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Modeling the role of competition and cooperation in the evolution of katydid acoustic synchrony

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The precise timing of individual signals in response to those of signaling neighbors is seen in many animal species. Synchrony is the most striking of the resultant timing patterns. One of the best examples of acoustic synchrony is in katydid choruses where males produce chirps with a high degree of temporal overlap. Cooperative hypotheses that speculate on the evolutionary origins of acoustic synchrony include the preservation of the species-specific call pattern, reduced predation risks, and increased call intensity. An alternative suggestion is that synchrony evolved as an epiphenomenon of competition between males in response to a female preference for chirps that lead other chirps. Previous models investigating the evolutionary origins of synchrony focused only on intrasexual competitive interactions. We investigated both competitive and cooperative hypotheses for the evolution of synchrony in the katydid *Mecopoda* "Chirper" using physiologically and ecologically realistic simulation models incorporating the natural variation in call features, ecology, female preferences, and spacing patterns, specifically aggregation. We found that although a female preference for leading chirps enables synchronous males to have some selective advantage, it is the female preference for the increased intensity of aggregations of synchronous males that enables synchrony to evolve as an evolutionarily stable strategy.
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In several species of animals, signals displayed by nearby individuals have precise temporal relationships with each other. The most striking of these is synchrony, which is seen in animals as diverse as fiddler crabs (Blackwell et al. 2006), fireflies (Buck 1938), frogs (Greenfield 1994), and katydids (Greenfield 1994). Acoustic synchrony has been reported from several species of katydids (Sismondo 1990; Greenfield 1994; Hartbauer et al. 2005; Nityananda and Balakrishnan 2007). The mechanism underlying this synchrony, however, differs in different species. In some species, synchrony arises due to an inhibitory resetting mechanism (Greenfield and Roizen 1993) where an internal oscillator is reset on every chirp. In other species like *Mecopoda elongata* (Hartbauer et al. 2005), synchrony is achieved due to a change in the rates of calling males such that the endogenous rhythms of both fast and slow individuals converge to a similar rhythm. In another species, *Mecopoda* "Chirper," the mechanism involves both chirp-by-chirp resetting and a change in the endogenous rhythm (Nityananda and Balakrishnan 2007).

Several hypotheses have been proposed to explain the evolution of synchrony (reviewed in Greenfield 1994). In some species, the evolution of synchrony could be better explained by cooperative hypotheses, where individuals in groups benefit from collective displays of synchrony. For example, synchrony might help preserve certain song elements required for species recognition by the female (Greenfield and Schul 2008). Alternatively, it could be more difficult for predators or parasitioids to localize individuals in synchronous groups (Tuttle and Ryan 1982). In this paper, the cooperative hypothesis we focus on is that synchronous groups will have a higher collective signal intensity than groups of individuals that do not synchronize their signals and hence attract a greater number of females (Wells 1977; Buck and Buck 1978).

In contrast to these cooperative hypotheses, Greenfield and Roizen (1993) suggested that acoustic synchrony in katydids could evolve as a consequence of competition between males in response to a female preference for leading chirps. Females of some katydid species have been shown to prefer chirps that lead others by a short period of time (Greenfield and Roizen 1993; Fertschai et al. 2007). This preference was restricted to chirps that led other chirps by a short window of time (the female preference window) and could be overridden by following chirps that were louder than the leading chirps by some decibels (the time–intensity trade-off point: Snedden and Greenfield 1998). Greenfield and Roizen (1993) and Greenfield et al. (1997) argued that competition to produce leading chirps in response to this female preference could lead to the evolution of a resetting mechanism in males, resulting in the phenomenon of synchrony. According to this hypothesis, synchrony evolves as a by-product of female preference, and individual males do not benefit from the collective synchrony.

Previous simulations of evolutionary processes (Greenfield and Roizen 1993; Greenfield et al. 1997) focused on species where aggregation was not a factor. Furthermore, these species were governed by inhibitory resetting mechanisms and did not have rhythms that varied during interactions with other males. In such species, it was found that synchrony could evolve as an epiphenomenon of a female preference for leading chirps and male competition to produce leading chirps. In our study species, *Mecopoda* "Chirper," however, the endogenous rhythm varies during interactions (Nityananda and Balakrishnan 2007), and individuals are found in aggregations in the field (Nityananda and Balakrishnan 2008). These differences in biology indicate that synchrony might have evolved along a different pathway in this species. Greenfield and Schul (2008) also suggest that the phenomenon of collective synchrony could evolve along different pathways in species with differing biology.

