

# Piep Piep Piep – Ich Hab’ Dich Lieb<sup>1</sup>: Rhythm as an Indicator of Mate Quality

Eva van den Broek and Peter M. Todd

Centre for Adaptive Behavior and Cognition  
Max Planck Institute for Human Development  
Lentzeallee 94, 14195 Berlin, Germany  
evdbroek@phil.uu.nl, ptodd@mpib-berlin.mpg.de

**Abstract.** Rhythm is common in courtship signals of many species. Here we explore whether regularly repeating rhythmic patterns can serve as indicators of underlying mate quality. We find through simulation that rhythmic signals allow the greatest discrimination between high- and low-quality males when low quality is associated with timing errors in artificial songs. However, rhythmic signals are difficult to evolve in our framework, leading to the conclusion that other pressures may have been involved in their appearance.

## 1 Introduction

Rhythmically repeated behaviors are common in nature: locomotion, breathing, chewing, and the like all rely on regular repetition for their effectiveness, and special neural circuits (central pattern generators, or CPGs) evolved early on to ensure that such behaviors would be performed with the proper rhythmic timing [1]. In addition to these important life functions, animal signals and displays often take a rhythmic form, from the regular flashing of fireflies or stridulations of crickets to the alarm calls of squirrels or the songs of birds and humans. Indeed, barring perhaps the performances of some Eurovision Song Contest entrants, rhythm is one of the most distinctive hallmarks of human music.

Given their prevalence, it is natural to ask whether the rhythmically repeated nature of these signals has some adaptive function. Perhaps rhythm is attention-grabbing; on the other hand, arrhythmic displays, by contrasting with commonly-seen rhythmic motor patterns, could be more surprising and draw more attention. More plausibly, rhythm may be used as a signal of an individual’s underlying traits, and in particular may indicate factors that are important in mate choice. Karl Grammer and his colleagues have been studying the traits that human rhythmic behavior may convey. In their studies, people were brought to the lab and asked to “dance to their own rhythm”. The participants’ movements were filmed and analyzed using neural networks which came up with surprisingly accurate estimates of the dancers’ personality

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<sup>1</sup> “Peep peep peep, I love you”, from the song “Guildo hat euch lieb”, by Guildo Horn And The Orthopaedic Stockings, Germany’s entry in the Eurovision Song Contest 1998: <http://willow.dyndns.org/rachel/doh/jukebox/guildo.htm>

traits according to the standard “Big Five” dimensions<sup>2</sup>—showing that traits that are often important in mate choice can be elicited from rhythmic motion patterns.

Further hints that rhythm may have the function of signaling mate quality can be found in the static visual domain. Regularly repeated forms that are easy to compare with each other can be used as quality indicators: Stripes and other regular patterns on fish, insects, snakes, and other animals might make errors stemming from developmental noise more salient. As Geoffrey Miller [2] put it, “From the viewpoint of signaling theory, repetitions across space (bilateral symmetry, radial symmetry, stripes) and across time (rhythm, repetition) are efficient ways to indicate developmental stability, a major component of fitness” (p. 67). This line of reasoning fits with the great amount of research in the past fifteen years devoted to finding the correlation between fluctuating asymmetry and developmental stress or genetic imperfection [3].

Besides revealing developmental noise, rhythmic displays in the temporal domain could heighten the salience of neural noise or disorders (leading to disruptions in motor control and in the generation of behavioral patterns), or show off positive aspects of quality such as respiratory fitness. In this paper, we test this function of rhythmic behavior as a proximate cue of underlying mate quality or fitness. We do this by constructing both coevolutionary and optimization models of populations of interacting artificial birds that produce and evaluate songs—temporal signals—for mate choice.

