Song Performance Rules in the Oriental Magpie Robin (Copsychus salauris)

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Abstract

Members of the thrush family (Turdidae) are renowned for a quite melodious but nevertheless complex mode of singing. Such holds true also for the Oriental Magpie Robin (Copsychus saularis) that settles in some tropical regions of Asia. We have studied the territorial singing of this species in the area of Biratnagar (Nepal), and present a list of first results here. Analysis of singing episodes of (duration ~ 40 min each) recorded from adult males (n=5) who were flagging their territories at the beginning of their breeding season (March 2007), yielded three sets of findings: (1) oriental magpie robins resemble some song performance rules of other thrushes, and such concern especially the time domain. (2) However, some interesting idiosyncracy were found as well. This was true, for instance, for the robins' repetitive singing style and their mode of motif type combination within and also across songs. (3) In addition, it was remarkable that neighbours did not share parts of their repertoires. These findings contribute to the discussion of two aspects; namely the use of 'song as an interactive tool' and the role of 'learning as an origin of pattern similarity'.

Keywords: Oriental magpie robin; Copsychus salauris; Repertoire size; Repertoire performance; Structural hierarchy.

Introduction

Biologists distinguish about 9000 species of birds and list about 4000 of them as passeriformes (oscines; Howard and Moore, 1991), or simply as 'songbirds'. These birds are named after a special category of acoustical signals, i.e. their so-termed 'songs' (Koodsma and Miller, 1996). Aside a few exceptions, songs are produced by adult males who thereby can address and attract females. In addition, they play a crucial role in flagging territories and repelling male competitors (Catchpole and Slater, 1998). In terms of these two functions, songs replace another category of acoustic signals that

normally are classed as 'calls'. Songs and calls differ in several important properties (Kroodsma, 1977; Krebs *et al.*1978; Catchpole, 1983; Hultsch 1980, 1993a). For example, the linkage between a given social context and a particular signal pattern is quite fixed in calls, but astoundingly flexible in songs. In other words, during an episode of singing, most bird species perform different song patterns without any evidence that the social context has changed. (Todt 1970a; Thompson 1972; Falls and d'Agincourt, 1982; Kramer and Lemon, 1983; Horn and Falls, 1988).

A further and even more fundamental difference between calls and songs concerns their development. In contrast to calls, songs are learned and generated by vocal imitation of individually experienced signals (Catchpole and Slater, 1995; Beecher, 1996; Todt and Hultsch, 1996). Such signal acquisition through auditory learning is rare in other non-human organisms. Until now, it has been documented only for a few families of birds (e.g. oscine birds and parrots; review in: Marler and Slabbekoorn, 2004) and mammals (e.g. marine mammals and bats; review in: Janik and Slater, 1997).

The singing of birds is performed as a stream of behavior that shows a clear-cut alternation of acoustical patterns and silent intervals (pauses). The most conspicuous pattern is the so-called 'song' (strophe) (Todt, 1970). In most European birds, songs have duration of about 3 seconds and are separated by pauses of a similar duration. From the perspective of information processing, song duration seems to be selected for providing optimal 'chunks' of information; i.e. a song is long enough to convey a distinct message and, at the same time, not so long to constrain a sensory check for signals of a neighbor or delay a potential reply (Todt and Hultsch, 1996).

In addition, songs form an intermediate level of a structural hierarchy in which the highest level is given by an episode of singing or a sequence of songs (term: intersong level). On hierarchically lower levels one can distinguish several structural compounds that compose the songs (term: intra-song levels). In a top-down order these are, for example, song sections, or phrases, motifs, syllables and elements or notes (Todt, 2004). The numbers of both phonetic song constituents and discerned intra-song levels vary a lot across species. Most

analyses, therefore, concentrate on the basic level of song organization which is given by the so-called 'song elements'. At this level units are compared and, according to parametric cues or values assessed by frequency spectrography, either told apart or lumped. The pool of classified song elements is then taken to categorize higher level patterns, e.g. types of motifs ore even types of songs, and to finally assess the repertoire of song-types (Todt, 1968; Lemon and Chatfield, 1971; Shiovitz, 1975, Bondesen. 1979: Kroodsma. Thompson et al. 1994; Todt and Hultsch, 1996).

