Precedence effects and the evolution of chorusing

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SUMMARY

The structured choruses produced by rhythmically signalling males in many species of acoustic animals have long-captured the imagination of evolutionary biologists. Though various hypotheses have been forwarded to explain the adaptive significance of such chorusing, none have withstood empirical scrutiny. We suggest instead that alternating and synchronous choruses represent collective epiphenomena resulting from individual males competing to jam each other's signals. These competitions originate in psycho-acoustic precedence effects wherein females only orient toward the first call of a sequence, thus selectively favouring males who produce leading calls. Given this perceptual bias, our modelling confirms that a reset-ting of signal rhythm by neighbours' signals, which generates either alternation or synchrony, is evolutionarily stable provided that resetting includes a relativity adjustment for the velocity of signal trans-mission and selective attention toward only a subset of signalling neighbours. Signalling strategies in chorusing insects and anurans are consistent with these predicted features.

1. INTRODUCTION

Most research on the sexual selection of song focuses on the potential information content of male advertise-ment calls and how females and males may use such information in choosing among available mates and assessing competitors, respectively (Andersson 1994). Thus, most investigations have examined signal char-acters such as rate, spectral structure, and energy, and inter-male variation in these characters. Only a few have examined the timing of a male's calls relative to those of his competitors and how such timing may influence female choice.

Recent findings that female preferences are influ-enced by call order suggest, however, that the relative timing of a male's calls may be as important to his mating success as the calls' properties themselves. Sev-eral studies of insects and anurans have identified 'precedence effects' (*sensu* Wallach *et al.* 1949; Zurek 1980; Wyttenbach & Hoy 1993) wherein females orient preferentially toward the leading of two identical calls presented in close succession. Thus, call timing may be a critical factor in the sexual selection of song. In re-sponse to selection from female precedence effects, signalling males may employ specialized mechanisms that modify their relative call timing, such that they increase their chances of producing attractive leading calls. For example, females in the acoustic insect *Neoconocephalus spiza* (Orthoptera: Tettigoniidae) prefer-entially orient toward male advertisement calls that precede others by 10–80 ms. Male *N. spiza* reset their calling rhythms upon hearing a neighbour, thus decreasing their production of non-attractive following calls. But a synchronous chorus results when *N. spiza* males, all using this resetting mechanism, call at comparable rates (Greenfield & Roizen 1993).

Can female preference for leading signals be ulti-mately responsible for the striking patterns of synchronous and alternating signalling observed among acoustic insects and anurans? To answer this question, we develop a general model of rhythmic sig-nalling in which calling is controlled by a central nervous system oscillator that may be inhibited and re-set by an acoustic stimulus such as a neighbour's call. We then run Monte-Carlo simulations of neighbouring signallers to determine whether male resetting mechan-isms can be maintained by female precedence effects and generate the structured choruses observed in natur-al populations. We report that when female orientation and choice are influenced by precedence effects, the ba-sic resetting modification in male signal rhythm is evolutionarily stable if it includes a 'relativity adjust-ment' for the velocity of signal transmission and 'selective attention' toward a subset of signalling neigh-bours. Signalling strategies in chorusing insects and anurans appear to incorporate these predicted features, and signallers may generate either synchronous or al-ternating choruses by default. This explanation contrasts markedly with previous hypotheses (see Greenfield 1994*a,b*) that male signallers chorus to establish a group-level condition in which their attractiveness to females and avoidance of natural enemies is enhanced.

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2. MODELLING OF SIGNAL RHYTHMS AND INTERACTIONS

(a) Resettable oscillator

Our model assumes that the calls of an isolated male are regulated by a central nervous system oscillator with a mean free-running period $\bar{T}$ (figure 1). The oscillator rises from a basal to a peak level and then returns to the basal level over interval r. Calls are triggered when the oscillator attains the peak level, but call onsets do not occur until a brief interval t has passed following triggering. This interval represents an 'effector delay', the time required for transmission of the neural message to the motor apparatus producing the call and for activation of that motor apparatus. When a male hears a stimulus (e.g. a neighbour's call) that begins after delay d relative to the onset of his last call, the oscillator descends immediately to the basal level, remains inhibited until the stimulus is no longer heard, and then ascends to the peak level at approximately the normal rate—or faster if $d \approx (\ T - t)$. Thus, a stimulus during the oscillator's ascent lengthens the concurrent period ($T' > T$), but one heard during its descent shortens the next period ($T' < T$) while leaving the call already triggered by the oscillator unaffected. This simple 'inhibitory-resetting' modification (Greenfield & Roizen 1993) is a 'phase-delay' mechanism (Hanson 1978; Buck 1988): it affects one period only, and the free-running rhythm resumes immediately thereafter. Playback experiments on acoustic insects (Jones 1966; Shaw 1968; Walker 1969; Minckley *et al.* 1995) and anurans (Loftus-Hills 1974; Lemon & Struger 1980;

Zelick & Narins 1985; Moore *et al.* 1989), as well as fireflies (Buck *et al.* 1981*a*), indicate that rhythms and signal interactions in many species fit these basic assumptions and the inhibitory-resetting mechanism.