We use birdsong as our domain for testing these more broadly applicable ideas about signal rhythmicity for two main reasons. First, birdsong is used as a courtship signal (among other functions), indicating its possible quality-revealing function. In many bird species, sexual selection has resulted in complex, elaborated songs with rhythmic elements [4]. Second, there is evidence that rhythm in birdsong is disrupted by low-quality aspects of an individual singer. Birdsong production depends on features of the brain that easily break down under developmental stress or poor nutrition [5] (making song a revealing handicap). Consistent variation exists among individuals with respect to the temporal aspects of song delivery [6], and differences in rhythm are not only perceived but also important in inducing responses [7]. Rhythm may also be disrupted by noise at the neural level, leading to unwanted song timing variations. Courting male zebra finches seem to attempt to overcome this by holding down their level of neural noise when their songs are directed towards a female [8]. Thus the amount of rhythmicity in birdsong may serve as an indicator of developmental noise, neural noise, or current condition (e.g., energy reserves), all of which may be useful for a discriminating female to assess in a singing male.

## 2 Modeling the function of rhythmic signals

Models of signal design have typically focused on aspects other than regularity or rhythmicity, with a few exceptions. Johnstone [9] used neural networks to investigate a universal sensory bias for symmetry. Enquist and Arak [10] proposed that regularity arose as a by-product of the need to recognize objects irrespective of their position (but see [11] for problems with this approach). In addition to the (pre-biased) sensory mechanisms of the receiver, the environment is a factor influencing signal design. In

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<sup>2</sup> <http://evolution.anthro.univie.ac.at/ishe/multimedia/alysis.html>

noisy environments, signals might evolve to be more redundant (which can be instantiated as rhythmicity) and therefore easier to discriminate from the background [12].

A coevolutionary modeling approach similar to that taken here was used by Werner and Todd to explore signal design in birds in terms of novelty rather than rhythm [13]. They emphasized neophilia and an evolutionary pressure towards constantly changing signals, as opposed to a female preference for regularity. In their model, females used inherited song preferences along with a “desire for surprise” to select males who evolved over time to perform a wide and ever-changing diversity of songs. This result is complementary to the approach taken here, because the pressure for novelty can only operate after a pressure for regularity has first given rise to specific (possibly rhythmic) patterns and hence expectations that can then be violated.

## 2.1 Performing songs with evolved templates

To explore whether regular repeated (rhythmic) signals could evolve as useful indicators of quality in mate choice, we constructed a set of models with two types of individuals: male and female “birds”. (In our models, the birds do not have a specific predetermined sex, but can be drawn from the population to serve either as a mother or a father.) Both types are born with a basic song template, which they inherit from their parents. We leave out learning and fix the template at birth (thus making the model more similar to non-passerines than passerine songbirds).

The lives of our artificial birds are simple: They merely seek mates and reproduce. As in nature, the *in silico* males have to advertise themselves to potentially interested females by singing. In fact, in the model this is *all* that males do: males are reduced to a song template performed by a singing mechanism. The way a template is expressed (i.e., the behavioral phenotype that is produced) depends on the quality of the male, as described below. Females are the choosy sex, because the number of offspring they can have is limited (they can only mate once per generation, whereas a particularly tuneful or lucky male could mate many times). They consist of a judging device that uses an inherited song template of the same form as used by the singing males.

The song template encodes a temporal sequence of a very simple sort, representing what is happening in the song at a sequence of equally-spaced points in time. Here we cut the notion of a “song” down to its simplest binary form: At each instant, a note can either be sung or not, so that the song template entry can be either on or off (1 or 0). Thus, an example of a template with ten time-steps (the length that we typically use here) specifying the sequence of notes from left to right could look like “0010110010”. Every individual has two templates, one of which is used depending on the individual’s current sex role: the male template that is expressed as a song, and the female template that is used to judge male songs.

Like most sexually selected traits, the expression of the song has both a genetically transmitted and a condition-dependent component. Whereas the template is inherited from the parents, the condition or quality (in range 0.0-1.0) is randomly assigned to males at birth (females do not have condition-dependent traits). Quality has two effects for males. First, it impacts on the song he sings as he tries to attract a female and be chosen by her for mating. The male attempts to copy his inborn template perfectly in his song, but he may make mistakes in relation to his quality. More specifically, the

probability that the male bird makes a mistake on any single note while singing his template is inversely related to his quality (noisiness =  $(1 - \text{quality})/5$ , so that the “average” male with quality .5 has a .1 chance of making a mistake at each note).

