Social Interaction Among Chorusing Pacific Tree Frogs, *Hyla regilla*

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A shift of call timing by *Hyla regilla* males in response to playback of recorded calls with various fixed repetition rates supports the hypothesis that alternate calling by chorusing males is true social interaction and not an artifact of body temperature. The observed patterns of phase shifting, inhibition of simultaneous calling and spatial distribution of individuals within the chorus support the hypothesis that social interaction serves to minimize call interference among neighboring males. This appears to be a strategy to maximize each male's chances of attracting a mate.

IN addition to serving as species isolating mechanisms of varying effectiveness (Bogert, 1960; Blair and Littlejohn, 1960; Awbrey, 1968), anuran vocalizations also function in social interaction among males of many species (Wells, in press). Silent frogs can be stimulated to begin calling by playback of recorded calls or even crude imitations of calls. Jones and Brattstrom (1961) concluded that calling in *Hyla crucifer* was facilitated by auditory interaction among males. Anderson (1954) showed that *Gastrophryne carolinensis* males call sequentially in small groups. Foster (1967) reported apparent vocal interaction by groups of two or three *Hyla regilla* males, but did not quantify these relations. These observations are consistent with the hypothesis that in some frog species, chorusing also represents true social interaction among males. Alternatively, this apparent social interaction could be an artifact of body temperature. For example, in calls of 57 individuals recorded during 1972 and 1973, water temperature and call period in *H. regilla* are highly correlated (period = 2.90–0.11 Temp., $r = .90$, $P < .001$). If one frog's calls stimulate his neighbor to begin calling, apparent call alternation would result if both frogs had similar call rates because of similar body temperature. Such behavior would not be true social interaction. The hypothesis of true interaction would be supported only if a frog changed his freerunning call rate (Loftus-Hills, 1974) to match that of another frog with a different call rate.

Change of call repetition rates in response to recorded or synthetic calls has been reported in *Eleutherodactylus martinicensis* (Lemon, 1971) and *Pholidoptera griseoaptera* (Jones, 1966a, b). Wells (in press) has reviewed call alternation and synchrony and concluded that it is most likely to occur in species with prolonged breeding seasons and with regularly spaced, repetitive calls, such as *H. regilla*. All such instances should be carefully analyzed to determine whether call alternation is real or apparent.

Two types of social interaction are possible. Calls might be separated temporally to minimize acoustic interference among neighboring males and thereby maximize an individual male's chances of attracting a female (Littlejohn and Martin, 1969; Rosen and Lemon, 1974). Alternatively, by calling in bouts, dominant males might interefere with other males and reduce their chances of attracting females (Whitney and Krebs, 1975b). Either strategy would require deliberate timing by the frogs. The temporal separation and interference hypotheses can be tested by determining whether frogs shift phase to overlap or to avoid overlapping one another's calls and whether the calls of one male inhibit simultaneous calling by other males.

METHODS

The population studied is located around a small reservoir on King Creek approximately 6 km north of Descanso, San Diego County, California. Elevation is 850 m.

All experiments were conducted in the field with unrestrained, naturally calling male *H. regilla*. In each experiment, a frog was presented sequentially with a series of tape loops, each with a period of 0.5, 1.0, 1.25, 1.5, 2.0 or 2.5 s (period is the reciprocal of the call repetition rate). All tape loops were of the same call and differed only in period. Background noise was removed as follows. A call with no detectable simultaneous calls was selected and multiple copies made of it. The tape segments containing the call were cut out and spliced onto the length of blank tape needed for each period at 19 cm/s tape speed. The 0.5 s tape loop contained two call replicates. Splice noise was measured with an oscilloscope and was at

TABLE 1. PHYSICAL CHARACTERISTICS OF DIPHASIC *Hyla regilla* CALL USED IN PLAYBACK EXPERIMENTS. Dominant frequency is mean over all pulses with range shown in parentheses. Call repetition period of original sequence measured with stopwatch over ten calls.

Call parameters	Phase 1	Phase 2
Pulse rate (Hz)	50	49
Number of pulses	8	4
Dominant frequency (Hz)	2450 (2375–2525)	2550 (2525–2590)
Duration (s)	.145	.065
Interphase interval (s)	.07	
Repetition period (s)	1.52	

least 40dB below signal level. The call used was recorded at the study site on 9 March 1972. Body temperature of the frog was 9.8 C. Characteristics, as determined with a dual beam storage oscilloscope and frequency counter, are listed in Table 1.