We transform the above description of inhibitory-resetting of a rhythmic process into a general linear model by determining a phase response curve (PRC) which regresses response phase, $[(\ T' - \bar{T})/\bar{T}] \times 360°$ against stimulus phase, $(d/\bar{T}) \times 360°$ (Walker 1969; Sismondo 1990). Given $r = t$ and equivalent call (x) and stimulus (y) lengths, the modified call period is

$$T' = (sd) + (\ \bar{T} + \epsilon) \tag{1}$$

where s is the PRC slope, a parameter reflecting the rapidity with which the oscillator rebounds from inhibition, and ϵ is a stochastic element in each call period; this designation for ϵ follows an experimental determination (Buck *et al.* 1981*b*) that variation in firefly flash rhythm originates in T rather than t. Relaxing the two restrictions above and accounting for the velocity (v) of signal (sound) transmission over the stimulus-focal individual distance (l) yield the more complete definition

$$T' = s \times [(d + l/v) - (r - t)] + (\ \bar{T} + \epsilon) + (y - x). \tag{2}$$

Because signallers may not hear during their own calls (Greenfield & Minckley 1993; Greenfield 1997), we correct equation (2) by subtracting $(y + d)$ from T' when the stimulus begins prior to the focal male's call and overlaps it (figure 1). When the stimulus begins after the focal male's call and overlaps its end, we
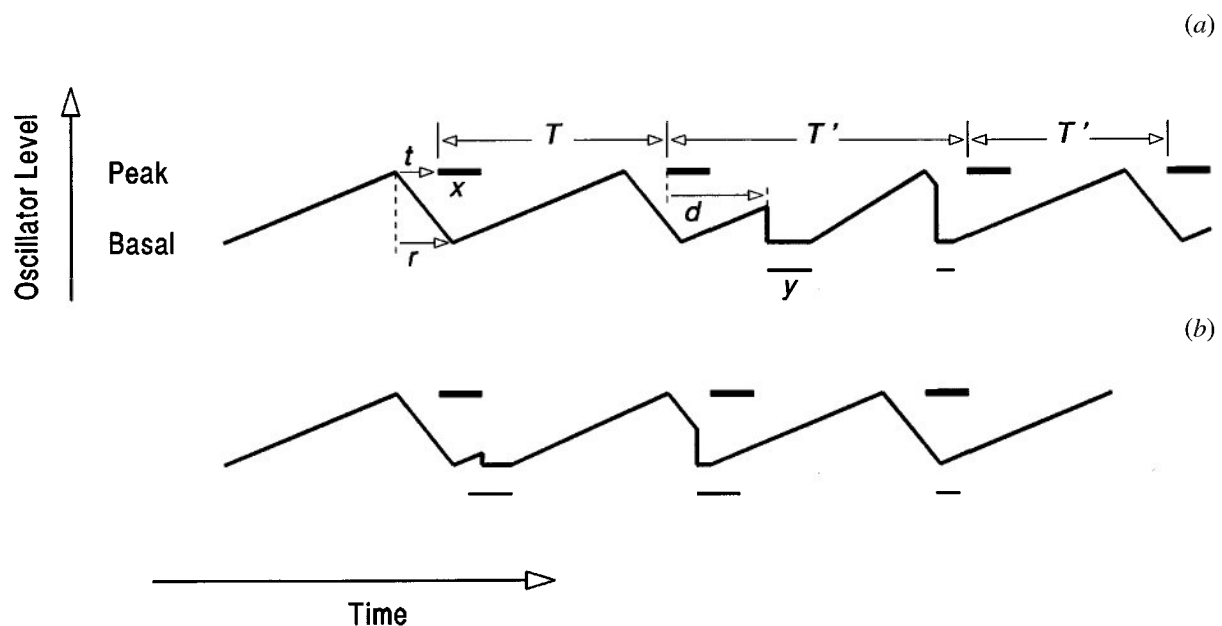
(a)

(b)

