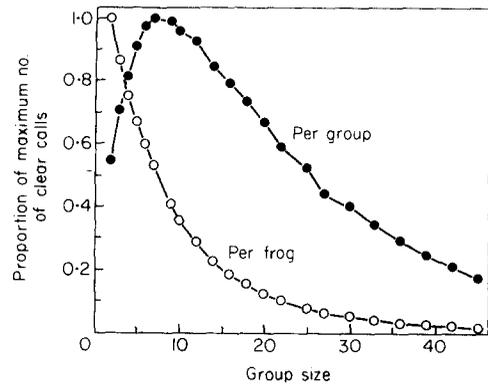


Figure 3. Relative proportions of total non-overlapped calls per group and non-overlapped calls per frog, as functions of group size, for an arbitrary value of π (0.05). The intersection point is at a group size of four frogs. This represents the optimum group size for this value of π based on optimizing both the fraction of the maximum possible number of non-overlapped calls per group and the fraction of the maximum possible number of non-overlapped calls per frog.

when individuals make no attempt to avoid overlap with their neighbours), and $\pi = 1.0$. In such a situation, every call is non-overlapped. Both individual and group interests can be taken into consideration as follows: for each value of the calling parameter, the proportion of non-overlapped calls per frog (relative to the maximum number of such calls at that value of π) is plotted as a function of group size on the same graph as the relative proportion of non-overlapping calls per group. These two curves intersect at a group size that maximizes non-overlapping calls, both per frog and per group (Fig. 3). A plot of this 'dual optimum' group size as a function of calling parameter, π , shows that, for values of π greater than ca. 0.05 , the group size for which the proportion of possible clear calls per group equals the proportion of possible clear calls per frog is three frogs (Fig. 4).

Comparisons of actual calling patterns of individuals within groups with those of frogs in simulated groups revealed which frogs were calling non-randomly with respect to one another. Active avoidance of call overlap was defined as having occurred when the degree of overlap between two males was significantly less ($Z \leq -1.65$, $P \leq 0.05$) than that observed between the corresponding simulated pair over 100 trials. In the two four-male groups and the two five-male groups tested

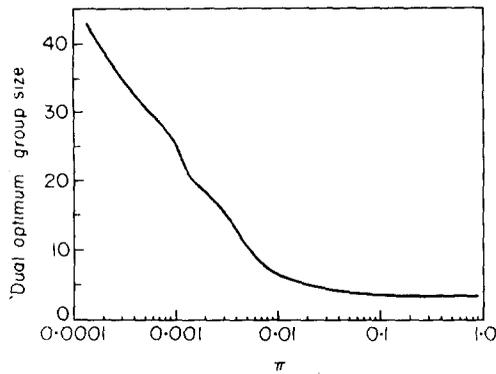


Figure 4. Optimum group size (see text) as a function of π .

($N=18$), 14 of 18 males were actively avoiding overlap with up to two of their neighbours, while one male was actively avoiding overlap with three of his neighbours. Three males had significantly more overlap with one of their neighbours than expected based on random call placement ($Z \geq 4.45$, $P \leq 0.01$), and were thus jamming the calls of that neighbour. The actual proportions of overlapped calls for one group of four males ranged from 0.0 to 0.08, while the degree of overlap in the simulations of that group ranged from 0.10 to 0.16, with standard deviations between 0.05 and 0.07.