Hyla regilla has several different calls with apparently different social functions (Snyder and Jameson, 1965; Allan, 1973) but only the biphasic mating call was used for these experiments.

A Uher 4000L tape recorder was used to play back the tape loops through a 12.5 cm diameter weatherproof high fidelity loudspeaker mounted in an 18 cm × 18 cm × 9 cm plywood enclosure. Sound level measured with a General Radio 1551-C sound level meter was approximately 85dB (C-weighted) at 0.5 m. This level was empirically determined to be adequate for good responses by the subjects. As a tape loop was played back, it was also re-recorded onto one channel of a Uher 4400 stereo tape recorder via a connecting cable. Simultaneously, the subject's calls were picked up by a microphone and recorded on the second stereo channel. By switching the loudspeaker on and off while continuing to record both the tape loop calls and the frog's calls, a record of his call timing was obtained which could be compared with a standard both when the frog could and could not hear the standard. All neighboring frogs calling within 5 m of the test subject were temporarily removed during the experiments to minimize external effects on the subject's call responses. In each experiment, a tape loop was placed on the playback machine and a

sequence of about 20 of the frog's spontaneous calls was recorded. The speaker was then switched on and another sequence of calls recorded. A poststimulus sequence was recorded when possible, but the frogs usually stopped calling when the speaker was turned off. When the subject resumed spontaneous calling, another tape loop was presented in the same way until he had responded to all six tape loops.

A random sample of the recordings of three of the males tested was chosen for analysis after listening tests and oscilloscopic examination of the recordings revealed a highly consistent response pattern among males. Limited sample size was necessitated by the fact that the available computer did not have simultaneous multichannel analog to digital conversion capability, so thousands of data points had to be hand-digitized. The small sample size still allows a valid test of the hypotheses because all tapes show the same general response pattern and because the test requires only that phase shift and/or call inhibition occur as predicted.

For analysis, both data channels and a 0.1 s timing pulse were displayed on a multichannel oscilloscope and photographed with an oscillograph camera at 1 cm/s. Data were digitized by using the timing marks as sampling points. For each data channel, a value of one was recorded if any portion of a call coincided with a timing mark, otherwise the value was zero. The resulting two series of ones and zeros were then transferred to computer data cards and subjected to autocorrelation and crosscorrelation analysis (Bendat and Piersol, 1971).

The autocorrelation function (Bendat and Piersol, 1971) is estimated by the following equation:

$$R_x(\tau) = 1/T \int_0^T x(t + \tau)\, dt \qquad (1)$$

It is a measure of the general dependence of data values $x(t)$ at time t on data values at time $t + \tau$, where τ is a time displacement or lag that may be varied from zero to the entire sampling time T. In practice, lag time was varied between zero and a maximum which was greater than the call period, yielding a plot of the autocorrelation function $v.$ time. In the plot, or correlogram, the values of R_x are correlation coefficients ranging between ±1. Periodicity in a signal shows up as peaks at intervals equal to the period, with height determined by the signal's degree of regularity.

