Constrained Performance in a Communication Network: Implications for the Function of Song-Type Matching and for the Evolution of Multiple Ornaments

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Abstract: Many species of territorial songbirds exhibit a behavior known as song-type matching, in which a male sings the same song type that his neighbor is singing. Song-type matching is associated with increased aggression, but researchers have not come to a consensus on its adaptive function. Building on studies that identify singing performance as a variable relevant to sexual selection, we hypothesize that higher-performance singers benefit from matching their opponent’s song type because matching improves eavesdroppers’ ability to compare the two males’ performances. We present a model of song-type choice that predicts that males that can outperform their rivals benefit by matching. In contrast, lower-performance males should avoid both matching and being matched. Our hypothesis is compatible with some existing hypotheses of song-matching function, but it is not compatible with the hypothesis that song matching is a conventional signal of aggression. We offer unique predictions that could be used to test our idea. We speculate that lower-performance individuals might have driven the evolution of repertoire complexity because they stand to benefit from novel, unmatchable songs. The phenomenon that dissimilar signals are less accurately compared than similar signals may favor the evolution of multiple ornaments and of plastic signal development (e.g., song learning) in general.

Keywords: alignable differences, birdsong, comparison, performance constraints, ritualization, song learning.

One of the primary goals in the study of animal communication is to understand the maintenance of honest signaling. For a signaling system to be considered honest, there must be a consistent correlation between the character of the signal and the state of the signaler or the environment (Searcy and Nowicki 2005, p. 3). Using the mechanisms that maintain honesty to classify animal signals, we recognize three types of signals. First, “index signals” are honest because they are impossible to fake (Maynard Smith and Harper 2003, p. 1). For example, only large-bodied common toads (Bufo bufo) are physically capable of producing low-frequency croaks, making croak frequency an index signal of body size in that species (Davies and Halliday 1978). Second, “handicap signals” come at a high production and/or maintenance cost. Thus, at evolutionary equilibrium, a low-quality individual’s best option is to save its energy and produce signals of lower quality than those produced by high-quality individuals (Zahavi 1975; Getty 2006). Third, “conventional signals” are signals of arbitrary form that are not costly to produce and that are associated with a specific meaning solely by convention. The honesty of conventional signals can be maintained “if social control of deception, in the form of punishment from aggressive individuals, is sufficiently severe” (Owens and Hartley 1991, p. 1187). Once a pattern of punishment is established, the threat of further punishment may be sufficient to enforce honesty.

Our present interest in conventional signals stems from the hypothesis that a common avian behavior known as song-type matching is best modeled as a conventional signal of aggressive intent (Vehrencamp 2001). Male songbirds of many species sing repertoires of two or more song types. It is common to observe two neighboring males singing at escalated rates and apparently directing their song at one another, a behavior known as countersinging. During bouts of countersinging, one or both singers may choose to match his opponent’s song type. Playback experiments have linked song-type matching (as opposed to nonmatching) to escalated response, indicating that
matching serves an adaptive function related to male-male competition (Krebs et al. 1981; Burt et al. 2001). Krebs et al. (1981) proposed that by matching an opponent’s song type, a bird communicates willingness to escalate an agonistic conflict.

Krebs et al.’s (1981) hypothesis raises the familiar question of signal honesty: Why don’t countersingers always match song and therefore maximize the probability of intimidating their opponents regardless of their true willingness to escalate? Vehrencamp (2001) reasoned that matching comes at a cost because it increases the probability that the receiver will retaliate by attacking the signaler. Thus, song-type matching is a conventional signal of willingness to escalate.

We propose a competing hypothesis in which costs and benefits are mediated by a communication network comprising the opponent and any eavesdroppers within hearing range of the interaction (McGregor 1993). We hypothesize that higher-performance singers benefit by song-type matching their opponents because this behavior increases the eavesdropper’s ability to compare the two males’ singing performances. By singing performance we mean the approach to physiological performance limits (discussed below). According to our hypothesis, song-type matching is not a conventional signal of aggressive intent directed at the opponent. Rather, we view matching as an emergent property of individuals attempting to maximize the effect of an index signal of quality (i.e., song performance). It is notoriously difficult to conclusively reject the hypothesis that conventional signaling is operating in a given system (Zahavi 1993). Our aim, therefore, is not to directly attack the conventional signaling hypothesis of song-type matching but rather to offer an alternative model based on reliable signaling and wait to see whether future experiments support the unique predictions of our model.

