

Song Grammars as Complex Sexual Displays

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Abstract

We study the complex evolution of song grammars of the Bengalese finch. Their mating songs have the remarkable feature that they are described by finite-state automata. (Honda and Okanoya, 1999) In addition, it has been experimentally confirmed that complex songs are preferred by females and that the Bengalese finch's song is more complex than that of its ancestors. (Okanoya, 2002) These facts suggest that complex grammar-like systems may have evolved as a result of sexual selection. In order to explore this hypothesis, we study the communication between male and female finches, modeling their co-evolution by asymmetric finite-state automata. By introducing a complexity measure for song grammars, we study the effect of females' preferences. We observe that a gradual transition from lower complexity to higher complexity grammars is associated with the changing of male birds' courting strategy.

Introduction

Language is where the phonemes of a vocal communication system are arranged in a complex, one-dimensional manner with precise articulation. Whether or not this language contains grammar is a main difference distinguishing human and animal communication (Hauser et al., 2002). Interestingly, such functional features of human language are very similar to the courtship songs of songbirds and whales and different to the vocal signals of chimpanzees (Aitchison, 2000; Michael and Allison, 2000). This suggests that grammatical language behavior may have evolved independently in different species. Therefore, we believe that the study of language-like behavior is one way to understand the origins and evolution of language.

In recent years, experiments studying the grammar of one particular songbird, the Bengalese finch (*Lonchura striata* var. *domestica*), have been carried out and the following facts were established: (Honda and Okanoya, 1999; Hosino and Okanoya, 2000; Okanoya, 2002; Okanoya, 2003)

- The courtship song of the male Bengalese finch consists of a combination of chunks, each of which is a sequence of sound elements. Unlike alarm calls and threats, these may be recursively constructed by finite-state automata.

- More complex songs are preferred by females over monotonous ones. They promote the reproductive behavior of females, for example, the frequency of nest-making and mating poses etc.
- The Bengalese finch is a domesticated species of White-Backed Munia (*Lonchura striata*). After domestication, the song of the Bengalese finch has become much more complex than that of the White-Backed Munia.

In light of these facts, it has been hypothesized that males with complex song grammars have been chosen by females and that song grammars have evolved as a result of sexual selection (Okanoya, 2002). To explore this hypothesis, we study the co-evolution of males' song grammars and females' preferences by a synthetic approach which represents birds as asymmetric finite-state automata (FAs).

A significant aspect of our modeling is the way in which female birds gauge the complexity of the songs they hear. While complex songs generated by a FA enhance the reproductive behavior of females, the frequency of this reproductive behavior tends to be relatively low when the females are listening to monotonous or random songs (Okanoya, 2003). This suggests that the female birds can innately discern grammatical features such as recursive arrangement of song elements, and therefore distinguish interesting songs from monotonous or random ones. We therefore assume that female birds may be sensitive for arrangement of chunks and may have innate preferences for phrasing and rhythm in a song, so that they can gauge songs according to her preferences. As a result, the song grammars of males may have become complex due to the diversity of females' preferences.

To model this process, we constructed artificial birds as asymmetric FAs, one type of which is used only for song generation, the other type being used only for listening. We then introduced the following communication interaction between males and females. The female interjects in synchrony with the male song (by wagging her tail or chirping softly, for example), measuring how many interjections succeed according to her preferences before she evaluates

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her satisfaction with the song. ¹ In this model, we call such an interaction “song-interjection” communication.

With this model, we demonstrate co-evolution of male song grammars and female preferences.

Model

Here the co-evolution of male song grammars and female preferences is modeled as a communication game.

Male and female birds

The song grammar of a male bird is expressed as a finite-state automaton (FA) with an output as follows:

$$G = (Q, \Sigma, \Delta, \delta, \lambda, q_0), \tag{1}$$

where Q is a finite set of states, q_0 is an initial state, Σ is a finite set of input symbols, Δ is a finite set of output symbols, δ is a state transition function, $Q \times \Sigma \rightarrow Q$, λ is an output function and $Q \times \Sigma \rightarrow \Delta$ (Hopcroft and Ullman, 1979). In this model, $\Delta = \{blank, A, B, \dots, J\}$, where each letter represents a song chunk and “blank” represents a silent interval between chunks. The bunch of combinatorial chunks between blanks expresses a phrase and the whole output sequence expresses a courtship song. A male bird arranges the chunks in accordance with his song grammar.