Figure 1. Central nervous system oscillator model depicting inhibitory-resetting, a phase-delay mechanism regulating interactive signalling in various acoustic insects and anurans. Thick (upper; length = x) and thin (lower; length = y) horizontal bars represent the focal male's calls and stimuli (or neighbour's calls), respectively. T is the free-running signal (and oscillator) period, t is the effector delay between triggering of a call and its onset, r is the oscillator return interval, d is the stimulus delay in absolute time, and T' is the modified period following perception of a stimulus. In these depictions the oscillator (sawtooth line) is reset to its basal level by an acoustic stimulus, remains inhibited at that level until the stimulus ends, and then ascends to its peak level more rapidly than when free-running. (*a*) Inhibitory-resetting by stimuli that do not overlap the focal male's calls. Positive ds yield T's $> T$, while negative ds yield T's $< T$. (*b*) Inhibitory-resetting by stimuli overlapping the focal male's calls. Because it is assumed that males do not hear stimuli during their own calls, the focal male is only reset and inhibited by that portion of a stimulus that does not overlap its own call.
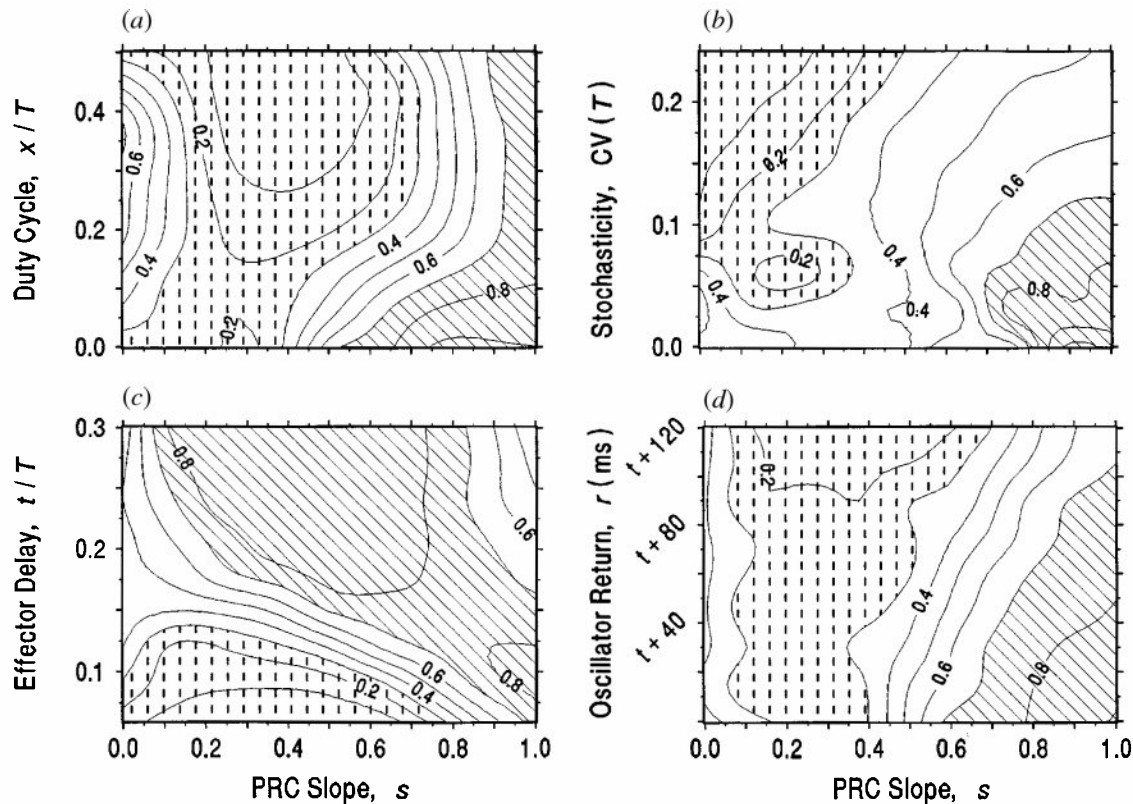
Figure 2. Conditions yielding synchrony versus alternation in pairwise simulations of two identical male inhibitory-resetters: see text for details of Monte-Carlo simulation. Contours indicate the synchrony index, the proportion of signals produced during all 100 runs of a given simulation that a female between the two males would register as leading (onset precedes that of the other males next signal by $\geqslant \gamma$, a minimum threshold separation, but by $\leqslant \beta$, a maximum threshold separation), following (onset occurs $\geqslant \gamma$ after onset of other's last signal but $\leqslant \beta$ after it), or tied (onset precedes (or follows) that of other's next (or last) signal by $< \gamma$). Signals not synchronized as such (singletons; onset begins $> \beta$ after onset of other's last signal and $> \beta$ before onset of other's next signal) recur in an alternating sequence with phase angles $\cong 180°$ separating successive males. The following default values, representative of various acoustic insects (table 1), including *N. spiza*, are used in all simulations: $\bar{T} = 500$ ms, t = 60 ms, x = 50 ms, (duty cycle = 0.1), r = 100 ms (t + 40), ϵ normally distributed with mean = 0 and standard deviation = 30 ms (coefficient of variation of $T = 0.06$), $\beta = x + 30$ ms, $\gamma = 5$ ms, l = 10 m, v = 343 ms^{-1}. PRC slope (s) is varied in 0.05 increments from 0.0 to 1.0 in the following four bivariate distributions exploring dependence of the synchrony index on pairwise combinations of parameters: (a) PRC slope and duty cycle (x/ $\bar{T}$ varies in 0.04 increments from 0.04 to 0.48). (b) PRC slope and stochasticity (coefficient of variation of T varies in 0.02 increments from 0.0 to 0.24). (c) PRC slope and effector delay (t/ $\bar{T}$ varies in 0.02 increments from 0.06 to 0.30). (d) PRC slope and oscillator return interval (r varies in 10 ms increments from t to t + 120 ms). Ruled and stippled areas indicate regions where the synchrony index is high (> 0.7) and low (< 0.3), respectively. Synchrony and alternation are largely dependent on high and low PRC slopes, respectively, although long effector delays combined with low PRC slopes yield increased synchrony. Similarly, high stochasticity or short effector delays combined with high PRC slopes yield increased alternation.