The Model

We developed a model that predicts the optimal singing strategy when song quality varies and eavesdroppers’ responses influence singers’ fitness. The model assumes that one bird (the opponent) has sung and that another (the actor) can choose to sing a matched song or a nonmatched song. A matched song is the same song type that the opponent sang, so it is made up of similar elements but is not perfectly identical to the opponent’s song. Importantly, both matched songs and nonmatched songs may differ in terms of performance level. Here, a song’s performance level is defined as its proximity to a population-wide performance constraint; it is assumed that high-performance songs are more attractive to females than low-performance songs. The opponent sings a song of mean performance level $Q_1$, and then the actor responds with a song of mean performance level $Q_2$. An eavesdropper listening to the interaction estimates relative performance level ($Q_2/Q_1$) after both males have sung, but the eavesdropper makes some degree of error in this assessment. If the actor matches his opponent’s song type, the error is equal to $e$, but if he sings a nonmatching song, the error equals $E$. Both errors are normally distributed random variables with mean $= 0$, but the variance of $E$ is greater than the variance of $e$, denoted as $\sigma^2_e > \sigma^2_E$. The ratio $\sigma^2_E/\sigma^2_e$ represents the matching clarification, the degree to which matching improves the eavesdropper’s ability to assess relative mean performance level. The eavesdropper’s assessment of $Q_2/Q_1$ is the currency to be maximized; behaviors that increase the probability that the eavesdropper will assess the actor’s performance as exceeding the opponent’s ($Q_2/Q_1 > 1$) are assumed to confer a fitness advantage.

We ran the model to simulate matching and nonmatching interactions over a range of relative song performance levels ($Q_2/Q_1 = 0.90, 1.00, 1.05, 1.10, 1.20, 1.30, 1.40, 1.50$) and matching clarifications ($\sigma^2_E/\sigma^2_e = 1.25, 2.00, 4.00$). After each song-matching event, the eavesdropper assesses the singer’s relative performance as $Q_2/Q_1 + e$, where $\sigma^2_e = 0.01$. We simulated 10,000 matching events at each level of relative male performance and recorded the number of times that the eavesdropper assessed the opponent as the superior performer (cases in which $[Q_2/Q_1 + e] < 1$). We followed the same protocol to simulate nonmatching interactions over the range of relative male quality with $\sigma^2_e = 0.0125, 0.02, 0.04$. We then determined the advantage (or disadvantage) conferred by matching. This was accomplished by subtracting the expected losses (events in which the actor was assessed to be inferior) given matching from the expected losses given nonmatching per 100 interactions at each level of relative male quality and matching clarification. The simulation was conducted in Microsoft Excel 2007 (Microsoft, Redmond, WA) equipped with the Poptools add-in (freely available at http://www.cse.csiro.au/poptools/).

The results of the simulation are intuitive (fig. 1). Matching is predicted to confer an advantage (i.e., matching advantage $> 0$) when the actor’s mean performance level exceeds his opponent’s (when $Q_2/Q_1 > 1$). According to our model, matching produces the greatest advantage when countersingers are closely matched for performance level (when $Q_2 - Q_1$ is small but positive) and when eavesdroppers’ ability to assess relative performance is strongly influenced by whether songs are matched (when $\sigma^2_E/\sigma^2_e$ is large).

So far our model considers the case where $Q_2/Q_1$ is constant across all song types of the two males. It is simple to extend the model to situations in which the relative
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Figure 1: Results of a model simulating two male birds countersinging while being assessed by an eavesdropper. Parameters of the model are the relative quality of the opponent ($Q_1$) and the actor ($Q_2$) and the degree to which matching improves the eavesdropper’s ability to assess relative mean performance level (the matching clarification, $\sigma/Q$). The matching advantage is the expected percentage of superior assessments garnered by song-type matching versus not matching. Matching is predicted to confer a fitness advantage when this value exceeds 0.

performance level varies among song types (app. A). The main conclusions of this extended model are the same.