Crosscorrelation is a similar measure of time relationship between two signals $x(t)$ and $y(t)$ and is estimated by:
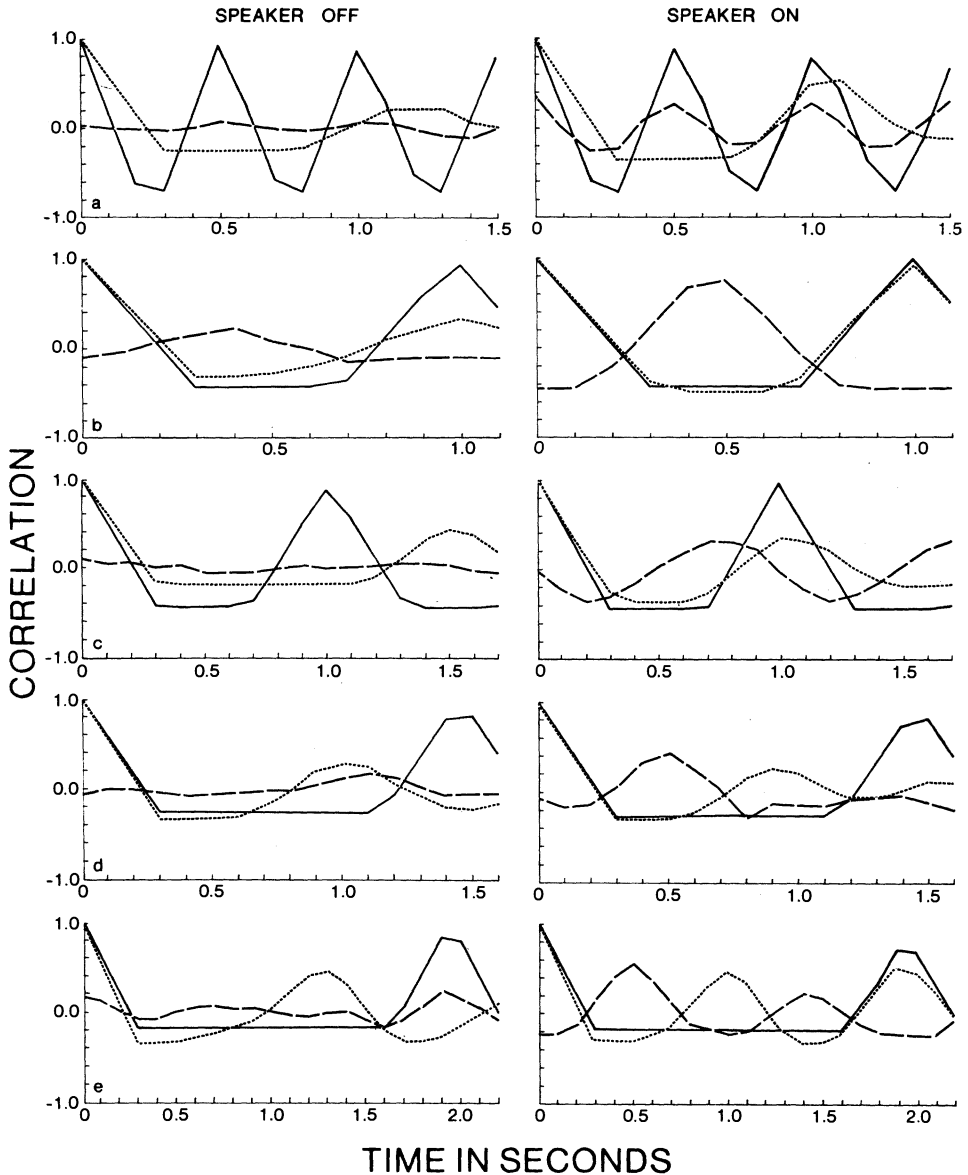
Fig. 1. Correlograms from playback experiments showing effects of hearing playback of recorded calls with various periods on call periods of unrestrained males. In the left-hand graphs, male could not hear the recorded call and was calling spontaneously. Graphs on the right side show what happened to call timing when loudspeaker was switched on. Solid line is tape loop autocorrelogram, dotted line is frog autocorrelogram, and dashed line is crosscorrelogram. a) 0.5 s tape loop period. b) 1.0 s tape loop period. c) Replicate 1.0 s tape loop period. d) 1.5 s tape loop period. e) 2.0 s tape loop period.

$$R_{xy}(\tau) = 1/T \int_0^T x(t)y(t + \tau)\, dt \qquad (2)$$

Boundaries of calling area and locations of the 23 calling frogs within that area were determined by using a surveyor's transit and steel tape to measure angle and distance to each point from a base point. A computer program was then used to convert the resulting polar coordinates to rectangular coordinates, plot a map, calculate distances from each frog to its neighbors and test the distribution pattern for randomness.

RESULTS

Responses of males to taped conspecific calls.— Responses of three different males to calls with varied periods are shown in a series of correlograms (Fig. 1). The autocorrelation functions show periodicity of tape loop and individual calls, each with reference only to itself. A perfectly regular call has an autocorrelation of 1.0 at its period. Variability reduces the correlation and broadens the peak. Any time relationship between the frog's call period and the recorded call is indicated by the crosscorrelation function. In Fig. 1a, the tape loop had a period of 0.5 s. When the frog could not hear the recorded call, his free-running call period was about 1.2 s but variable (actual range for ten calls was 1.0 to 2.1 s). His maximum autocorrelation was 0.27, $P > 0.05$. When the loudspeaker was switched on, the frog's call period changed to between 1.0 and 1.1 s and became highly regular (maximum autocorrelation = 0.54, $P < .02$). He called once for every two taped calls and 14 to 18 calls were at exactly the same time as a taped call.