Correlograms were made for two groups of four

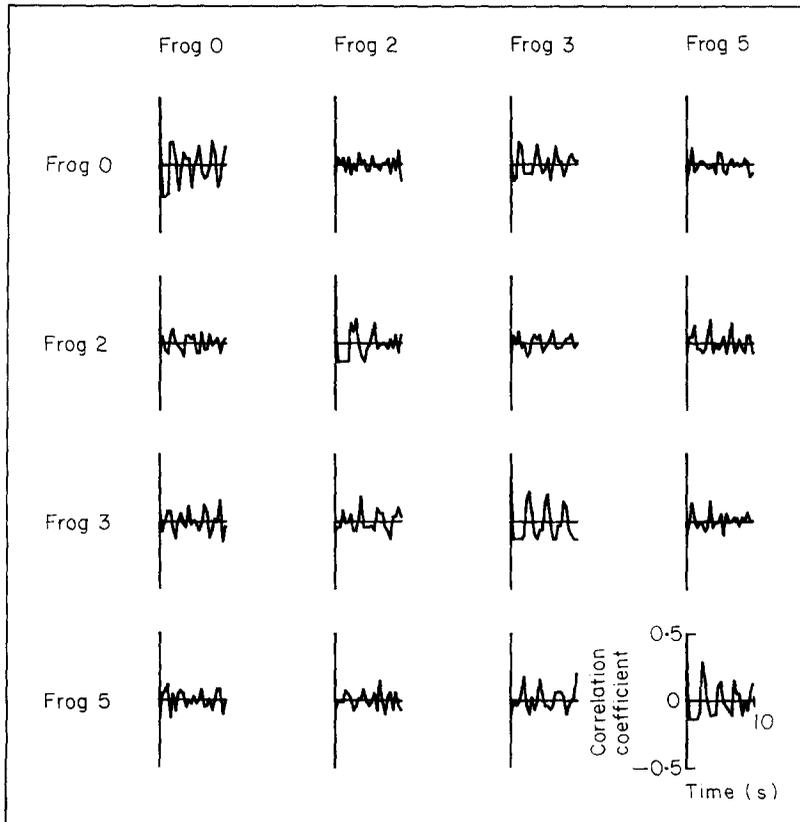


Figure 5. Correlograms for a representative assemblage of four frogs (numbers 0, 2, 3 and 5). Each of the 16 combinations is plotted: the ordinate ranges from -0.5 to $+0.5$, while the abscissa runs from 0 to $+10$ s. The $+1.0$ peaks of the functions for $i=j$ at $t=0$ were omitted to conserve space. The plot in the j th column and the i th row characterizes the calling behaviour of frog j following frog i . The height of the curve at time t is the probability of observing the onset of a call by frog j at a time t seconds after the onset of a call of frog i .

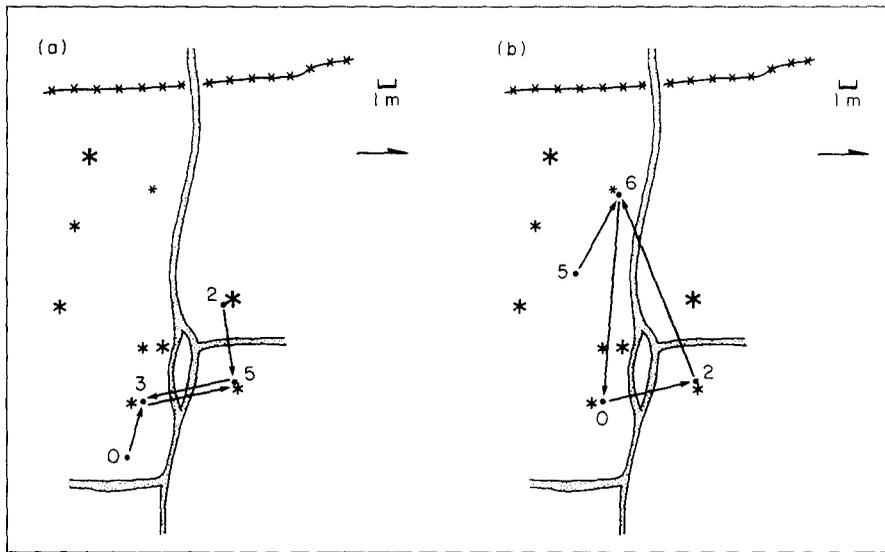


Figure 6. The study site in El Verde, Puerto Rico with the locations of the frogs (closed circles and associated numbers) used on 6 September (a) and 9 September (b). Symbols represent trees, the shaded lines represent trails and the crossed line represents a wire fence. An arrow from frog i to frog j indicates that frog j was the primary follower of frog i . These relationships were deduced from correlograms similar to those presented in Fig. 5.