replace *d* by *x* in the first term of equation (2) and then subtract $(x - d)$ from T'. A stimulus that is overlapped entirely by the focal male's call is simply not perceived.

(b) *Monte-Carlo simulations*

To model pairwise interactions among male signallers, we simulate rhythmic calls of two identical individuals, allowing both to initiate and maintain calling in accordance with the rules of inhibitory-resetting. The pair has fixed locations on a plane, identical $\bar{T}$, *t*, *s*, *r*, and *x* values, and identical means and variances of ϵ. A random number generator, RAN3 (Press *et al.* 1989), sets the times for the initial calls of each male. Subsequent calls of each are timed according to equation (2); in every period, the random number generator selects the value of ϵ from among its distribution. The simulation, programmed in VISUAL BASIC, is continued until the pair

produce a total of 100 calls (one run); for a given combination of the six defining parameters above, this process is repeated until 100 runs are completed. Absolute times of call onsets and endings are corrected to times when these events would arrive at a representative female between the two males. From these corrected times, we compute the proportion of calls produced during all 100 runs of a given simulation that the female would perceive as synchronized (onsets of both males' signals occur in close succession; figure 2) or alternated (call periods of the two males are separated by phase angles $\cong 180°$).

We found that our simulated pairs alternated most of their calls when the PRC slope was low ($s \lesssim 0.5$) but synchronized an increasing proportion of calls as *s* approached 1.0 (figure 2). When the oscillator can quickly rebound from inhibition experienced at a high stimulus phase ($s < [(\bar{T} - 2t)/(\bar{T} - t)]$), each male may call soon after hearing and becoming inhibited by
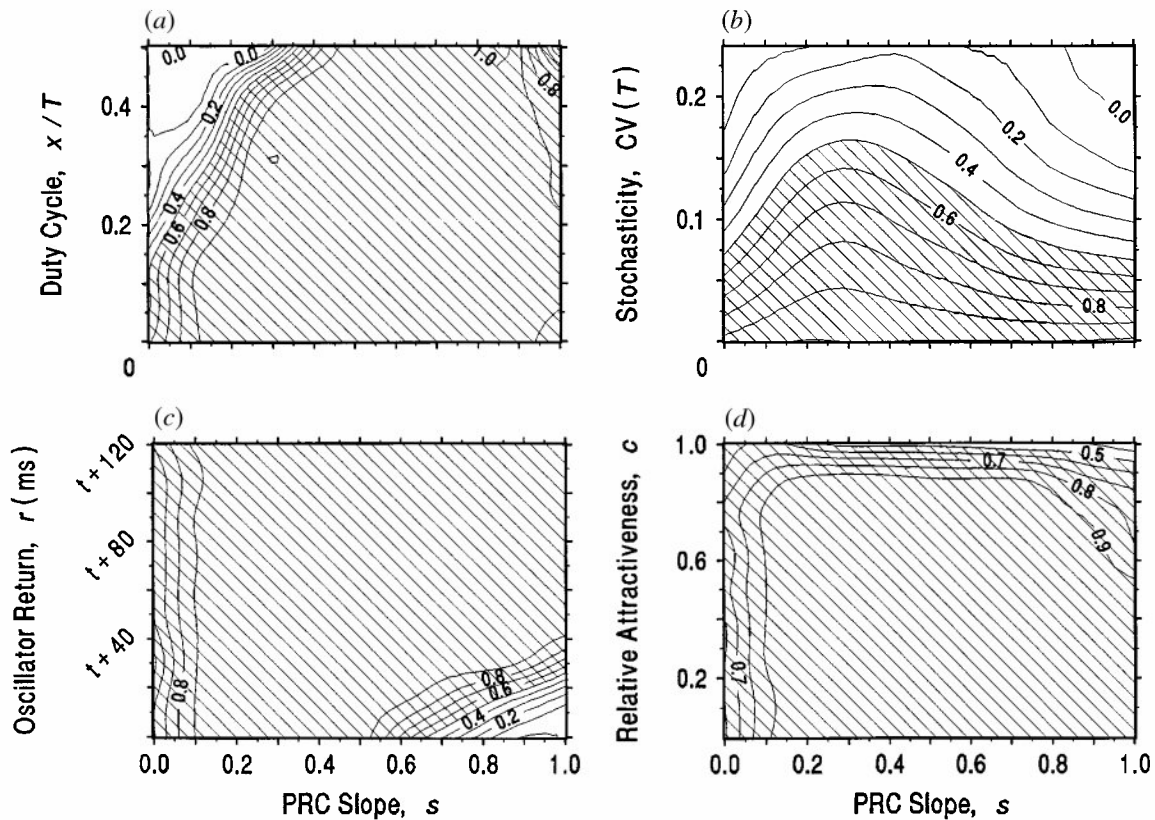
Figure 3. Conditions in pairwise simulations wherein an inhibitory-resetter (I) is more attractive to a centrally located female than is a signaller (R) who ignores his male neighbour. Leading and following signals are registered as $(l/l + c)$ and $c/(1 + c)$ 'points', respectively, where $0 \leqslant c \leqslant 1.0$; ties and singletons are registered as 0.5 and 1.0 points, respectively. Points accrued by each male are tallied separately during a simulation run; these totals are their attractiveness values. Contours indicate the proportion of the 100 