On the other hand, the preference of the female bird is expressed by a FA with an input:

$$P = (Q, \Sigma, \delta, q_0, F), \tag{2}$$

where $Q, \Sigma, \delta,$ and q_0 are the same as above, and F is a set of accepting states, which is a subset of Q . This expresses a female’s preference for the phrasing, rhythm, and arrangement in a courtship song. She changes her internal state by listening to the song and interjects if she is in an accepting state. Examples of male and female FAs are shown in Fig.1. Note that every node in a female’s FA has one transition for every possible input, which is completely different from males’ FAs.

Communication and co-evolution

Given the number of male and female birds, N^{male}, N^{female} , in the initial state, communication occurs as follows.

Each male bird attracts a female at random and sings a song for length L_{song} according to his grammar, G , where L_{song} denotes the length of the courtship song. Since a male’s song must be a signal for tempting a female, “novelty” is an important factor in a courtship song (Miller and Todd, 1993; Werner and Todd, 1997). So, we assume that females may pay attention to the novelty of males’ song as follows:

¹The female Zebra finch has been observed to chirp in synchrony with the male song. However, no such observation has yet been made for the female Bengalese finch.

Examples of song grammar (G) and preference (P)

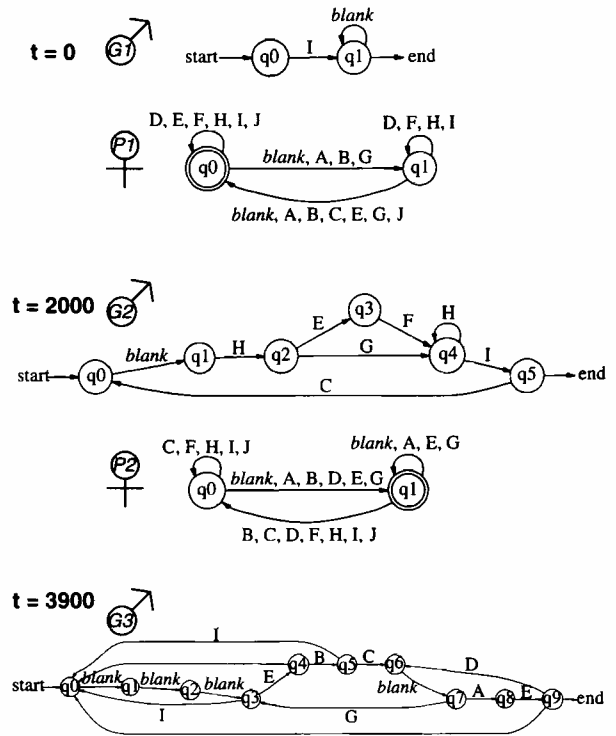


Figure 1: Examples of song grammars (G) and preferences (P): G_1, G_2 and G_3 shows male song grammars and P_1, P_2 show female preferences. G_1/P_1 and G_2/P_2 are well-suited pairs that yielded good communication at $t = 0$ and $t = 2000$, respectively. G_3 shows a grammar more complex than G_1 or G_2 . The double circle represents a accepting state.

- (i) There must be at least one chunk in the song which is not blank.
- (ii) The female must make at least one mistake in interjecting. This is because a song to which a female can interject perfectly (i.e. which is perfectly predictable by her FA) is boring for her.

Unless these conditions are satisfied, the birds involved are not eligible candidates for mating. Listening to a novel song that fulfills the above conditions, a female bird interjects to the song in accordance with her preference, P and evaluates her contentment. Each male bird can sing for a length up to L_{song}^{max} and can sing to several females within this length, where L_{song}^{max} denotes the maximum length he can sing. For example, if a male bird has $L_{song} = 10$ and $L_{song}^{max} = 50$, he can attract five females. Each time step, every male bird behaves in the above way.

On the other hand, the female interjects to all songs that she hears and that she is satisfied with according to her preference P and the above novelty criteria (i) and (ii). In this

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Examples of communication

t = 0
G1($N^{node}=2, L_{song}=10, LI=0.67$) vs. *P1*($N^{node}=2$)
 I I I I I
 ###_##
 score = 0.38

t = 2000
G2($N^{node}=6, L_{song}=13, LI=0.67$) vs. *P2*($N^{node}=2$)
 _HEFIC_HGI_HE
 #_#_#_#_#
 score = 0.43

t = 3900
G3($N^{node}=10, L_{song}=148, LI=0.63$) vs. *P3*($N^{node}=8$)
 _ I _BC _EBI _EBI _ I _EBC_GBC _ I _ I _ I _EBC_GEC _EC _EBI...
 ###_###_###_###_###_###_###_###_###_###_###_###_###_###_###_###_###...
 score = 0.74

t = 2000
G4($N^{node}=9, L_{song}=28, LI=0.64$) vs. *P4*($N^{node}=2$)
 GEGEJC_IGEJC_EGEGIC_IGIC_IJC
 ##_#_#_#_#_#_#_#_#_#_#_#_#_#_#
 score = 0.0