In this study, we have incorporated our previous results on the physiology and ecology of chorusing in the katydid *Mecopoda* "Chirper" (Nityananda and Balakrishnan 2007, 2008;

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Nityananda et al. 2007) into physiologically and ecologically realistic simulation models that investigate both cooperative and competitive hypotheses for the evolution of synchrony in this species given different aggregation regimes.

METHODS

The evolutionary scenario was modeled using the programing language MATLAB 7.0. The field was modeled as a 30 × 30 m grid. Ten males were assigned to points on the grid either randomly or in groups of two or three (see descriptions of individual simulations for details). Each of them was assigned a set of values for different call features including chirp sound pressure level (SPL), chirp period, and threshold SPL for resetting. The values for these call features were randomly picked from normal distributions with mean values and standard deviations observed in natural populations (Nityananda and Balakrishnan 2007; Nityananda et al. 2007).

We modeled two male strategies: "Responder (R)" and "Nonresponder (N)." R males interacted and synchronized with other males. Using previous measurements of attenuation in the habitat (Nityananda and Balakrishnan 2008), the SPL of each male was calculated at every point in the grid. Acoustic interactions were carried out between males that perceived each other to be louder than a behavioral threshold (Nityananda et al. 2007). Interactions were modeled as chirp-by-chirp resetting (Nityananda and Balakrishnan 2007) with the additional incorporation of period change: Periods were shortened for every consecutive chirp heard and lengthened when external chirps were not heard. To model the chirp-by-chirp resetting, the rhythm of each male was modeled as a phase counter that increased from 0 to 1. The increment of the phase counter was the reciprocal of the intrinsic chirp period assigned to the male. Whenever the counter reached 1, it was reset to 0 and a chirp was produced.

If multiple external chirps were received before the counter reached 1, each chirp reset the counter according to a Phase Response Curve (PRC) depending on the phase that the counter had reached.

The PRC was described by the equation

$$y = -1.3x^3 + 1.4x^2 + 0.3x + 1 \quad \text{if } x \leq 0.7$$

and

$$y = -33.2x^3 + 88.1x^2 - 78.2x + 24.3 \quad \text{if } x > 0.7,$$

where x is the phase in the chirp cycle at which an external chirp is received after sound transmission delays and y is the response phase, that is, the value in phase to which the chirp period of a male is adjusted in response to the external chirp. The phase at which each chirp reached any male was calculated taking into account the time of onsets of the other males' chirps and the delay caused due to sound transmission between the males. The programs modeling the resetting mechanism are given in the Electronic Supplementary Material. Interactions lasted 30 s in each bout. N males called regardless of their neighbors' calls. The R and N strategies were played off in multiple simulations.

Each simulation was run for a variety of possible female preference features that determined the attractiveness of a leading chirp given the timing and intensity of a following chirp. Every male perceived by a female to be above an assumed hearing threshold of 30 dB SPL was evaluated. The number of chirps of each male perceived as attractive by each female was determined using different criteria for female evaluation: different preference windows and time–intensity trade-off points. The female preference window is the time window after the onset of a leading chirp within which any other following chirp would be considered unattractive. The time–intensity trade-off point is the value of relative intensity between a following and a leading chirp for a given preference window above which a following chirp would be considered more attractive than a leading chirp. This was varied from 3 to 12 dB in steps of 3 dB. For each of the values of the time–intensity trade-off point, the female preference window in consecutive runs was assigned one of six values: 5, 15, 25, 50, 100, and 150 ms. A hundred bouts (= one run) were run for each combination of female preference features modeled (Figure 1).

Within a bout, a male was evaluated by a female at every point in the grid (1×1 m^2) except in the simulations where female aggregation was modeled. In these simulations, males were evaluated at every point on the grid where a female was present. In all cases, wherever chirps at the position of the female were above a female hearing threshold of 30-dB SPL, the points (females) were assigned to the male perceived to have the most number of attractive chirps and the entire bout was assigned to the strategy that attracted the greater mean number of females per male. R males and N males were represented in the next generation in the ratio of the proportion of bouts won in each run. Twelve successive generations were simulated for every combination of female preferences. A strategy was deemed evolutionarily stable if the proportion of males with that strategy reached 1. A diagram of the basic algorithm of a single simulation is given in Figure 1.