runs of a given simulation in which I accrues a higher attractiveness value than R. $(a-c)$ The three bivariate distributions, simulations, and default values are the same as in figure 2a, b, and d except that one male signaller is an R (as for I, the random number generator sets the time for R's initial signal and the ϵ values in all its subsequent periods ($= \bar{T} + \epsilon$)) and the default value for c is 0.25. (d) PRC slope versus relative call attractiveness (c varies in 0.05 increments from 0.0 to 1.0); other parameters are set to default values as above. The ruled area indicates region where I is more attractive in > 50% of runs.

the other, and alternation results (except during events, occurring by chance $\propto t/\ T$, when both males begin at the same time and remain locked in phase (Sismondo 1990; Greenfield 1994*b*)). If rebound intervals always approximate the free-running period ($s \cong 1.0$), however, a male inhibited in this way may not call again until the other one's next call has been triggered, and runs of synchrony ensue. Neither call duty cycle $(x/\ \bar{T})$ nor oscillator return interval (r) influence the outcome strongly, but high stochasticity (ϵ) or a short effector delay (t) combined with a high PRC slope yields decreased synchrony, and a long effector delay combined with a low PRC slope yields increased synchrony.

3. EVOLUTION OF THE RESETTABLE OSCILLATOR
(a) Pairwise interactions

What selection pressures may have influenced the evolution of inhibitory-resetting mechanisms in acoustic species? Recent findings (Dyson & Passmore 1988; Greenfield & Roizen 1993; Greenfield 1994*a*; Minckley & Greenfield 1995) that female call preferences are

influenced by precedence effects would appear to offer a cogent explanation, because males who use an inhibitory-resetting mechanism should produce attractive, leading calls more often than males calling at equivalent rates who do not. We tested this expectation by simulating the calls of two males again, except that one (I) was an inhibitory-resetter and one (R) called without regard to its competitor's signals. Calls that the representative female, equidistant from the two simulated males, would hear were then registered separately for I and R. Calls were given weighted female attractiveness values, with following calls assigned a lower value than leading ones (figure 3). A male's attractiveness during a simulation run was then computed by totalling the attractiveness values of all his calls.