Figure 1b shows first a sequence of 17 frog calls while the loudspeaker was off. Both signals had a period of 1 s but the frog's call period was irregular (range = 0.7–2.6 s) and crosscorrelation was low. Six (35.3%) of the frog's calls overlapped taped calls. When the speaker was switched on, the frog shifted phase to call almost exactly 0.5 s after the start of each taped call. In the sequence of 25 calls analyzed, periods ranged only from 0.9 to 1.2 s and 22 (84.6%) had a period of 1.0 s. There were no overlaps.

Another frog, with a free-running call period of 1.5 s (Fig. 1c), changed his period to match that of the tape loop when the 1.0 s tape loop was switched on, calling 0.7 s (range = 0.5–0.9) after the taped call. If two consecutive taped calls coincided with his own, the usual response of the frog was to skip his next expected call, then call 0.5 to 0.6 s after the next taped call.

In Fig. 1d, the taped call period was 1.5 s while the frog had a free-running call period of 1.0 s. When the loudspeaker was switched on, he at first matched call rates with the tape loop, calling 0.5 s after each taped call as shown by the major crosscorrelogram peak, then tried to revert to the 1 s period. This resulted in his call being "interrupted" by the taped call, so he phase shifted by skipping his next call and waiting until 0.5 s after the next taped call before calling again. This was followed immediately by a series of short period (0.8–1.0 s) monophasic calls which were not well correlated with the tape loop. This timing pattern shows as two low peaks in the frog's autocorrelogram at 0.9 and 1.5 s. A few calls either nearly or actually coincided with taped calls resulting in a minor crosscorrelogram peak at 1.3–1.4 s.

In Fig. 1e, the frog's free-running period was 1.3 s. When the taped call with a period of 1.9 s was presented, he shifted his period to 1.0 s and called twice for each taped call. Typically, he called 0.5 s after the beginning of the taped call and then called again 0.9 s later. The resulting crosscorrelogram peak at 1.4 s is lower than the 0.5 s peak because the second call was sometimes omitted.

A consistent feature of the call patterns of all frogs recorded in these experiments is the delay between the beginning of a playback call and the beginning of the frog's next call. In the two frogs with a free-running period of 1 s (Fig. 1), the delay tended to be about 0.5 s,
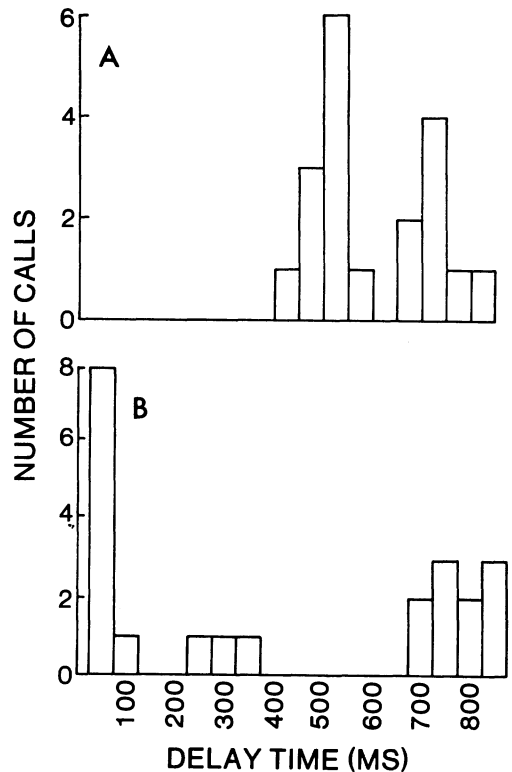