Figure 2: Examples of communication: *G1* vs. *P1*, *G2* vs. *P2* and *G3* vs. *P3* lead to suitable communications. *G4* vs. *P4* shows an example of poor communication.

model, the male can't discern the female's contentment for his song; only the female herself knows how much she likes a particular song. Some examples of communication are illustrated in Fig.2.

After a pair of birds communicate, their communication is assigned a score calculated as follows:

$$S = \frac{1}{3} \left\{ \frac{1}{N^{th}_{interj}} \min(N^{succ}_{interj}, N^{th}_{interj}) + \frac{N^{succ}_{interj}}{N^{all}_{interj}} + \frac{N_{chunk}}{L_{song}} \right\}, \quad (3)$$

where $0 \leq S \leq 1$. The first term denotes the evaluation of the number of successful interjections. The score is proportional to the number of successful interjections N^{succ}_{interj} below the threshold N^{th}_{interj} . If $N^{succ}_{interj} \geq N^{th}_{interj}$, the female bird's evaluation is saturated and the first term becomes 1. The second term denotes the success rate of interjection, that is, the ratio between the total number (N^{all}_{interj}) and successful number (N^{succ}_{interj}) of interjections. The third term denotes the fraction of non-empty chunks in a song. In other words, in total communication score (3) considers the evaluation of both quantity and quality of interjection, and the richness of song elements. In this way, females prefer longer songs

to which they may relatively easily interject, based on their preferences with the novelty criteria (i) and (ii).

According to the communication scores, females select the males with the highest score as their mating partners. Assuming that they produce offspring in proportion to their communication score, the number of offspring is calculated as $C_{offs} \cdot S$. Then, their offspring's genders are randomly assigned and they are added into the system as new child birds.

Since child birds study songs from their fathers or may have similar song preferences to their mothers as a result of their upbringing, their characters become similar to those of their parents. Therefore, in our model child birds inherit the FAs of their parents, changed according to the following genetic mutation operations:

- (a) **Arrow Mutation:** Change the transitions of the FA with the number of nodes remaining fixed.
- (b) **Node Mutation:** Change the number of nodes (± 1) and then add or remove arrows as required.
- (c) **Random Mutation:** A new FA is made at random.

These (a)-(c) express the possible inaccuracy in child birds inheriting their parents' characteristics, song grammars *G* and preferences *P*. In particular, the accuracy of inheritance is highest in (a) and (c) represents complete failure to inherit any characteristics.

In addition, the following mutation is performed in the male bird population only:

- (d) **Song Mutation:** Change L_{song} (± 5), and change L_{song}^{max} (± 2)

In this artificial ecosystem, each bird has a life time T_{life} , after which they are removed from the system. In order to limit the maximum number of birds, some birds are removed due to a fixed ecological capacity of $C_{echo}(N^{male} + N^{female})$.

In our simulations, these procedures are iterated over time.

Simulation Results

Here we describe the typical results of this artificial evolution.

The parameters of our simulations were as follows. The initial populations of males and females were 100 respectively. Every male bird had a FA constructed randomly with $N_{node} = 2, L_{song} = 10$ and $L_{song}^{max} = 50$. The maximum length of song was 500. Meanwhile, every female bird also had a randomly constructed FA with $N_{node} = 2$. Two examples of initial FAs are shown in the top of Fig.1. Other significant parameters were $N^{th}_{interj} = 100, C_{offs} = 3.5, T_{life} = 5$ and

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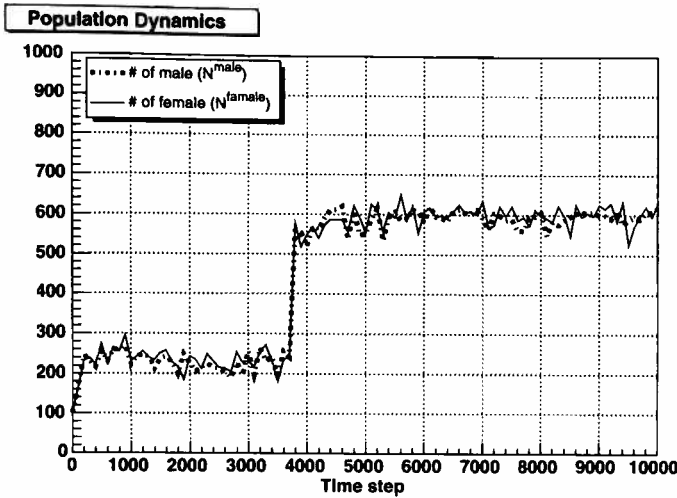


Figure 3: Population dynamics: Step-like evolution is observed. After the critical period around $t = 3700$, the number of birds rapidly increases.