Is a male (I) who uses the inhibitory-resetting mechanism more attractive to females than a male (R) who calls regardless of his neighbour's signals? We found that male I was more attractive to females than R was over a wide range of PRC slopes, call duty cycles, and relative call attractiveness values (ratio of values of following:leading calls) providing that stochasticity was not high and the oscillator return interval (r) was
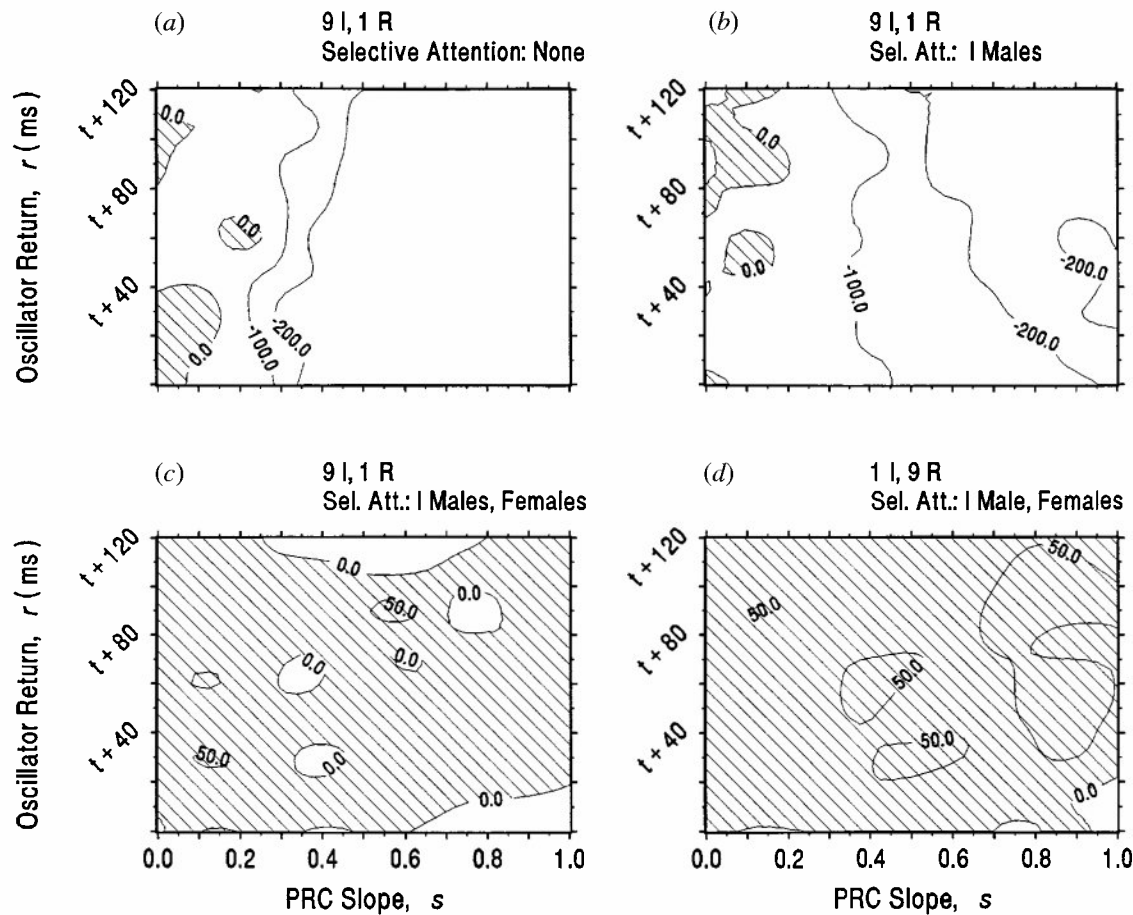
Figure 4. Conditions in simulations of ten males wherein an inhibitory-resetter (I) is more attractive to ten females than is a signaller (R) who ignores his male neighbours. Simulations of *n* male signallers are constructed according to the method for pairwise simulations (figures 2, 3). Signal timing of an I is influenced by signals of all perceived neighbours except those signals that, from I's perspective, follow another (figure 2); this stipulation assumes that a comparable precedence effect occurs in males and females. Males are randomly distributed on a 20 × 20 m plane; their locations are re-randomized at the start of all 100 runs of a given simulation. *f* females are also randomly distributed on the 20 × 20 m plane and re-randomized at the start of all runs. In each run of a given simulation, the points accorded each male by each female are computed (figure 3). Here, leading (or tied with leading) and following signals are registered as $1/([1 + (k - k^*) c] \times (k^*+1))$ and $c/[1 + (k - k^*) c]$ points, respectively, where k^* is the number of (perceived) males whose signals are tied with the leading signal, and k is the number of (perceived) males whose signals follow or are tied with the leading signal; singletons are registered as 1.0 points. For each male, the number of females that accord him an attractiveness value higher than that accorded all other males is determined: this is the number of females attracted by him in that run. Contours indicate the number of females attracted by an average (or single) I minus the number attracted by the single (or average) R, summed over the 100 runs of a given simulation. (*a*) Simulations of nine Is and a single R; Is and females hear all males. (*b*) Simulations as in (*a*) except that an I hears only the nearest male. (*c*) Simulations as in (*a*) except that an I hears only the nearest male and a female hears only the two nearest males. (*d*) Simulations of a single I and nine Rs; I hears only the nearest male and a female hears only the two nearest males. Increments in the bivariate distribution and default values are as in figure 3*c*. The ruled area indicates the region where, summed over 100 runs, an I attracts more females than an R.