Four sets of simulations were run. The first set of simulations examined whether either the R or the N strategy was an ESS, given no aggregation of either females or males. Males were evaluated

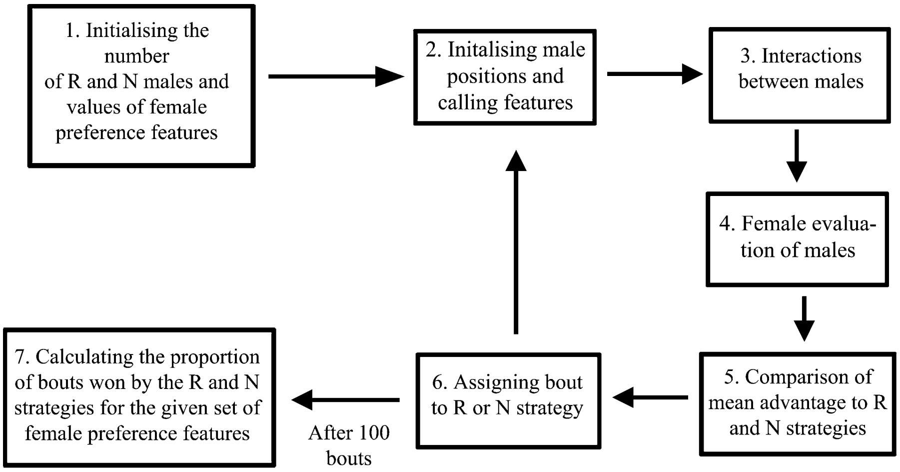


Figure 1
Diagram illustrating the algorithm of a single simulation run. One run was carried out for every combination of female preference features. R = Responder, N = Nonresponder.

by females at every point on the grid. In simulations that examined whether the R strategy was an evolutionarily stable strategy (ESS), the initial population of animals had a ratio of 9 R males to 1 N male. Simulations examining if the N strategy was an ESS had the reverse ratio.

In the second set of simulations, we investigated how the evolutionary payoffs to these strategies might change if males evolved a tendency to aggregate. The initial ratio of N and R males was the same as the results of the previous simulation at the end of 12 generations. Aggregation was modeled by creating groups of two or three animals. Two-animal groups were modeled by randomly placing the two animals within 5 × 5 m squares randomly specified on the grid. Three-animal groups were modeled by randomly placing the animals within 7 × 7 m squares randomly specified on the grid. The nearest neighbor distances obtained were comparable with those seen in natural choruses (4–5 m, Nityananda and Balakrishnan, 2008). Three possible aggregation regimes were modeled: 1) males aggregate regardless of responder or nonresponder roles, 2) only R males aggregate, and 3) R and N males aggregate in different groups.

In the third set of simulations, we modeled aggregation of females as well as males. Female aggregation was modeled similar to male aggregation. The number of females was set at 10, and their aggregation was modeled similar to that of males. Four simulations were run with males being nonaggregated or aggregated according to each of the three aggregation regimes described previously.

In a final set of simulations, we investigated the relative attractiveness of males in aggregations based purely on sound intensity without taking the female preference for leading chirps into account. Playback experiments with natural calls were used to model how loud animals were in groups. A series of chirps was played out at a period of 490 ms in an anechoic room (approximate dimensions: 2.4 × 2.2 × 2.4 m) from either one, two, or three speakers, and the peak SPL was noted using a Bruel and Kjaer Sound Level Meter (Naerum, Denmark) 2231 with a ½" microphone (4410, frequency range: 4 Hz to 20 kHz).

The chirps were played back at an output rate of 200 kHz using a NI-DAQ AT-MIO-16E-2 card through either a Tucker Davis Technology (Alachua, FL) ES1 speaker (frequency range: 2–110 kHz) using a Tucker Davis Technology ED1 electrostatic speaker driver or an Avisoft Ultrasonic Scanspeak speaker (frequency range: 1–20 kHz) using an Avisoft amplifier. The chirps played out were taken from a previous recording (Nityananda and Balakrishnan 2007) of a solo calling male made using a Bruel and Kjaer Sound Level Meter type 2231 with a ¼" microphone (4939, frequency response: 4 Hz to 70 kHz) and digitized at a sampling rate of 200 kHz using a NI-DAQ AT-MIO-16E-2 card and the software Labview 6.0. When played out from either of the speakers, the SPL of chirps at the position of the microphone was 85.5 dB (re 2×10^{-5} N/m^2).