Co-evolution

The population as a function of time is shown in Fig.3. We see a step-like evolution in which the population increased rapidly at about $t = 3,700$ and then remained almost constant.² After this period, we can see a change of strategy in the courtship behavior of both males and females. In Fig.4, we can see a rapid increase in the length of males' songs, L_{song} . Before this period, the male birds sang relatively short songs, even if the maximum song length was much higher. They could find partners successfully by singing to many females. This is clear from the N_{court} in Fig.5., which represents the average court count a female bird. Before the critical period at $t = 3700$, the communication scores were low in Fig.4., but N_{court} was very high in Fig.5.

On the other hand, shortly after that period, a trend in preferring longer songs emerged. Once such a trend appeared in the system, the character of males and females was drastically changed as may be seen in Fig.4 and Fig.5. In particular, Fig.5 shows that the male birds began to sing longer and more complex songs as the number of FA nodes increased. Subsequently, the female birds had a tendency to become sensitive to the arrangement of song chunks and also had FAs with increasing numbers of nodes. It is because of larger FAs with many nodes that females could distinguish the order of complex male songs.

The male birds never sang for the maximum length L_{song}^{max} shown in Fig.4. This results from a kind of dilemma. The

²Whether or not we see such a stepwise change depends on both the parameters N_{inter}^{th} and C_{offs} that affect the number of offspring. The step-like evolution is observed in wide region of these parameters, provided they are not too big or too small (i.e. the production rate is not too high or too low).

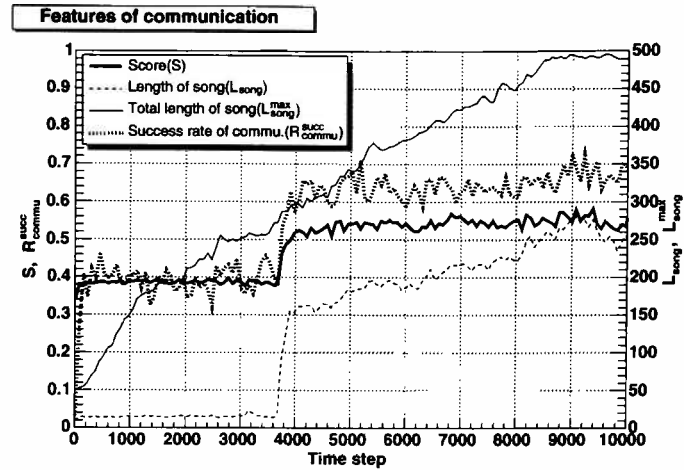


Figure 4: Features of communication: Shortly after the critical period $t = 3700$, a trend in preferring longer songs emerged. Subsequently, communication scores and successful communication rates increased.

male birds wanted the females to listen to their songs to get high scores, but if their affinity was bad, the cost of failure would be more serious. We can say that the male birds evolved a survival strategy as a result of co-evolution, avoiding the risky behavior of singing to only one female a song of length close to L_{song}^{max} .

On the whole, the communication evolved to become quite successful judging from the change in average communication score and the success rate of communication which represents the frequency non-zero scores in Fig.4.³

In summary, the emergence of male birds which could sing novel and longer songs triggered the co-evolution of song grammars and female preferences.

Complexity of song grammars

For the following discussion, we require a measurement of song complexity. We can define LI , the linearity of a song grammar as

$$LI \equiv N_{node} / N_{arrow}, \tag{4}$$

where N_{arrow} is the number of arrows leaving a node. If $N_{node} = N$, this value ranges between $1/N \leq LI \leq 1$ as N_{arrow} varies from N^2 to N . More complex FAs have lower values of LI . However, when the number of nodes is low, this index isn't suitable for measuring the complexity of song grammars. For example, the song grammars $G1$ and $G2$ of Fig.1 have the same value of $LI(= 0.67)$, but the song generated by $G2$ is clearly much more complex as may be seen in Fig.2.