long (figure 3). This latter requirement reflected the finite velocity of signal transmission from R to I and from I to the female. Were *r* brief (and PRC slope (*s*) high), inter-male distances as short as 1–2 m would allow I to produce many calls that are leading from its perspective but not as perceived by the female. A lengthy *r*,

$$r > [d_{\min}(1 - 1/s) + (l/v) + t] \tag{3}$$

however, automatically induces a relativity adjustment that advances each reset call by at least l/v and thereby allows I to produce attractive, leading calls.

(*b*) *n-male choruses*

Calling males are unlikely to interact with only one neighbour, and the pairwise interactions simulated above would seldom occur in nature. We therefore extended our model to simulate the calling of *n* males and evaluation of them by *f* females ($2 \leqslant n \leqslant 10; 1 \leqslant f \leqslant 10$). Females and I and R males were spaced randomly, or in various regular arrays, on a plane with specified dimensions. We re-examined the advantage of inhibitory-resetting by designating a single R and comparing the number of females attracted by it with the average number attracted by an I male. Thus, we determined whether R could successfully invade a population of I males.

Table 1. *Known phase response curves (PRCs) of rhythmically signalling acoustic insects and anurans*

(Slope (s), intercept (i), and correlation (cf) of least-squares regression are shown. $\bar{T}$: mean period; t: effector delay; x: signal length. Chorus type: A, alternation; S, synchrony. Precedence effect (prec.) in female orientation: Y, yes; ?, unknown.)

species (family^; subf.)	s	i^*	cf^+	$\bar{T}, t, x,$ (s)	chorus	prec.	reference
Insecta							
Ephippiger ephippiger (Tett.; Ephippigerinae)	0.46	$^* - 68°$	$^+ 0.52$	1.8, 0.15, 0.3	A	Y	unpublished data. W. A. Snedden & M. Ritchie
Ligurotettix coquilletti (Acrid.; Gomphocerinae)	0.39	$^* - 96°$	0.31	1.0, 0.1, 0.02	A	Y	unpublished data, M. D. Greenfield & Y. Jang
Ligurotettix planum (Acrid.; Gomphocerinae)	0.61	$^* - 98°$	$^+0.49$	10, 0.2, 0.4	A	Y	Minckley *et al.* (1995)
Mecopoda sp.	0.1	$0°$		2,	A	?	Sismondo (1990)
(Tett.; mecopodinae)	0.9	$0°$		2,	S		
Neoconocephalus spiza (Tett.; Conocephalinae)	0.96	$^* - 27°$	$^+0.85$	0.45, 0.06, 0.05	S	Y	Greenfield & Roizen (1993)
Oecanthus fultoni (Gryll.; Oecanthinae)	0.86	$^* - 18°$	$^+0.97$	0.46, 0.2, 0.1	S	?	Walker (1969)
Sphyrometopa femorata (Tett.; Agraeciinae)	0.7	$^* - 24°$	$^+0.59$	0.55, 0.13, 0.2	S	?	Greenfield (1994*a*)
Physalaemus pustulosus) (Leptodactyl.;)	0.74	$^* - 109°$	$^+0.66$	2.0, 0.03, 0.3	A	Y	unpublished data, W. A. Snedden, A. S. Rand & M. K. Tourtellot

^ Acrid.—Orthoptera: Acrididae; Gryll.—Orthoptera: Gryllidae; Tett.—Orthoptera: Tettigoniidae; Leptodactyl.—Anura: Leptodactylidae.
$^* i <$ threshold value, $- [(l/v)/ \ \bar{T}] \times 360°$, for $l = 5$ m; see equation (3).
$^+ cf$ significant at $\alpha = 0.05$.