Second, quality also determines the relative number of offspring a male can have, if a female chooses him. The function mapping male quality to the number of offspring controls the speed of evolutionary convergence. There must be enough difference between the fertility of low- and high-quality males to ensure that evolution can proceed appropriately, but without resulting in premature convergence. To achieve this balance, we let each mated pair containing a male of quality  $Q$  produce  $6 \cdot Q$  eggs. These eggs get put into the “egg pool” from which a fixed number (typically 200) are drawn at random to “hatch” and yield the next (non-overlapping) generation. Because the father’s randomly assigned quality only influences the number of eggs produced, quality should be regarded in this model as male investment and is not a heritable feature (as opposed to “good genes” models).

What kind of errors can a male make in his song? Given that he can only produce one kind of note or a pause at each time-step (1 or 0), we only need to consider a small set of possibilities. Specifically, a male could introduce a gap at some point and shift the rest of his song one time step forward (a note *insertion*), or he might forget a note, thereby shifting his song one time step backward (a *deletion*) [14]. We assume every insertion to be a pause, putting a zero on the actual time step and shifting the rest of the template one position to the right, thereby dropping the last note. A deletion is implemented by shifting the rest of the template to the left and inserting a zero at the end. These two ways of making mistakes are combined by defining an equal chance for either mistake to be made at each position in the template.

## 2.2 Evaluating songs with templates and preference tables

Each female’s goal (evolutionarily speaking) is to select a high-quality mate with whom she will have many offspring. However, she cannot assess quality directly, and so must rely on some aspect of the male songs to make her choice. Whether or not rhythm is one of the aspects that will evolve to aid in this choice is what we want to find out. All of the females get to select a mate, but they do not listen to the songs of all the males in the population before choosing; instead, a “choir” of a fixed number of singing males is selected randomly for each female to pick from. This limited sample reflects the time pressure to mate that real birds face. The number of males that a female can choose from regulates the force of selection. The larger her choir, the more strongly she can express her preferences (because she is more likely to find a male that she strongly prefers), and the more quickly the population may converge.

We build in a psychological mechanism by which the female makes her choice. The female follows a best-of- $N$  rule [15], picking as her mate the male in her choir whose performed song (phenotype) is closest—in some sense, defined below—to her own template (genotype). Given the possible noise in the male’s singing, similarity between his (hidden) genotype and his (heard) phenotype is not guaranteed; but when noise rates are low, each female will on average pick the male with the song template genotype that is closest (again, in some defined sense) to her own template genotype.

How does the female judge the similarity between the male song she hears and her own internal song template? The calculated similarity or distance depends on her preferences, for instance whether she is annoyed by missing notes, or by new notes that she was not expecting, or both. Exactly how a female judges is captured in her preference table (see Table 1), which defines how she rates what she hears (in the male song) at each moment against what she expected (in her template). These preferences are then summed over all time-steps in the song to yield the female's judgment of that male.

**Table 1.** Female preference table for judging male songs

	Expected	0	1
Heard	0	X1	X2
	1	X3	X4

As an example, a simple symmetrical preference table, one which is not biased towards a prevalence of either ones or zeros, is expressed by  $X1...X4 = \{1, 0, 0, 1\}$ . A female using this table effectively just calculates the Hamming distance between her template and the male song. Another psychologically possible preference table is an asymmetrical one in which there is no reward for producing a pause at the right time (X1), but there is a big punishment for being off the beat by producing a note in the wrong place (X3), so  $X1...X4 = \{0, 0, -1, 1\}$ . There are a number of other plausible preference tables that a female could use, so to keep from biasing our results with an arbitrary choice we have explored the space more widely. Assuming that the four values in the preference table come from the set  $\{-1, -0.5, 0, 0.5, 1\}$ , we limit ourselves to considering those preference tables where  $X4 = 1$ , and  $X4 \geq X1 > X2 \geq X3$ . In other words, the value placed on an expected note (X4) is always greater than or equal to the value for an expected pause (X1). Furthermore, expected events are always valued more than unexpected events, and an unexpected pause is penalized less than an unexpected note (i.e., a female's expectations will be violated more by an unexpected note than by a pause—see [16]). There are 20 such preference tables in all, shown in Table 2.