Bird species differ in the sizes of their song-type repertoires (review in Catchpole and Slater, 1995). Chaffinches (Fringilla coelebs) and Great Tits (Parus major), for instance, sing three to eight different songs, whereas size in Eurasian Blackbirds (Turdus merula) is approx. 50 and Common Nightingales (Luscinia megarhynchos) even master more than 150 types of song (Hultsch and Todt, 1981). In spite of such species-typic diversity, the composition of vocal repertoires reveals a basic principle in most songbirds: The sizes of element-type repertoires are larger than the sizes of their song-type repertoires. If we compare this principle to relations documented for units and higher level compounds in human language, a crucial difference appears. In the latter case a small number of basic units (e.g. phonemes) serve as a pool to compose an almost unlimited amount of verbal patterns, such as words or sentences. Nevertheless, for reasons to be treated later in this chapter, songs appear somehow comparable to sentences: both can be regarded as units of interaction where they obviously play a role as chunks of exchanged information ('units of sense').

Lessons from the structural hierarchy of bird song have stimulated studies on the rules encoded in the sequencing of songs or song elements, respectively, and these rules have been described by a procedural hierarchy. The concept of a procedural hierarchy allows investigating significance of sequential positions, namely by assuming that a given pattern can be taken as a 'hierarch' for the next unit in the sequence. Such studies showed that the sequencing of songs reflects a remarkably high degree of freedom. That is, in principle, no song-type succession is excluded, and this facilitates pattern specific during vocal responses interaction. Nevertheless, one can find preferred sequential combinations of particular types of songs, which according to recent studies can be explained as a result of individual learning. On the intra-song level, however, the sequencing of elements is much less flexible than that of songs. With the Eurasian Blackbird and the Common Nightingale as typical species procedural hierarchy on the intra-song level can be described by the following rules. First, particular types of elements occur at a particular song position only. Second, songs share initial types of elements, but differ in the subsequent ones. Thus the intra-song branching usually reflects a 'diffluent flow' schema (one-to-many principle). In terms of decisional aspects this means that a bird has a number of alternative options to continue a song after the first element has been produced (Todt, 1970a; Hultsch, 1980; Naguib et al. 1991; Naguib and Kolb, 1992).

To summarize, the singing of birds reveals a complex structure and there are distinct rules that specify its dynamic properties. Evidence form European birds, especially thrushes (Turdidae) have shown that such rules or structural features, respectively, are closely related functional aspects. Since a few months, we began to clarify whether these relationships hold true also for some Asian thrushes, namely the Shama Thrush (Copsychus malabaricus) and the Oriental Magpie Robins (Copsychus saularis). Profound studies on these organisms are still lacking. Here we present first results of an inquiry into the vocal accomplishments of the Magpie Robins inhabiting in Nepal. Our main questions were: (1) Do the birds mediate their messages by signal patterns that match the characteristics of songs? (2) How large is a given songster's vocal repertoire, and how is such a repertoire performed? Do neighbours share parts of their song repertoires, and do they engage in vocal matching? -Answers to these questions will be compared to rules of song organization and singing reported for other thrushes, mainly species from Europe and Africa, which acquire and use complex repertoires of vocal patterns.

Materials and methods

Subjects

Subjects were Oriental Magpie Robins (Copsychus saularis) living Biratnagar, Nepal. The species is insectivorous and common in suburban areas, but also outside residential areas. Breeding takes place within nesting-holes and can last from March to August. The acoustical material used in this study was recorded in March 2007 during the dawn singing of territorial males (n=5). Four of the five subjects settled within earshot of each other, while the remaining male was out of earshot farther away.