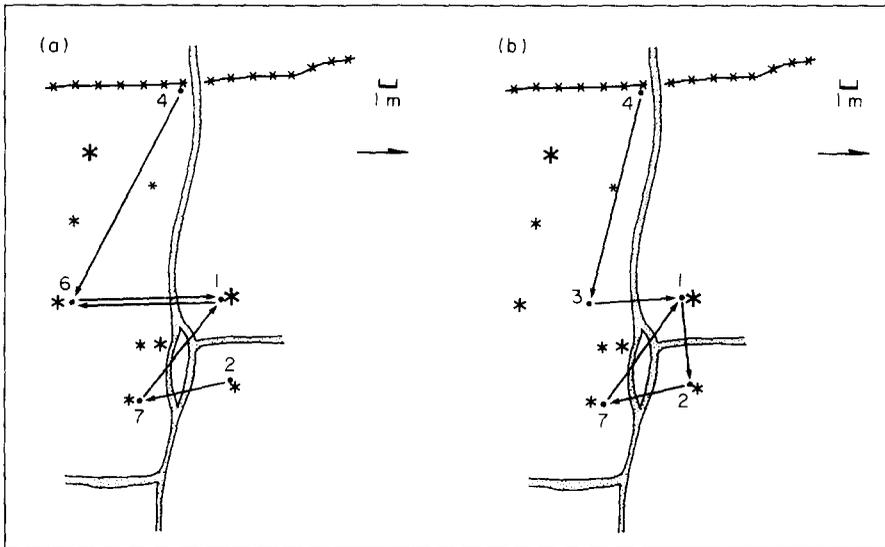


Figure 7. The study site with the locations of the frogs studied on 29 August (a) and 30 August (b). See Fig. 6 for details.

frogs and two groups of five frogs. Correlograms from one group of four frogs recorded on 6 September are shown in Fig. 5. Chorus diagrams constructed from the correlograms revealed that any one frog was the primary follower of either zero, one or two frogs, but not more than two frogs (see Figs 6 and 7).

DISCUSSION

Several advantages to clumping, either in space or in time, of signals by male organisms have been proposed. The most commonly invoked explanation for male clustering has been increased mate attraction through increased signalling (Littlejohn

1960; Hamilton 1971; Pierce & Ralin 1972; Cade 1981; Lloyd 1983). That is, males in clusters are presumed to be capable of emitting more signals per unit time, or (through synchronization) emitting more intense signals, thus attracting more females. However, Alexander (1975) and Bradbury (1981) proposed an alternative reason for male clustering: simply, that females prefer males in clusters so that they (females) can choose between several potential mates on a relative basis.

Regardless of the underlying reasons for male clustering, increased population densities may lead to an increase in the proportion of a given male's calls that are temporally overlapped by calls of his near (loud) neighbours. This can disrupt species-specific temporal features of calls (Schwartz 1987), which, in turn, could impair the ability of nearby females to discern whatever aspects of the call are important for mate choice (Gerhardt 1978). If a male were to attempt to avoid calling when any other male was audible to him, he would probably cease calling completely, due to the large numbers of nearby calling frogs (Stewart & Pough 1983; Narins & Smith 1986). Therefore, a given male should only actively avoid acoustic overlap with a small number of his neighbours. When a given male is actively avoiding call overlap with only one or two of his nearest (or loudest) neighbours, he will be ensuring that most of his calls which are overlapped will be overlapped by fainter calls of more distant males. Thus, any nearby females may be better able to discern the important features of his calls. The idea of a limited cluster size is supported by the results from our simulations, namely that the best group size over a wide range of π is three males. This is also supported by the observations of chorus structures: in the two four-male groups and the two five-male groups tested ($N=18$), no males actively spaced their calls relative to more than two neighbours. In the case of *E. coqui*, optimum group size will be limited by the typical call repetition rate (one call every 2–3 s), and call duration (ca. 0.5 s). In theory, if the frogs were able to schedule their calls perfectly, a group size of five or six should be obtainable while maintaining total acoustic avoidance. Since perfect scheduling is rarely achievable even in deterministic systems we may well expect the limiting group size to be less than optimum, namely on the order of three or four frogs, as suggested by both simulations and field data.