The chirps were played out in two different scenarios. In the first, the chirps played out from different speakers were in synchrony with each other. This mimicked aggregations of two to three R males. In the second, the chirps played out from different speakers were not synchronized with each other. This mimicked aggregations of two to three N males. In these playback experiments, synchronous two-male choruses were 4.6 dB louder and asynchronous two-male choruses 1.8 dB louder than individual males. Synchronous three-male choruses were 6.2 dB louder and asynchronous three-male choruses 2.1 dB louder than individual males. These SPLs were used to model the SPLs in the final set of simulations.

The field was modeled as a 300 × 300-m grid with aggregations modeled as single points on the grid. Every male was assigned the same SPL value. This value was picked from a normal distribution having mean and standard deviation as seen in the natural population. The increase in SPL from one to two or three males observed in the playback experiments was used to model the SPLs of two- or three-male aggregations. Two male aggregation regimes were modeled: 1) only R males aggregate and 2) R and N males aggregate separately. For each of these conditions, two scenarios were modeled with females aggregated in one and not in the other.

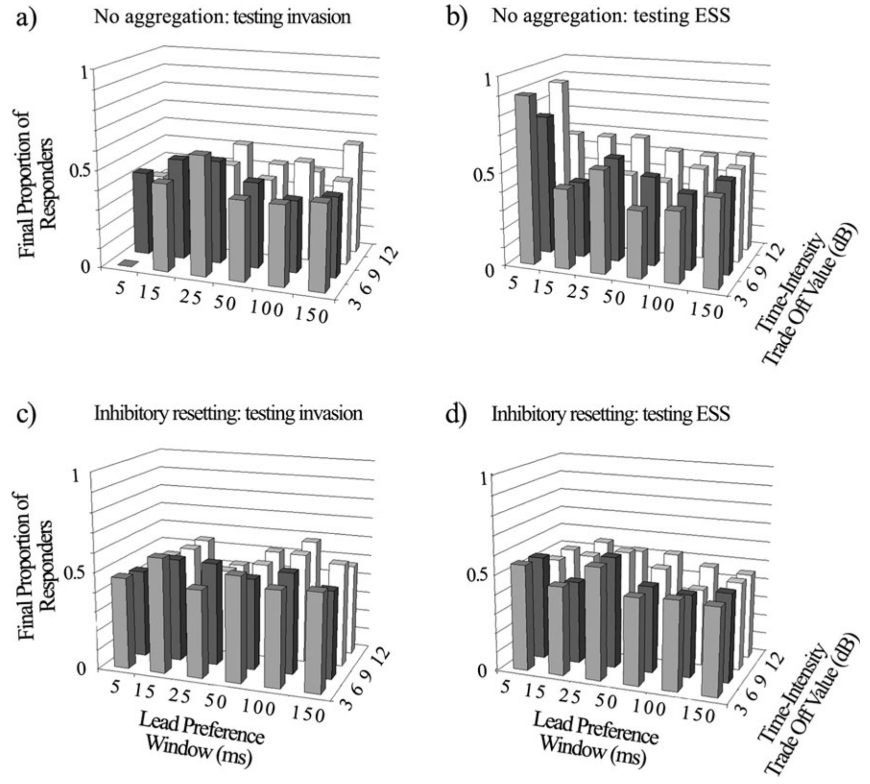
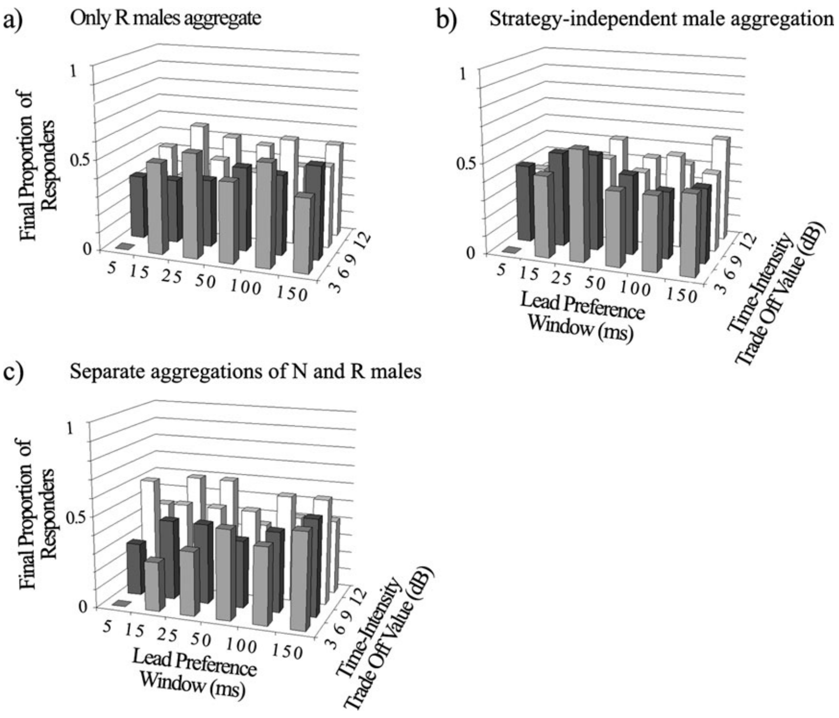