³If a male's song doesn't fulfill the novelty criteria (i) and (ii), the male gets no score. Moreover, if a target female cannot interject properly at all, the male is also unable to get a score.

In the initial state, only simple song grammars like $G1$ exist in the system. In such a case, even grammars that could only generate *blank* and chunks in turn could get a score. As the evolution proceeds, the song grammars became more complex. In Fig.1, more complex song grammars $G2$ and $G3$ are shown. $G2$ has a feature typical of more complex songs. That is, it has a node, q_4 which may be reached by two different paths, $q_1 \rightarrow q_2 \rightarrow q_3 \rightarrow q_4$ and $q_1 \rightarrow q_2 \rightarrow q_4$. Song grammars which include such branches can arrange non-deterministic chunks, thereby avoiding perfect interjection, which is a prerequisite for song novelty (ii). However, if LI is less than 0.5, song grammars have more than 2 branches per node and it becomes difficult for female birds to successfully interject.

The evolution of song grammar linearity is shown in Fig.5. In this picture, we see that LI decreases gradually from 0.6 to 0.4 over time. LI never reaches 0 or 1. Such song grammars are not too simple and not too stochastic. This suggests that the song grammars have to be understandable by female birds. Therefore, we may conclude that the novel song-interjection communication is itself a driving force of the evolution of song grammars while at the same time placing an upper bound on their complexity.

In addition, we can confirm in Fig.5 that before the critical period at $t = 3700$ where the male birds sang only short songs, LI was almost constant. On the other hand, shortly after this period, the number of females' nodes increased rapidly and LI started to decrease, i.e. the song grammars became complex. This suggests that the female birds require longer songs before they can evaluate them.

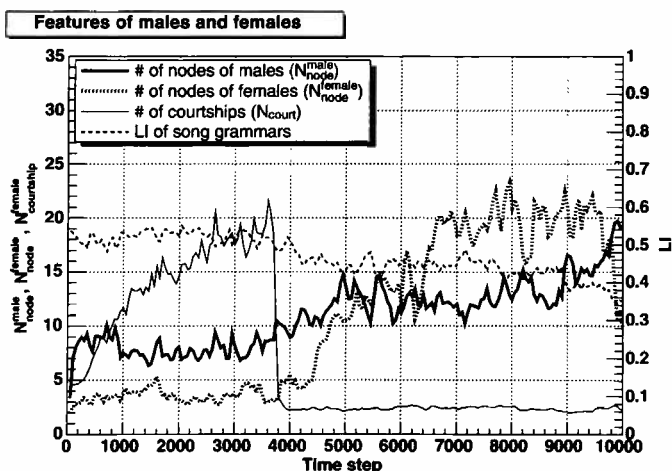


Figure 5: Features of males and females: The number of times the male birds sang to females N_{COURT} and the number of nodes of females N_{node}^{female} drastically changed at the critical time $t = 3700$. On the other hand, the number of nodes of males N_{node}^{male} and the linearity of song grammars LI changed gradually over time.

Discussion

It has been suggested by Okanoya that the mating song of the Bengalese finch may have evolved as a result of female preference. In the case of male peacock's sexual displays, the females' preferences are said to be the shapes and hole patterns in the males' plumage (Zahavi and Zahavi, 1997). We wonder, what kind of characteristics do female Bengalese finches prefer? If they prefer complex song grammars, how could these have evolved?

In order to explore these issues, we have modeled the co-evolution of male and female birds by asymmetric FAs. As a result of our simulations, we confirmed that song grammars could evolve to become complex via relatively brief, "novel song-interjection" communications. In this system, successful communication and song novelty are key concepts. Our results suggest that the driving force behind the evolution of grammar-like systems could be communication itself, not a diverse external environment (Suzuki and Kaneko, 1994; Hashimoto and Ikegami, 1996; Steels, 1999; Komarova et al., 2001; Sasahara and Ikegami, 2003).

The process of song grammar evolution observed in our model may be thought of as a "runaway process" (Zahavi and Zahavi, 1997). That is, singing a complex song doesn't assist a male bird in his survival. However, if this character, which is preferred by females, can be inherited by his offspring, complex songs could have an advantage in the conservation of his genes.

In addition, by introducing a complexity measure for song grammars, we studied the effect of females' preferences. We found that the linearity of song grammars LI gradually decreased from 0.6 to 0.4. This suggests that the song grammars may have evolved as a result of the cognitive ability of the female birds, in agreement with Okanoya's hypothesis.

Acknowledgments

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