Data sampling and analyses

Acoustic data were recorded by applying a Sanyo mini-tape recorder with an in-built microphone. For analysis, these data were transferred to a computer where all recordings were digitalised with sampling rate of 22,05 KHz and 16 bit resolution using Avisoft SasLab Pro software (R. Specht, Berlin). This program is easy to access, very well proven and allows a detailed analysis of signals. In addition. it provides clear-cut spectrographic displays of vocal patterns. Hard copies of spectrograms were made at 8 kHz in order to compare and sort the different types of song patterns. All further of analysis followed steps data conventional procedures of avian sound research (see Todt 1970; 2004; Hultsch and Todt, 1981; 1989; 2004).

To examine structural similarities or differences between song patterns, two persons, who were not informed about the aim of our study independently, did the following analyses. They visually compared spectrographic displays of the recordings and counted the number of vocal patterns belonging to the same type of song. The acoustic precision of most songbirds allowed for an objective assessment of this variable. Our test persons classed two song patterns to the same song-type if these did not differ in (a) their syllables or elements and also (b) the sequential succession of their constituents. Differences in the amount of syllable or element repetitions (trill sections), however, accepted for a given type, and measured as a kind of song variation (Hultsch and Todt, 1998).

For logistical reasons, i.e. because the amounts of song material available for the various species were too different, statistical data analyses were kept rare and constrained.

This procedure followed suggestions of Mundry and Fischer (1998) that are appropriate if samples are too small for asymptotic tests (see also Siegel and Castellan 1988).

Terminology

As this study was a first approach to the singing of Nepalese thrushes, it was designed to clarify both matters: first, some fundamental properties of these birds' signal behaviour, and second, which terminology would be appropriate to describe the accomplishments. With this as a reference we keep a-priory terminology as reduced as possible and limited to a distinction of terms related to a genuine physical domain, or the time domain of vocalisations, respectively (Figure 1). Accordingly, we suggest the following definitions:

Songs: Vocalisations ('strophes') that compose an episode of singing and are segregated from each other by silent intervals (=inter-song pauses) of ≥ 0.5 s. Note: (a) Songs have been shown to serve as 'units of vocal interaction' and to have a limited duration (< 10 s) for this purpose (see 'Discussion). (b) Silent intervals larger than 20 s are regarded to separate different episodes of singing (Hultsch and Todt, 1981; 1982; 1998).

Elements: Vocalisations ('notes', 'strophenelements') that compose the songs and are segregated from each other by silent intervals (=within-song pauses) of < 0.5 s. Note: (a) Song elements form temporally coherent sound figures that usually reoccur without conspicuous variation. In addition, also the sequential combination of such elements is quite regular (Hultsch and Todt, 1981; 1982; 1998).

Results

Song features

The singing behavior of all subjects showed a clear alternation between acoustically filled intervals and silent intervals. Comparing the duration of these intervals allowed identifying patterns that according to conventional criteria merit to be called songs. That is, silent intervals segregating them were longer than 0.5 s and preferentially around 4 s (Figure 2). Interestingly, most songs lasted for about 2 s, what pointed to their interactive role.

Regardless of such congruencies, subjects differed however in another time related parameter, namely, their song rate. Whereas one bird A produced about 500 songs (11 songs /min) within 40 mins, bird E did reach only an amount of less than 200 (4 songs per min). The other birds (B, C, D) showed a song rate of about 7.5 songs/min (Figure 6).

Repertoire Composition

Application of parametric analyses and procedures of categorization brought into light acoustic patterns that reoccurred in a rather persisting configuration. Most of these are illustrated in Figure 3. Due to this property we suggest to term them "motifs" and to sort them according to composition of the same types of elements (see methods). In other words, motifs of the same type were identical in the types of their acoustic elements. As this suggestion is founded on the material that currently had been analyzed, and our analysis is going on, we consider this definition as preliminary.

The motifs were composed by 5 to 10 elements that were displayed in a frequency ranged between 2.5 to 6 kHz. The mean repertoire size of motif types was 7.4, ranging from 10 types (bird D) to 5 (bird A, Figure 6).