Fig. 2. Post-stimulus histograms showing time delay between playback call and frog's call. Tape loop period is 1.5 s. A) Sequence of 19 frog calls with loudspeaker on. B) Sequence of 22 calls by same frog with loudspeaker off.
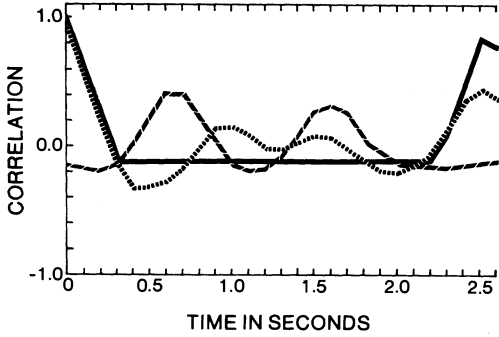
Fig. 3. Correlograms showing call inhibition. Loudspeaker was on, tape loop period was 2.5 s. Symbols as in Fig. 1. Note absence of third cross-correlogram peak at 2.6 s.

which would allow two males to alternate calls with little chance of overlap. The consistency of this 0.5 s latency period is evident in the correlograms. This is also shown in post-stimulus histograms which contrast times from beginning of a taped call and the frog's next call when he could (Fig. 2A) and when he could not (Fig. 2B) hear the 1 s tape loop. Delays of less than 0.4 s are uncommon and occur most often when the taped call has a period which is not a simple multiple of a male's free-running period. The frog's response in such situations often is to begin either monophasic or slow trill calling at rates independent of that of the tape loop.

Call inhibition.—Figure 3 illustrates a typical case of call inhibition. In the sequence recorded before the loudspeaker was switched on, this frog had been calling with a free-running period of 1.8 s and was not synchronized with the tape loop, which had a 2.5 s period. When the loudspeaker was switched on, the frog decreased his period to about 0.9 s, which would result in almost three of his calls to one taped call, but his third call would overlap the next taped call. As shown by the crosscorrelation curve, his pattern was to call 0.7 s after a taped call, wait 0.9 s and call again, and then wait about 1.6 s to call again. This third call thus came 0.7 s after the next taped call instead of during it as would be expected if 0.9 s timing were followed. Inhibition of overlapping calls is shown by the lack of a crosscorrelogram peak at 2.5 s. Only 1 out of 30 (3.33%) of his calls overlapped the taped call and in this instance he began calling 0.1 s before the taped call and did not call again for 2.2 s. His major autocorrelogram peak at 2.5 s indicates that he was
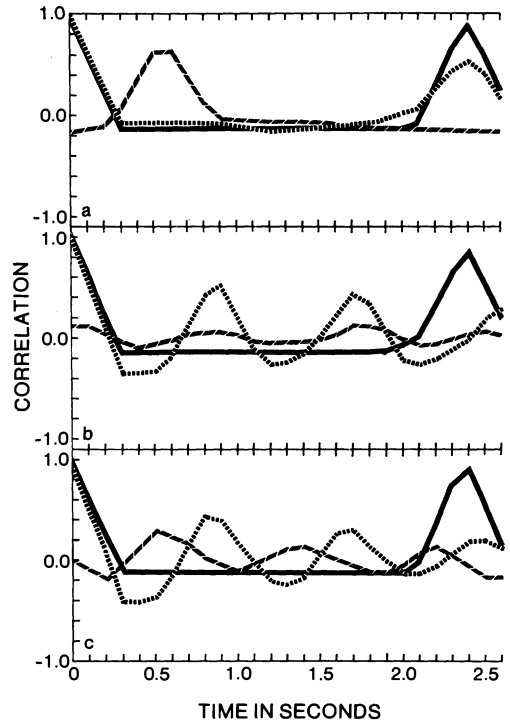

Fig. 4. Correlograms showing range of call periods in a single male. Tape loop period was 2.4 s. a) Loudspeaker on. b) Loudspeaker off. c) Loudspeaker on. Symbols as in Fig. 1.

in phase with the 2.5 s taped call period. Inhibition is also seen in Fig. 1d.