Once every female (that is, every individual in the population in their female roles) has chosen a mate, offspring are made from combinations of the templates of the parents. Crossover happens (with low probability) only between the two female- or male-associated templates, so that the templates used for judging cannot be mixed with those for singing. (This excludes a Fisherian runaway process, but correlations between the two templates within individuals can still arise). The mutation probability at each time-step is 0.01. Finally, as mentioned earlier, some number (depending on the father's quality) of the mated pair's eggs hatch and are placed in the offspring pool from which the next generation is randomly selected. Males in the new generation again are assigned a random quality.

### 3 Results: High expectations and poor performances

Given this framework, we now ask what types of male songs females can use to judge male quality and make good mate choices. Next, because good mate choices would lead to more offspring, we ask whether appropriate female templates will evolve to allow such choices, and whether male songs will coevolve to the same patterns, as is necessary for female choice to work. Our simulations aimed to find out if the female expectations and male performances could evolve to interact in this way.

#### 3.1 Template discriminability

Some songs that males could sing may make their quality evident—that is, any errors they produce would be obvious—while other songs would hide their quality. For instance, a totally silent “song” (0 at every time-step) would not allow any timing errors to be perceivable, because there are no notes to shift about in time. Females will gain an advantage if they (and the males) use song templates that allow them to judge male quality most effectively, discriminating accurately between high-quality low-error males and low-quality high-error ones. Which templates are the most discriminable for our female birds, given particular preference tables? We addressed this question using an optimization approach, looking for highly-discriminable templates for each of the plausible preference tables (in Table 2) in the following manner.

For each of the 1024 possible templates with length 10, we created a series of “noisy songs” by using an error rate that on average gives each song one insertion or deletion error. We computed the female’s preference for each noisy song given the current preference table, and then normalized each of these by dividing by the maximum possible preference rating for this template, which is the score, from 0-10, that the female gives if she hears an exact copy of this template. (Otherwise in some cases, for instance for an asymmetric score table, there could be an undesired difference between the scores for the templates with different numbers of notes.)

The gap between the best normalized score possible for each template (given a certain fixed preference table), which is 1.0, and the mean over all noisy performances of that template, is a measure of how well a female with this template can discriminate between low quality (one mistake on average) and high quality (no mistakes) males. For each of the 20 preference tables, we compared all of the templates to find the one with the largest such difference. This most discriminating template is then optimal for a female with this preference table, in the sense that it maximizes her quality-assessing abilities which determine how well her genes will be passed on.

As shown in Table 2, across the 20 psychologically plausible preference tables the most discriminating song template was rhythmically alternating (1010101010 or 0101010101) in all but four cases. (Two of the 16 rhythmic templates added an additional 1 at the end, but in these cases the fully rhythmic template had very similar discriminability). Only the four non-rhythmic templates had  $X1 \leq 0$ . Thus, placing a positive value on producing a pause when it is expected ( $X1$ ) seems essential for rhythmic templates to be the most discriminating. Given this caveat, rhythmic song templates appear to be the most useful type of signal, for our simulated birds at least, for discriminating high quality males from low quality ones.

**Table 2.** The 20 psychologically plausible preference tables where  $X4 \geq X1 > X2 \geq X3$ , along with the most-discriminating song template found for each. Only four preference tables have a non-rhythmic pattern as most discriminating.