Simulations revealed that R was consistently superior for $n \geqslant 3$, unless attention was selective (figure 4). R's attractiveness occurred because an I male that could produce many leading calls in a pairwise interaction with an R male was nonetheless inhibited repeatedly, and rarely called when surrounded by a multitude of neighbours. If both I males and females recognized only the nearest calling neighbours, however, the advantage of inhibitory-resetting was restored. When such selective attention operated, an I male was more attractive under all tested values of n and f; an I male also retained this advantage in simulations in which it was the only one of its kind among $n - 1$ Rs.

Assuming that attractiveness reflects reproductive success, the expected fitness payoff to a single R in an I population $[E(R,I)]$ is less than the average payoff to an I $[E(I,I)]$, and I is therefore evolutionarily stable (Maynard Smith & Price 1973). Moreover, the success of an I in an R population implies that $E(I,R) > E(R,R)$ and that I can increase in frequency when initially rare.

4. DISCUSSION

(*a*) *Do empirical data support the model?*

We surveyed the available literature and our own (unpublished) findings on rhythmic signalling in acoustic insects and anurans. Those data pertinent to signal interactions are largely consistent with the assumptions of our model and the predictions of our Monte-Carlo simulations. PRCs reported for acoustic insects and anurans are described adequately by least-squares linear regression, with slopes ranging from < 0.5 to nearly 1.0; synchronizing species are characterized by values $\gtrsim 0.7$ (Greenfield 1994*a*; 1994*b* and references therein; table 1). And in seven of the eight species that

we examined or were reported in the literature, the PRCs (adjusted for stimulus–animal distances) pass below the origin by at least $[(l/v) \ \bar{T}] \times 360°$, typical inter-neighbour distances being substituted for l (table 1). Thus, these rhythmic signallers incorporate relativity adjustments in their resetting mechanisms as demanded by our simulations (see equation (3)).

Neurophysiological investigation (Pollack 1988) and playback experiments on acoustic insects (Römer 1993) and anurans (Gerhardt & Klump 1988; Narins 1992; Schwartz 1993) demonstrate also that hearing may be tempered by selective attention to loud, nearby neighbours and stimuli as demanded by our n-male chorus simulations. Our ongoing experiments on *Ligurotettix* spp. (Orthoptera: Acrididae) show that such general hearing selectivity can apply to inhibitory-resetting mechanisms, as males presented with several audible stimuli are reset by only the nearest (and loudest) ones (Minckley *et al.* 1995). Similar results have recently been obtained for the Tungara frog, *Physalaemus pustulosus* (W. A. Snedden, unpublished data).

(*b*) *Synchronous and alternating chorusing as epiphenomena*

Synchronous and alternating chorusing have been suggested as means by which spatially aggregated males cooperatively adjust the timing of their calls to minimize predation risks, preserve species-specific call rhythms, or maximize attraction of females to the group (Walker 1969; Otte 1977; also see Lloyd (1973) and Buck & Buck (1978) on bioluminescent signal interactions). Significantly, none of these explanations are supported by a single empirical study (Greenfield

1994*a*; 1994*b*). Our model offers a simple alternative to previous functional interpretations of chorusing. Monte-Carlo simulations based on this model are consistent with findings in natural populations, and confirm that striking patterns of collective signalling activity can emerge as incidental consequences of intermale competition for the attentions of females. Given only a precedence effect wherein females prefer leading calls and a resettable oscillator controlling male calling, observed patterns of chorus synchrony and alternation can arise as incidental by-products of competition between signalling males to produce attractive leading calls.

Precedence effects are now known among various caeliferan and ensiferan Orthoptera (table 1). Such phylogenetic diversity may imply that precedence effects represent a conservative sensory bias. We propose that this sensory bias was exploited by male signallers during the initial evolution of inhibitory-resetting mechanisms, with synchronous or alternating chorusing arising as coincidental effects. Once an inhibitory-resetting mechanism arises among male signallers, though, precedence effects in female choice might be selectively maintained by a feedback loop: males who call at faster rates, an energetically-based signal property generally favoured by females (Greenfield 1997), are also those most likely to produce leading calls. Thus, precedence effects, in conjunction with inhibitory-resetting mechanisms, may establish a means by which females reliably choose rapid callers in complex acoustic environments.

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