Figure 2
Neither the Responder nor Nonresponder strategy is a pure ESS given only competitive interactions. Both converge to a polymorphic state across different female preference features. Each graph shows the final proportion of R males in the population after 12 generations for different female preference features. Aggregation was not modeled. The starting ratio of R males to N males was equal to (a,c) 1:9 and (b,d) 9:1. The mechanism governing interactions in (a) and (b) involved both a chirp-by-chirp resetting and change in chirp rate as seen *Mecopoda* "Chirper". The mechanism governing interactions in (c) and (d) was inhibitory resetting modeled with the slope of increase of the oscillator level set at 0.6, the effector delay set at 123 ms and the rebound time set equal to the effector delay.



a) Only R males aggregate

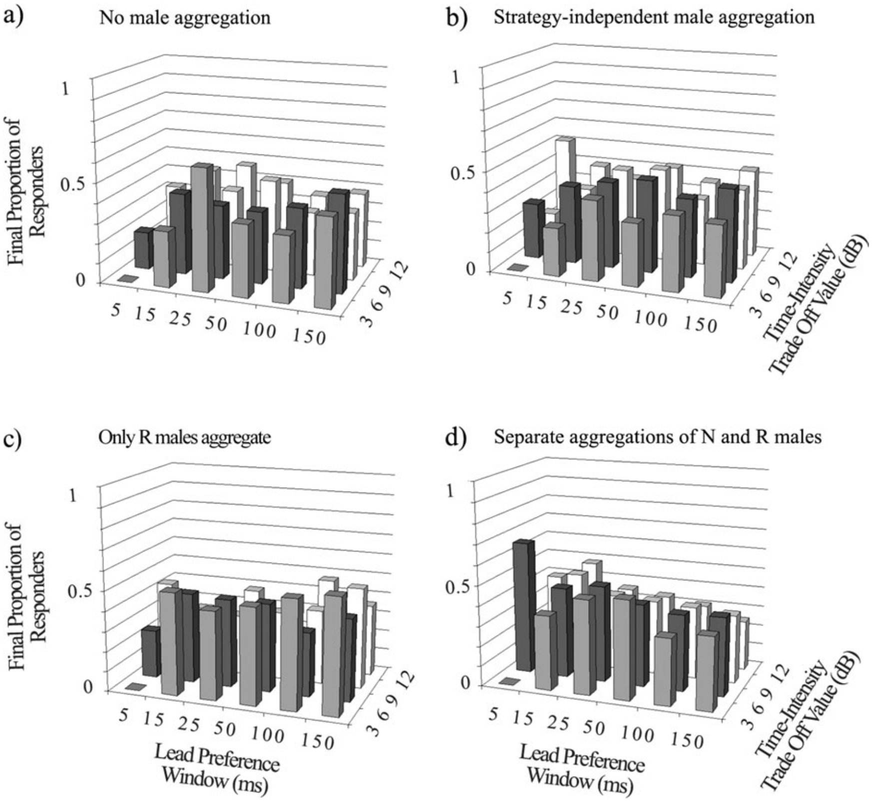
b) Strategy-independent male aggregation

c) Separate aggregations of N and R males

Figure 3
Male aggregation does not enable the Responder strategy to completely invade the population. The graphs show the final proportion of R males in the population after 12 generations for different female preference features. Female aggregation was not modeled, and male aggregation was modeled with (a) only R males aggregating, (b) males aggregating independent of whether they were R or N males, (c) R and N males aggregating separately. The starting ratio of R to N males was equal to the final ratio obtained in the simulations investigating invasion without aggregation (Figure 2a).