Comparison across individual songsters did not deliver evidence for sharing of motif

types or repertoire sharing respectively. This result is notable because repertoire sharing is common for many thrushes especially when they are neighbours. Currently it remains open whether a repertoire sharing may occur between birds which settle far away from each other, because of limited data base. Note: Only one bird (E) represents a distant songster but its song material is constrained and does not allow making prediction about his final repertoire.

Repertoire performance

Analysis of motif type succession allowed ascertaining three remarkable performance rules. These were:

- 1. Many songs were composed by only one motif. However repetitions of a given type of motif within one song could occur as well (Figure 4). In a few cases, a songster could even compose a song by using two different types of motifs Such occurrences were constrained however to those types of motifs that seemed to be related sequentially, also during the performance of songs (Figure 6, bird A and C).
- 2. Analysing the retrieval time of song performance, which is measured between the start of two successive songs showed a multimodal distribution. One peak was found at 2 s, and another one for 5 s. The first modal value referred to songs composed of one type of motif only, whereas the second modal value concerns multi-motif songs (Figure 5).
- 3. In general, Magpie Robins used to repeat songs composed by the same type of motif. This characteristic is common in birds with a limited repertoire size. Besides this, however, our species showed a particular

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Singing (=bout of songs)

Songs

Elements

Figure 1. Structural hierarchy of song organization (for details see Todt 2004).

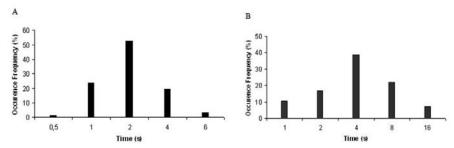


Figure 2. Temporal characteristics of singing in oriental magpie robins. Top: Frequency distribution (histogram) of song lengths (linear scale of time classes). Bottom: Frequency distribution (histogram) of durations measured between songs (pause lengths; geometrical scale of time classes). Note: the data confirm that a use of the term 'song' is appropriate in the test species as well.

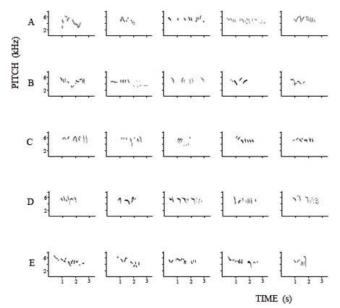
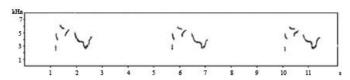


Figure 3. Frequency spectrograms (sonagrams) of motif types composing the vocal repertoires of 5 male magpie robins. Capitals (A, B,... E) refer to the birds. The songsters did not share parts of their repertoires (see text).

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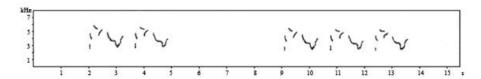


Figure 4. Frequency spectrograms illustrating how motif types can compose successive songs. Top: Single occurrence. Bottom: combined occurrence (see text.)

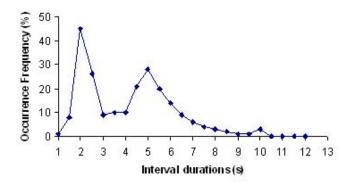


Figure 5. Retrieval time of song performance given by a frequency distribution of intervals measured between the starts of two successive songs. The first frequency peak referred to songs composed of one type of motif only, whereas the second peak concerns multi-motif songs.

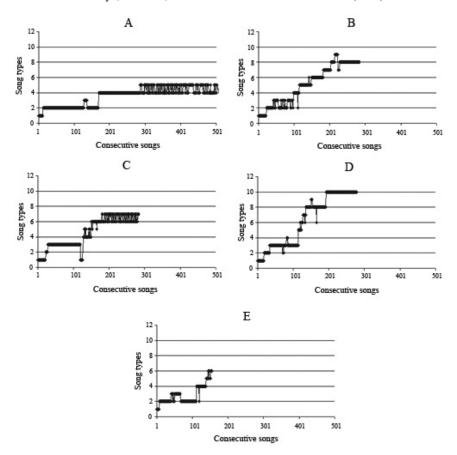


Figure 6. Shape of a 'repertoire curve'. Capitals (A, B,... E) refer to the birds. This type of data distribution is used as a tool to test whether a given repertoire is complete (criterion: further songs do not bring new song types). Here, however, the distribution serves to illustrate the rules encoded in a process of song performance: This application has been suggested by Todt and Hultsch, 1996).

accomplishment; i.e. birds switched between types of motifs. This was not at random but accumulated only between successions of a few selected types of motifs (Figure 6, bird A, B and C).