It has been suggested that the rhythmic calling

behaviour of anurans is based on a neural oscillator (Loftus-Hills 1973, 1974; Zelick & Narins 1985), such as that presented by Segundo & Kohn (1981). Similar oscillators have been proposed as the driving force in other organisms which modify their signalling rate in response to their environment, such as crickets (Jones 1966a), fireflies (Buck & Buck 1978; Lloyd 1983) and electric fish (Bullock et al. 1972; Heiligenberg et al. 1978). Since call repetition rate is one of the least stereotyped of *E. coqui*'s call parameters (Narins & Capranica 1977), some mechanism must be acting to modify the output if any inherently periodic oscillator exists in the vocal system of this animal. Several workers (Schmidt 1964; Foster 1967; Loftus-Hills 1974; Rosen & Lemon 1974; Lemon & Struger 1980) have suggested that call timing is lengthened or shortened from the natural period of the oscillator depending upon when an acoustic stimulus is detected. Stimuli occurring too soon after the end of a call (in the inhibitory phase) are postulated to increase the delay until the next call onset, while those occurring later (in the excitatory phase) decrease the delay by stimulating a call. These ideas are supported by observation of entrainment to external stimuli over a wide range of stimuli rates in several species (Lemon 1971; Loftus-Hills 1974; Lemon & Struger 1980; Zelick & Narins 1985). All of these studies and the existence of some non-random call placement patterns and distinctly organized chorus structures reported here indicate that *E. coqui* males are indeed modifying their behaviour based upon that of their neighbours, which supports the assertions of Awbrey (1978), Wells & Schwartz (1984) and Schwartz (1987), that calling male frogs actively interact with their acoustic environment.

Many workers have suggested that the function of this behaviour (change in call period, entrainment, etc.) is for a calling frog to minimize acoustic overlap with his neighbours (Littlejohn & Martin 1969; Whitney & Krebs 1975b; Narins & Capranica 1978; Narins 1982a; Zelick & Narins 1982) and increase reproductive success (Hardy 1959; Brattstrom 1962; Whitney & Krebs 1975a; Awbrey 1978; Fellers 1979). Others propose that, since some predators locate frogs via their calls (Jaeger 1976; Tuttle & Ryan 1981), calling frogs can to some degree avoid predation, either by calling more or less in synchrony (Tuttle & Ryan 1982) or by cessation of calling behaviour upon detection of a predator (Tuttle et al. 1982). Indeed, Rand & Ryan

(1981) suggest that the calling behaviour of frogs is a trade-off between maximizing mate attraction and minimizing predation risk. In light of the data presented here, some of the ideas regarding male aggregations, and the fact that calling is one of the most energy-intensive behaviours of which a male anuran is capable (Bucher et al. 1982; Taigen & Wells 1985), we suggest that an important function of call pattern modification behaviour is to allow a calling individual to maximize the communicative effectiveness of his calls.

We have used a simple model of a natural system to generate testable predictions about the acoustic behaviour of individuals in groups. To enhance the accuracy of our model, we could incorporate several additional features, such as allowing each frog to have a different calling parameter, introducing variability of call lengths, using a two-note call instead of one note, etc. However, the results of the natural experiments were compatible with both the predictions of even the simple model and the current literature regarding the behaviour of these organisms, demonstrating the power and usefulness of models in gaining an understanding of the dynamics of group behaviour.

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