Assumptions

First, our model assumes that actors can choose to match their opponent’s song, restricting its application to cases in which the actor shares the song type being sung by the opponent (factors affecting a bird’s ability to type-match are reviewed in Beecher and Brenowitz 2005). A second assumption of the model is that eavesdroppers err in their assessments of relative mean song performance quality ($Q_2/Q_1$). This assumption follows from the fact that stochastic variation—in song performance, transmission, reception, and decoding—is bound to affect the eavesdropper’s ability to accurately estimate the mean relative performance quality from a single song (Morton 1975; Wiley 1994). We suspect that few readers will find these two assumptions objectionable, so we will not discuss them further. Three remaining assumptions, however, require additional attention.

Song Performance Level Varies among Males and Is Recognizable by both Males and Females

Our model assumes that song performance level is a trait that varies among males. Receivers probably attend to several variable features within each song (Gil and Gahr 2002), but variation in individual song features has been demonstrated to strongly affect female choice (e.g., Drăganoiu et al. 2002; Ballentine et al. 2004). The model further assumes that actors and eavesdroppers agree on what constitutes a high-quality performance.

Physiological limitations that constrain vocal performance (reviewed by Podos and Nowicki 2004) generate measurable variance in song performance among males, which is perceptible to both male and female receivers. A song that closely approaches a population-wide performance constraint is an index signal that the singer is near the population limit of the constraining factor (e.g., motor control). If female receivers prefer to copulate with singers that approach such limits, or if male receivers prefer to avoid them, song performance level represents an aspect of song quality. Identified performance constraints include a trade-off between bandwidth and trill rate in sparrows (Podos 1997; Hoese et al. 2000) and banded wrens (Thryothorus pleurostictus; Illes et al. 2006), an upper limit to trill rate in canaries (Serinus canaria; Vallet and Kreutzer 1995), and a lower limit to amplitude modulation in dusky warblers (Phylloscopus fuscatus; Forstmeier et al. 2002). Both males and females attend to constrained aspects of song performance, with females consistently preferring songs that approach or exceed the performance constraint (Vallet and Kreutzer 1995; Vallet et al. 1998; Drăganoiu et al. 2002; Forstmeier et al. 2002; Ballentine et al. 2004; Illes et al. 2006; Cramer and Price 2007). We conclude that male singers and male and female eavesdroppers perceive variation in singing performance and that they can be
expected to agree, in a statistical sense, on relative song quality.

\textit{Eavesdroppers Assess Quality Based on Relative Singing Performance, and Their Assessments Have Fitness Consequences for the Actor}

Our hypothesis assumes that eavesdroppers listen to countersinging contests, that what they hear during these contests influences their future behavior, and that their future behavior has fitness ramifications for the actor. Importantly, high-performance singers must accrue greater benefits from singing than low-performance singers. Both male eavesdroppers, who must decide whether to challenge either of the contestants, and female eavesdroppers, who must decide whether to copulate with them, are of interest here. The results of several studies support our assumption that female birds eavesdrop on male countersinging contests and that their responses exert fitness consequences (via gained and lost paternity) on the countersinging males (Otter et al. 1999; Mennill et al. 2002, 2003; Leboucher and Pallot 2004). Similar results have been found when eavesdroppers are male (Naguib and Todt 1997; Naguib et al. 1999; Peake et al. 2001, 2005).

\textit{Eavesdroppers Are Better at Assessing Relative Quality of Matched Songs versus Unmatched Songs}

Our model assumes that performance comparisons between two songs of the same type are more accurate (i.e., include less error) than comparisons between two songs of different types. When singers match song types, eavesdroppers may directly compare the trill rate, amplitude modulation, or any other constrained feature of the two songs to estimate relative performance levels. If the males do not match song types, comparisons must additionally take into account the variation between the two song types, necessarily resulting in increased error.