RESULTS

Neither of the two strategies proved to be an ESS (Figure 2a and b). Both strategies could invade a population of the other strategy up to a point at which they had approximately equal proportions in the population. This is in contrast to the natural population where all males respond to and synchronize with their neighbors, that is, all males follow the R strategy. The only condition in which the R strategy was uninvadable was when females were modeled to have a very small preference window, that is, chirps were considered leading only if they led by a very short time (less than 5 ms). Studies of female preference windows in other species show that these windows are



a) No male aggregation

b) Strategy-independent male aggregation

c) Only R males aggregate

d) Separate aggregations of N and R males

Figure 4
Female aggregation does not affect the evolutionary outcome of competitive interactions. Each graph shows the final proportion of R males in the population after 12 generations across different female preference features, with the starting ratio of R to N males equal to the final ratio in the simulation shown in Figure 2a. Female aggregation was modeled and male aggregation was modeled with (a) no aggregation, (b) males aggregating independent of whether they were R or N males, (c) only R males aggregating, and (d) R and N males aggregating separately.

comparable with the chirp length (Greenfield and Roizen 1993; Römer et al. 2002). A female preference window of 5 ms would therefore be unrealistic in *Mecopoda* "Chirper", which has an average chirp length of 110 ms. Even if the preference window were 5 ms, however, synchrony would not evolve as a pure strategy in the first place (Figure 2a).

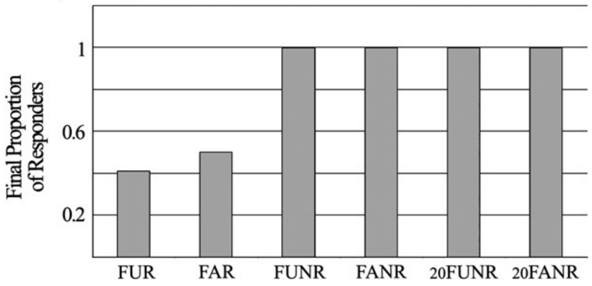
Similar results were also obtained (Figure 2c and d) when we modeled a different male mechanism (inhibitory resetting: Greenfield and Roizen 1993; Greenfield et al. 1997) and had selective attention restricted to the nearest neighbor for males and the nearest two males for females, as carried out previously for *Neoconocephalus spiza* (Greenfield et al. 1997).

In the second set of simulations, examining the effect of male aggregation regimes, the proportion of R males remained at approximately the same level at which they had started across all combinations of female preference windows and time–intensity thresholds (Figure 3a–c). This was found in all three aggregation regimes. The proportion remained around 0.5 and never exceeded 0.7 after 12 generations. For a female preference window of 5 ms, the proportion of responders remained low, unless it happened to fluctuate above 0.3. In such cases, the proportion increased until it also stabilized at around 0.5.

Similarly, the proportion of R males in the population did not increase beyond 0.7 (Figure 4a–d) in any of the male and female aggregation regimes in the third set of simulations. The population evolved to a mixture of R and N males in all cases except when the female lead preference window was very small (5 ms) when synchrony did not evolve (Figure 4a).

In the final set of simulations, we modeled the intensity differences between aggregations of synchronous and asynchronous males using results obtained from playback experiments. The proportion of R males in these simulations stabilized at approximately 0.5 if only R males aggregated (Figure 5, females unaggregated, only R males aggregated [FUR], and females aggregated, only R males aggregated [FAR]). If, however, both N and R males aggregated separately, the R strategy proved to be an ESS (Figure 5a, females unaggregated, N and R males aggregated separately [FUNR], and females aggregated, N and R males aggregated separately [FANR]). It was also able to completely invade a population of N males (Figure 5b, FUNR and FANR). This was true regardless of female aggregation and also when we repeated the simulation with 20 males and 21 females (Figure 5, 20FUNR and 20FANR).