Range of responses.—Figure 4 illustrates the maximum range of periods observed for calls of a *H. regilla* male. While the male was quiet, a tape loop with a period of 2.4 s was switched on. As can be seen in Fig. 4a, he began calling in alternation with the tape, answering each taped call 0.5 to 0.6 s later. In sequence of 15 calls, only 1 (a slow trill) was out of phase. When the loudspeaker was switched off, the frog stopped calling for about one minute, then resumed with a free-running period of 0.9 s (Fig. 4b). Phase match between the frog's calls and the tape loop which he could not hear was poor, with several overlapping calls. The speaker was then turned on (Fig. 4c) and the frog shifted his call period to 0.8 s, calling three times for each taped call. His third call was frequently interrupted by the taped call. Instead of skipping a call to reestablish alternation, he began monophasic calling. The last 10 of the 36 calls in this sequence were monophasic. During a subsequent non-calling period

in which he could not hear the tape loop, he resumed calling with a 1.2 s period. When the speaker was switched on again, he changed his phase but not his period and called 0.6 s after the tape and again 1.2 s later. Calls which would have occurred less than 0.6 s after the beginning of a taped call were usually skipped, again showing inhibition. The resulting second autocorrelation peak was .18 compared to .28 for the same peak when the frog had the same timing but could not hear the tape and, consequently, did not skip simultaneous calls.

Spacing of males.—The males in this pond are not randomly distributed. None were closer than 0.73 m to their nearest neighbor and 16 of 23 were members of reciprocal nearest neighbor pairs. Compared with the distribution of distances between 23 random points located by computer within the same boundaries, there are more frogs at distances between 1 m and 5 m from their neighbors than expected ($\chi^2 = 3.40$, $P = .01$). Although mean distances to both nearest and next nearest neighbors are different (1.41 m and 2.03 m, $t = 2.17$, $P = 0.4$), the corresponding ranges are nearly identical (0.73 m–4.35 m and 0.77 m–4.78 m).

In observations of hundreds of calling pairs of nearest neighbors in several different localities I have found that a distance of less than 20 cm between calling males virtually always results in at least one of the pair switching to slow-trill calling. If the second male does not stop calling and move away, a "fight" usually follows in which one male climbs atop the other but does not attempt to clasp him. The usual result is that the two frogs move apart more than 20 cm and resume normal mating calling. Occasionally they remain within 20 cm or less of each other but only one resumes calling and apparently ignores the other.

DISCUSSION

Although the high correlation between body temperature and call period in *H. regilla* males could account for call alternation among neighboring frogs in a chorus, time series analysis clearly refutes this hypothesis. The alternative hypothesis that call alternation among neighboring males is the result of active interaction is supported by the observation that individuals change call period in response to playback of recorded calls with different periods. If the recorded call has a period sufficiently different from his own free-running period, a frog may call at a multiple or fraction of the recorded call period. If a frog is unable to alternate precisely with a recorded call because it is too different from his free-running period, he will sometimes shift to either monophasic or slow-trill calling, both of which appear to function in aggression (Allan, 1973).

Time series analysis supports the hypothesis that *H. regilla* males attempt to avoid simultaneous calling. A male calling with the same period as the playback of a recorded call will shift phase to avoid call overlap. By mutually adjusting timing and phase, three frogs could call with a 1 s period and not overlap calls. Longer periods would allow more frogs to interact without acoustic interference. The timing of diphasic calls seems consistent with Loftus-Hills' (1974) acoustic pacemaker hypothesis, although these experiments do not test that hypothesis. Further support for the hypothesis of minimum interference is provided by the apparent suppression of calls which partially overlap those already started by a neighbor.

A third observation which supports the minimum interference hypothesis is maintenance of a minimum interindividual distance between chorus members. *H. regilla* males apparently compete strongly for mates (Whitney and Krebs, 1975a, b). For a given male to attract a mate successfully, he should be readily locatable in a place to which a female is likely to come. If the number of favorable calling areas at a breeding locality is limited, limiting density of males within an area would increase an occupant's chances of mating (Whitney and Krebs, 1975a). In *H. regilla*, density within an area is limited by aggression which is triggered when neighbors interfere with each other's calls and when a male attempts to call from a site too near another. This minimum interindividual distance might depend on the loudness of the calls a male hears at his calling position and so would be a function of distance and terrain. Temporal spacing would allow two or three neighbors to call without reducing each other's locatability and interindividual distances would serve to remove others to a distance at which their simultaneous calls would not prevent a female from locating a nearby male. There is no need for a male to attempt to interfere with other males and reduce their chances of attracting a mate (Whitney and Krebs, 1975b) because he would also be reducing his own locatability.

The observed pattern of physical and temporal spacing among calling *H. regilla* males appears to be a strategy in which each male

attempts to maximize his own chances of attracting a mate.

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