Psychologists have developed a body of theory that addresses the comparison of similar and dissimilar entities, such as matched and unmatched song. Markman and Gentner (1993) propose that when comparing two entities, humans rely on “alignable differences” and “nonalignable differences.” The authors define alignable differences as differences between aspects of the common structure of the two entities being compared. For example, a person comparing two vehicles might recognize that car 1 gets 20 km/L while car 2 gets only 15 km/L. In contrast, nonalignable differences are not related to the common structure. Suppose in this case that car 1 comes with a global positioning system while car 2 offers an extended warranty. Applying this framework to birdsongs, pairs of type-matched songs include more alignable differences and fewer nonalignable differences than pairs of unmatched songs. Experiments show that human subjects compare entities more easily and estimate the relative value of entities more accurately when alignability is high (Slovic and MacPhillamy 1974; Tversky and Kahneman 1986; Gentner and Markman 1994; Zhang and Markman 1998; Zhang et al. 2002).

Zahavi (1980) suggested that male displays are often strongly ritualized because this makes it easier for females to directly compare the performance of the displaying males. In other words, ritualization serves the alignability of signals. We agree with this logic; females should pay greater attention to signals that are alignable than to nonalignable ones. By this mechanism, females put pressure on males to standardize their displays. Our model, however, suggests an amendment to Zahavi’s idea: both females and superior males benefit from increasing the alignability of male displays, but inferior males stand to benefit from decreasing alignability.

\textit{Compatibility with Other Functional Hypotheses}

There exist several hypothesized functions for song-type matching, but two related functions have received the bulk of scientific attention. First, it has been hypothesized that by song-type matching, a bird can target a single receiver (Brémond 1968, cited in Vehrencamp 2001) and so direct his signal of territoriality at a particular individual. The other major hypothesis is that matching functions as a high-intensity threat signal (Krebs et al. 1981). The hypothesis that matching is a conventional signal of threat (Vehrencamp 2001) is a variant of this second hypothesis.

The directed-signal hypothesis is compatible with the hypothesis we advance in this article. In our model, the opponent who is matched may be more likely to know he is being “sung at” than if he were not matched (the relative timing of the songs may also function to identify the target of a song; Hyman 2003). It may be, however, that the identification role of song matching is a selectively neutral outcome of the comparative role that we have proposed.

The relationship between our hypothesis and the graded-intensity-threat hypothesis is more complicated. If, as we suggest, matching can expose an opponent’s inferiority to eavesdroppers, a poor singer may benefit by developing a reputation as a “punisher” who is quick to attack birds that type-match him (here we assume that poor singers are not necessarily poor fighters; see Forstmeier et al. 2002). If punishment for matching is common, actors would do well to weigh the benefits of matching against the retaliation costs that are likely to be incurred. So although our model does not consider song-type matching a signal of aggressive intent, the model indirectly predicts that matching will be associated with el-
evated levels of aggression. If the threat of retaliation is an important deterrent to song-type matching, we might subtract the costs of matching from the fitness advantage gained by matching, shifting downward all three curves in figure 1.

Our model of song matching is not compatible with the hypothesis that matching is a conventional signal of aggressive intent. Recall that "conventional signals … are communication signals of arbitrary form that are associated with specific contexts by convention" (Vehrencamp 2001, p. 1637). In contrast to this definition, we propose that song-type matching is a nonarbitrary signal form whose structure is inherent to its function. Our model does not require any convention to associate matching with superiority because only high-performance singers will benefit by inviting direct comparison. In a conventional signaling system, bluffing is prevented by retaliation or the threat of retaliation (Vehrencamp 2000, 2001). Although we suspect that senders may incur retaliation if they match, we do not agree that the costs associated with retaliation are necessary to prevent bluffing. We suggest that bluffing is not "prevented" so much as it is impossible. Only superior performers stand to gain fitness by matching; inferior performers would actually lose fitness if they chose to match (represented by the negative matching advantages when $Q_2/Q_1 < 1$; fig. 1).

**Predictions**

Many predictions of our model are shared with other functional hypotheses of song-type matching and so are of limited value for testing the validity of our hypothesis (e.g., both our hypothesis and the aggressive-intent hypothesis predict more matching early in the breeding season; Beecher et al. 2000). Below, we focus on three classes of testable predictions that are unique to our hypothesis.