a) Testing ESS



b) Testing invasion

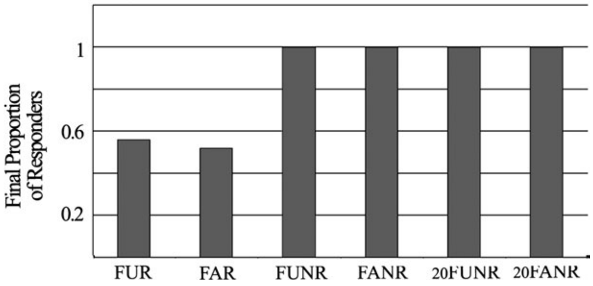


Figure 5
The Responder strategy is an invasive ESS due to cooperative effects when R and N males form separate groups. The graphs show the final proportion of R males in the population after 12 generations with female evaluation of males based purely on the differences in SPL between groups of R and N males. Starting ratio of R males to N males equal to (a) 9:1, (b) 1:9. Abbreviations: FUR, females unaggregated, only R males aggregated; FAR, females aggregated, only R males aggregated; FUNR, females unaggregated, N and R males aggregated separately; FANR, females aggregated, N and R males aggregated separately.

DISCUSSION

The results of the simulations across almost all combinations of female preference features and male and female aggregation regimes indicate that the evolutionary payoffs to males with the R (respond and synchronize) and N (do not respond) strategies in a population of either R or N males are equal if the sole selective pressure is the female preference for leading chirps. Neither the R strategy nor the N strategy can therefore be a pure ESS in this scenario, and the population would be a mix of R and N males.

When R and N males aggregate separately, however, the difference in intensities between the two groups would be expected to bias female choice such that the payoff to an R strategy male is greater than that for an N strategy male in a population of R strategy males, indicating that the R strategy is an ESS. Furthermore, the payoff to an R strategy male is greater than that for an N strategy male in a population of N strategy males, indicating that the R strategy can invade a population of N strategy males.

We therefore hypothesize that acoustic synchrony in *Mecopoda* "Chirper" can evolve as a pure ESS only after aggregation evolves, with the R males subsequently avoiding aggregations of N males (Figure 6). R males would be expected to do this because selective attention is poor in this species (Nityananda et al. 2007) and R males would consequently be continuously reset by N males. Although the formation of separate aggregations of N and R males and the corresponding difference in sound intensity between the aggregations is both necessary and sufficient for the evolution of synchrony as a pure ESS, the presence of a female preference for leading chirps could also contribute to the evolution of synchrony. This could occur either before or after the evolution of aggregation (Figure 6, dotted boxes).

The evolution of aggregation is therefore fundamental to the evolution of acoustic synchrony in this species and

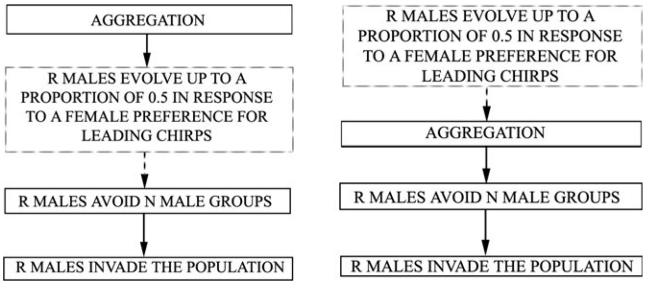


Figure 6
Two alternative evolutionary pathways leading to synchrony in the katydid *Mecopoda* "Chirper". Dotted boxes indicate possible but unessential steps in the process.

explanations based on interindividual competition alone are insufficient, though they could also operate in parallel. Aggregation could have several advantages unrelated to synchrony, which could lead to its initial evolution (reviewed in Parrish and Edelstein-Keshet 1999). These could include protection from predators (Lazarus 1979; Landeau and Terborgh 1986), improved defense against heterospecific competitors (McAuliffe 1984), and gaining informational cues from conspecifics (Kiester and Slatkin 1974). Once aggregation evolves, the increase in intensity as well as other cooperative advantages conveyed to aggregates of synchronizing males, such as the preservation of the species-specific call pattern and reduced predation risks, may enable them to invade the population and synchrony to evolve as a pure ESS. Acoustic synchrony in *Mecopoda* "Chirper" thus appears to be better explained by cooperative hypotheses than by those based on interindividual competition.

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