Discussion

Our study revealed that Oriental Magpie Robins resemble some song performance rules of other thrushes, and such concern especially the time domain. However, some interesting idiosyncrasy was found as well. Such was true, for instance, for the robins' singing style and their treatment of motifs within and also across songs. In addition, it was remarkable that neighbours did not share parts of their repertoires. These findings invite a brief discussion of two aspects; namely the use of 'song as an interactive tool' and the role of 'learning as an origin of pattern similarity'.

Interaction by song

Interaction by song is an essential part of communication (Marler Slabbelkoorn, 2004). From a formal perspective interactions are distinguished, for instance, in terms of relationships that exchanged signals show in the time and the pattern domain (Hultsch and Todt, 1982; Wolffgramm and Todt, 1982). From a functional perspective, in contrast, interactions are specified in terms of social relationships among signallers and distinguish, for instance, behaviours between partners, such as mates, or behaviours between rivals, such as territorial neighbours. Mated birds often interact via elaborated vocal duets (Todt and Fiebelkorn, 1979; Todt et al. 1981; Farabaugh, 1982) whereas rivals typically engage in forms of counter-singing, i.e. vocal duets (Todt, 1970a, b; Kroodsma, 1979: Falls et al. 1982: Kramer and Lemon.

During auditory exposure to a singing conspecific, territorial birds may modify the patterning of their song performance. Such modification can affect different hierarchy levels of song organisation, and at the same time also reflect a tonic or a phasic response. In a tonic response, a bird alters the quality of his singing gradually over an extended span of time, for instance by increasing the volume or duration of his

songs. In a phasic response, in contrast, a bird selects a particular song type of his own repertoire and vocalises this song as a reply to a stimulus song. Examples of this form of responding are song matching and cases of coordinated switches between bouts of songs. Song matching is quite common across species (Lemon, 1968; Smith and Reid. 1979: Falls et al. 1982: 1988: Beecher et al.1996), and is particular impressive in songsters who, such as Eurasian Blackbirds (Todt, 1970a; 1975; 1981) or Nightingales (Todt, 1970b; 1971a; Hultsch, 1980), have large song repertoires and sing with an immediate versatility (e.g. A-B-C-D-..). Coordinated song type switching, in contrast, is found in species that repeat renditions of a particular song type several times before starting to sing another one (e.g. A-A-A-B-...), like e. g. Abessinian Ground Thrushes (Todt, 1971b), Great Tits (Falls et al., 1982, Mc Gregor et al. 1992), Western Meadowlarks (Falls and d'Agincourt, 1982; Horn and Falls 1988) and Song Sparrows (Kramer and Lemon, 1983, Kramer et al.1985; Nielsen and Vehrencamp, 1995).

Pattern specific responses depend on species typical properties, but they also build on prerequisites in the vocal repertoires of the individuals involved. This dependence is particularly evident in song matching. Per definition, song matching (synonymous term: 'equivalent response') states that a song X is responded to by a song with an equivalent pattern X'. Thus matching can take place only between individuals who share song-types in their vocal repertoires.

Given the remarkable differences that species in various domains of their singing it is not surprising that several hypotheses have been proposed to explain the

proximate functions of pattern specific responses in vocal interactions (Todt, 1971a; 1975; 1981; Kroodsma, 1979; Falls et al. 1982; Krebs et al. 1978, Kramer and Lemon, 1983; Hultsch and Todt, 1986). For vocal matching, which to date is the most extensively studied response category, such hypotheses range from very straightforward ones, like 'addressing an opponent' (Todt, 1975) or 'sending a keep-out signal' (Falls, 1985; Shackleton and Ratcliffe, 1994), to more controversial ones like 'distance estimation' (Falls et al. 1982: Morton, 1982: Naguib, 1997) or 'attracting the attention of a third party', like females or other males (Todt, 1981).