**Choice to Match Will Depend on Relative Performance**

We predict that in natural encounters, males that sing at a low performance level will be matched by those that sing at a high level more often than the opposite scenario. Extended bouts of song matching should only occur when males are closely matched for quality. If singing quality correlates positively with fighting ability, the conventional-signal hypothesis would also predict matching in response to lower-quality songs. The two hypotheses could be teased apart with a playback experiment using altered versions of the males’ own song as stimuli. We predict that males will match reduced-performance stimuli (e.g., those with artificially slowed trills) but will avoid matching increased-performance stimuli even when the mean performance level of the subject and the playback are equal. Importantly, these predictions apply to countersinging between territories; our hypothesis is not relevant to playback experiments that simulate a territory intrusion.

**Female Eavesdroppers Will Exhibit Stronger Preferences in Response to Matched Songs**

Our hypothesis predicts that females exposed to two songs of the same type should exhibit a stronger preference for the higher-performance song than females exposed to two different song types. Preference might be determined in a laboratory experiment by counting copulation solicitation displays or measuring approach in response to each stimulus type after a period of exposure to simulated countersinging (similar to Leboucher and Pallot 2004). We predict a stronger preference after females hear song-type matching because females exposed to type-matched stimuli should be less likely to mistakenly prefer the lower-performance stimulus. Ideally, stimuli would be balanced across treatments and would be synthetically generated (or altered from natural songs) to eliminate the variation in nontargeted song characteristics.

**Low-Performance Singers Will Choose Unmatchable Songs**

Males that cannot outperform their neighbors with shared song types should avoid being matched by choosing songs that are not in their neighbors’ repertoires. This line of reasoning requires the additional assumption that eavesdroppers do not discount unmatchable songs to such a strong degree so as to cancel out their potential benefits to actors. Given that assumption, our hypothesis predicts that low performance singers will tend to sing unshared song types more often than high performance singers.

**Implications for the Evolution of Multiple Ornaments**

The question of why animal displays frequently involve multiple ornaments has typically been addressed from two different angles (Candolin 2003; Hebets and Papaj 2005). Taking a female perspective, researchers have asked why females should pay attention to more than one trait. One answer is that multiple measurements should increase the reliability of assessment. Alternatively, signal complexity itself may be the most revealing quality indicator (multitasking hypothesis; Hebets and Papaj 2005). From a male perspective, it has been argued that multiple signals should be more successful at being detected and at exploiting sensory biases (Rowe 1999; Hebets and Papaj 2005).

While it has been realized that multiple ornaments or complex displays are more difficult to assess than single, one-dimensional traits (Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1996), the question of who
benefits from complicating the assessment of displays has received little attention (see Johnstone and Earn 1999). Generally, females and males have incongruent interests regarding the honesty of signals used in female mate choice: females benefit from gathering reliable information about male quality, but males benefit from being assessed superior irrespective of true quality differences. Thus, a male that is inferior to his opponent with regard to ornament A should downplay the importance of A by highlighting his superiority in another ornament, B. Females should resist this male-driven process of increasing dimensionality only to the extent that assessing an additional ornament is more costly than the gains from a more precise estimate of male quality. So we expect males to display their best ornament set within the range determined by the females. Without wanting to discount the importance of female preferences, we see the primary reason for the existence of complex and multiple displays in the general tendency of males to highlight their strengths. This tendency, combined with the inevitable genetic and environmental variation in male traits, leads to the multidimensionality of ornaments and displays at the population level.

Advertising displays such as birdsong come in several natural dimensions along which individuals can strive for superiority, such as endurance, maximum level of performance, versatility, and innovation. Many bird species have evolved large and complex song repertoires despite the fact that this should render species recognition more difficult. The most commonly used explanations for this are that song complexity might reflect male genetic quality (Catchpole 2000) or that it exploits female sensory biases (Collins 1999). However, there are species with large song repertoires in which female preference seems to target singing performance but not repertoire size (e.g., Forstmeier et al. 2002). If performance improves with practice, as in human singing, inferior males may specialize on being innovators rather than perfectionists. Innovators would initially produce novel song types at a higher performance level (due to the head start in terms of practice) before being outcompeted by the imitating perfectionist, which is when the innovator should drop this song type from his active repertoire. This scenario is consistent with the high rates of turnover of song types observed in many species (e.g., Forstmeier and Balsby 2002; Forstmeier et al. 2006). In contrast, the observation that song types are frequently dropped from an individual’s active repertoire (e.g., Nelson et al. 1996) is not consistent with the view that the displayed repertoire size itself is subject to directional selection through female mating preference.