X1	X2	X3	X4	Template
-0.5	-1	-1	1	0010101001
0	-1	-1	1	0000000001
0.5	-1	-1	1	0101010101
1	-1	-1	1	0101010101
0	-1	-0.5	1	0000000100
0.5	-1	-0.5	1	0101010101
1	-1	-0.5	1	0101010101
0.5	-1	0	1	0101010101
1	-1	0	1	0101010101
1	-1	0.5	1	0101010101
0	-0.5	-0.5	1	0000000001
0.5	-0.5	-0.5	1	0101010101
1	-0.5	-0.5	1	1010101011
0.5	-0.5	0	1	0101010101
1	-0.5	0	1	0101010101
1	-0.5	0.5	1	0101010101
0.5	0	0	1	0101010101
1	0	0	1	0101010101
1	0	0.5	1	0101010101
1	0.5	0.5	1	1010101011

### 3.2 What will evolve?

Now that we have found that rhythmic templates allow the greatest discrimination of error-prone males, the next question is whether or not they will arise during evolution. Will the rhythmic templates be of sufficient help to their female owners in enabling them to pick more males with a higher quality, thereby producing more offspring that inherit the same adaptive template? It all depends on how the male songs evolve at the same time. To find out, we built a co-evolutionary model with a population of 200 birds seeking mates and reproducing to form the next generation. In this model, it is assumed that the female judging system is not perfect with regard to the information it receives. To increase the need for using highly discriminable templates, we added Gaussian noise ( $sd = 1.5$ ) to each female's appraisal of a male song.

We began by exploring what would evolve when we initialized male and female templates at random, using the basic symmetric preference table ( $X1 \dots X4 = \{1, 0, 0, 1\}$ ) in 100 simulation runs with a choir size of 20. We measured the average number of alternations between 0 and 1 notes in all evolved templates in each generation (where the maximum, for the fully rhythmic length-10 template, is 9, and the ran-

domly expected mean is 4.5). The average number of alternations after 1000 generations is only slightly higher than the randomly expected mean, indicating that the population tends to converge to essentially random templates over time. On the other hand, we did find some indication that females with more alternating (rhythmic) templates are able to choose higher-quality males, but this effect does not seem strong enough to drive the evolution of rhythmic templates very far.

While rhythmic templates do not seem to “pop up” in our simulations, we can proceed to ask whether they would be stable over time if they arose in the population for some other reason. To answer this question, we started evolutionary runs from particular initial populations. First, we set all templates in the initial generation, both male and female, to the rhythmic template with nine alternations (1010101010). As the population evolves, the mean number of alternations per template starts diminishing after 300 generations. The resulting number of alternations after 1000 generations is 7.5, averaged over 10 runs. Conversely, when the population is initiated with a constant template (1111111111), it evolves at a higher rate toward random levels of alternation. Thus, the rhythmic template does appear to be evolutionarily more stable than the nonrhythmic template, but not entirely impervious to drift.

## 4 Discussion

Our model shows that rhythmic songs are more discriminating with regard to the sorts of mistakes that male birds make. However, rhythmic song templates are not easy to evolve in our binary-encoding framework, nor particularly stable against change once they have predominated in a population. Given that rhythmic signals do seem to be useful quality indicators, but are difficult to evolve in our model, the question arises whether other selective pressures or historical contingencies favoring rhythm may have been present in the evolution of those rhythmic signals we find in the world today. One plausible source of such historical contingencies exists at the neural level, where preexisting central pattern generators originally used for other purposes such as locomotion may have been exapted for new use in creating rhythmic signals. Such rhythmic circuits may also have led to sensory biases in the receivers to prefer regularly repeating displays. A promising direction in which to extend our models here would therefore be to build song templates in both males and females on top of a neural substrate in which rhythmic circuits could naturally arise, for example Jordan- or Elman-style sequential connectionist models or continuous-time recurrent neural networks (some of which have already been explored in the context of music production and perception—see [16]).

Further evidence for or against the mate-quality-indicator hypothesis for rhythm may come from uncovering the neural structures leading to rhythmic behavior and the genetic and environmental factors that can impact on the production of rhythmic signals. If a lack of noise (whether on a developmental, neural, or condition level) is indeed correlated with a fitness advantage for a bird, a rhythmic song might be the sonic equivalent of the peacock’s tail through which a male can reveal his mate quality.<sup>3</sup>

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<sup>3</sup> Whether or not this can help explain why Guindo Horn only placed seventh in the 1998 Eurovision Song Competition remains to be examined.



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