The basic 'addressing' account of vocal matching is a candidate mechanism to deal with the general problem of signalling to a particular male in a community of songsters. The interesting issue is that a more specific message of the signal can be encoded in its timing, as has been shown in Nightingales and Eurasian Blackbirds (Wolffgramm and Todt, 1982; Hultsch and Todt, 1986). These species use song matching in two temporally different forms. In the rapid matching, a song-type A is responded to by A' quickly after its onset. Thus the matcher overlaps the other male's song. In the delayed matching, in contrast, the matcher waits until the other bird has ended his rendition of A, thus inserting the response into the intersong interval of that male. The message to infer from rapid matching is similar to that one described for temporal overlapping, a vocal threat. Rapid matching dominates at the beginning of the singing season when songsters set up territories, i.e. mainly during highly agonistic interactions. In contrast, delayed matching can be found particularly when territories are established and when other song features of neighbours indicate that they sing in a somehow relaxed way. This response, therefore, was interpreted as a vocal 'greeting ritual' (Todt, 1974, 1981).

To recall, our study has shown that neighbouring magpie robins did not share parts of their repertoires, and thus can not engage in vocal matching. On the other hand, the birds shared a few singing properties (e.g. small repertoire, repetitive performance style) with species such as great tits (Falls et al. 1982; Mc Gregor et al. 1992), and song sparrows (Kramer and Lemon 1983; Kramer et al. 1985; Nielsen and Vehrencamp, 1995). Therefore, we expect that our robins could use the same kind of vocal interaction as these species communicate for example, 'coordinated song type switching' (Todt and Naguib, 2000). It would be interesting now to examine whether and when this expectation may be confirmed by novel field studies in Nepal.

Learning as an origin of repertoire sharing

Birdsong is a learned behaviour (reviews in Catchpole and Slater, 1995; Kroodsma and Miller, 1996; Hultsch and Todt, 2004). In conjunction with the evolution of song as a culturally transmitted behaviour, birds have developed a system of adaptations which ensure the biologically adequate use of song as a signal system. Among them are phenomena like age-bound auditory learning (sensitive phases), a preference for the species-typical song pattern (signal selectivity), and a preference to acquire song from a socially significant individual (social selectivity). Large differences among species exist among species in the extent to which these mechanisms become effective during the perceptual phase of song acquisition, and constraints seems to be tightly related to the particular ecology of a given species or even population (for reviews see: Kroodsma and Miller, 1982; Slater, 1989; Marler, 1987, 1991; Baptista, 1996; Beecher 1996; Kroodsma 1996).

Song learning is a kind vocal imitation. It begins with a memorization of auditory stimuli, usually conspecific song patterns, and continues with a development of vocalisations which – aside a few exceptions – match the pattern of the perceived originals (Marler 1987; 1991). The mechanisms underlying these accomplishments are currently a hotspot of memory research. Thus, there is a huge amount of knowledge about how birds achieve a sharing of their signal repertoires Marler, 1987, 1991; Baptista 1996; Beecher 1996; Kroodsma 1996).

In philopatric bird species the percentage of song sharing decreases with an increasing distance between songsters. With this as a reference, our finding that neighbours did not show any pattern sharing is quite notable and call for an explanation. Currently, however, we don't have sufficient data and thus can offer the following 'working-hypotheses'. Hypothesis I: It postulates that Oriental Magpie Robins are not philopatric but leaves their native areas and invade into other suitable habitats. The advantage of this dispersal is a reduced risk of inbreeding. As there is already evidence that they are able to learn and imitate some avian vocalizations, we would like to examine the cited hypothesis by follow-up studies on the dispersal pattern of these thrushes. In addition it would be interesting to expose the territorial males to playbacks of their own song and thereby to explore whether they are able to immediately match the perceived patterns. In other words, there are a number of open questions to be studied in this most interesting member of the thrush family.

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