Our hypothesis that inferior males drive the evolution of signal complexity is compatible with the finding that multiple ornaments are especially common in species with a lekking or polygynous mating system (Møller and Pomiankowski 1993). In these systems, high mating skew puts strong selection pressure on inferior males to find alternative ways (such as the above-mentioned trait B) to impress females. Also, the finding that female mate preferences are weaker in species with multiple as opposed to single ornaments (Møller and Pomiankowski 1993) could be interpreted as males having succeeded in complicating the assessment.

Our model suggests that a male songbird’s fitness depends on his ability to match inferior singers and to not match superior singers. Thus, both novelty and matching may be beneficial, depending on the circumstances. Song learning and song innovation may allow songbirds to maintain a flexible strategy with regard to song-type matching.

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APPENDIX

Modeling Variable Relative Quality among Song Types

The actor has the choice to respond to a given song-type A produced by the opponent (mean quality = Q_{A,1}) with his own rendition of the same song type of quality Q_{A,2} (matching) or with a different song type of quality Q_{B,2} (nonmatching). For the sake of simplicity, we initially assume that Q_{A,2} = Q_{B,2}. Then the matching advantage (the Y-axis of fig. 1) becomes the percentage gained probability of winning this single interaction by matching (where winning means being judged superior). This extended version of our model now predicts that males should match only those song types where they outperform the opponent.

Finally, we consider what happens if Q_{A,2} \neq Q_{B,2}. This leads to six possible constellations of relative qualities, which
are shown in table A1. With most constellations (scenarios 2 and 4–6), the actor is generally best off when using his higher-performance song type. All of these are trivial cases. If the actor’s matching song type is better than his nonmatching song type ($Q_1 < Q_2$), then he should always match. In contrast, scenario 1 is nontrivial, because using the lower-quality matching song type may still be advantageous if the gain through increased comparability is larger than the loss due to the quality difference between $Q_1$ and $Q_2$. Likewise, in scenario 3, it may pay the inferior actor to respond with the lower-quality nonmatching type ($Q_1$) if the increased uncertainty is large enough to compensate for the lower quality. In other words, if eavesdroppers can clearly tell that $Q_2 < Q_1$, the actor can never win this contest by matching, but if the quality $Q_2$ (relative to $Q_1$) can only be assessed with great uncertainty, the actor may sometimes be perceived as superior.

### Table A1: Predictions of whether song-type matching is advantageous given relative performance quality

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Opponent</th>
<th>Relative qualities</th>
<th>Prediction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Inferior</td>
<td>$Q_1 &lt; Q_2 &lt; Q_2$</td>
<td>Matching may pay</td>
</tr>
<tr>
<td>2</td>
<td>Inferior</td>
<td>$Q_1 &lt; Q_2 &lt; Q_2$</td>
<td>Matching always pays</td>
</tr>
<tr>
<td>3</td>
<td>Superior</td>
<td>$Q_2 &lt; Q_2 &lt; Q_1$</td>
<td>Nonmatching may pay</td>
</tr>
<tr>
<td>4</td>
<td>Superior</td>
<td>$Q_2 &lt; Q_2 &lt; Q_1$</td>
<td>Nonmatching always pays</td>
</tr>
<tr>
<td>5</td>
<td>Intermediate</td>
<td>$Q_2 &lt; Q_1 &lt; Q_2$</td>
<td>Nonmatching always pays</td>
</tr>
<tr>
<td>6</td>
<td>Intermediate</td>
<td>$Q_2 &lt; Q_1 &lt; Q_2$</td>
<td>Matching always pays</td>
</tr>
</tbody>
</table>

Note: $Q_1$ stands for the quality of song-type $A$ produced by the opponent, $Q_2$ for the quality of matching song-type $A$ produced by the actor, and $Q_B$ for the quality of the actor’s nonmatching song-type $B$.

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