journal of interdisciplinary music studies
spring 2012, volume 6, issue 1, art. #12060103, pp. 55-85

O Canto do Uirapuru: Consonant intervals and patterns in the song of the musician wren

Emily Doolittle[1] and Henrik Brumm[2]

[1] Music Department, Cornish College of the Arts
[2] Communication and Social Behaviour Group, Max Planck Institute for Ornithology

Background in music theory, ethnomusicology, and zoomusicology. People have long recognized a similarity between bird and other animal songs and human music. Bird and animal imitations are used in music from around the world, and cultures as diverse as the Luiseño people of California, the Tuvans, and the ancient Chinese have credited animals with the origin of music. This paper takes as a starting point the zoomusicological premise that some animal songs are sufficiently similar to human music that techniques originally developed for the analysis of human music can be usefully and instructively applied to them. The song of the musician wren (*Cyphorhinus arada*), famed both in its native Amazon rainforest and abroad for its apparent musicality, consists primarily of timbrally pure, sustained notes, and is thus a perfect candidate for intervallic and motivic analyses similar to those typically performed on human melodic music. We discovered that the musician wrens preferentially used perfect consonant intervals (those based on the simplest ratios of 1:2, 2:3, and 3:4), which are also the intervals most likely to be considered consonant (or stable or restful) in diverse human musical cultures, including western classical music, Indian music, Chinese music, and the music of the ancient Greeks. As well, some musician wren songs have repeated patterns of contour and duration which appear to be used similarly to motifs in human music.
Background in biology. Scientific investigations of birdsong typically focus on its production or function rather than on the construction of the song. However, the tools of bioacoustic analysis, such as the use of sound spectrograms to represent the songs and statistical methods to interpret findings, can equally well be applied to an analysis focusing on pitch selection, structure, and other "musical" aspects of the song. An analysis which incorporates these scientific methods may offer greater reliability and accuracy than one based on subjective musical methods alone.
Aims. This paper shows how musicians and biologists working together can gain a deeper understanding of an animal song than people working in either discipline alone. We seek to understand the song of one particular bird, the musician wren, while also suggesting a method for future interdisciplinary study of other bird and animal songs.
Main contribution. Through combined music theoretical, bioacoustic, and statistical analysis, we show some striking similarities in interval selection and structure between musician wren song and some human music, suggesting why this bird's song is so widely considered "musical". In particular, we show that this species favors consonant over dissonant intervals, and perfect consonances over imperfect consonances, leading to some passages which may sound to human listeners as if they are structured around a tonal center. As far as we know, this is the first study to show a performance preference for successive perfect consonances (octaves, fifths and fourths) in a non-human animal. Using a sound perception experiment we were able to confirm that musician wrens' interval usage is indeed what makes their songs sound musical to human listeners. Though we cannot generalize from our findings to the songs of other "musical" sounding bird species, the interdisciplinary method developed in this paper could equally well be applied to the analysis of other species' songs.
Implications. Even though both musicians and biologists are interested in birdsong, they tend to focus on very different aspects of the song. Combining tools of musical and biological analysis leads to deeper understanding of the song and more accurate interpretation of the results.

Keywords: music theory, music analysis, ethnomusicology, zoomusicology, birdsong, bioacoustics, ornithology, musician wren

• *Correspondence*: Emily Doolittle, Music Department, Cornish College of the Arts, 1000 Lenora St., Seattle, WA, 98112; tel: +1 206 777 5212, e-mail: edoolittle@cornish.edu
• *Received:* 22 August 2012; *Revised:* 20 September 2013; *Accepted:* 23 September 2013
• *Available online:* 15 October 2013
• doi: 10.4407/jims.2013.10.003

Introduction

As far back as oral or written records can tell us, people from all over the world have been fascinated by the calls and songs of birds. The Sultantepe tablets, which date back more than 2600 years, are one of the oldest sources to tell of this fascination. In these cuneiform scripts, each bird is connected with a Babylonian god, and the bird's songs are transliterated into phrases that both describe the song and tell of events in Babylonian mythology (Lambert, 1970). Today, bird songs continue to intrigue musicians and scientists alike. They figure prominently in music of many genres and from many cultures (Doolittle, 2008; Brumm, 2012). In science, bird song is an important model for the study of animal behaviour, and is investigated by biologists from many different fields, such as neurobiology, behavioral ecology, and evolution (Slater, 2003).

The invention of the sound spectrograph immediately after the Second World War launched the scientific study of bird song as we know it today. Before this time naturalists, like the writers of the Sultantepe tablets, used onomatopoeic descriptions to record birdsongs, or they used music notation. In either case, they relied entirely on their ears, and thus on the subjectivity of their hearing. Nowadays, biologists employ computer-based acoustic sound analysis tools, which allow a more objective, in-depth analysis of the physical properties of the sounds. The scientific study of the complexity of birdsong is grounded in evolutionary theory, which explains how sexual and environmental selection shapes the structure and performance of songs (Searcy and Anderson, 1986; Gil and Gahr, 2002; Brumm and Naguib, 2009). A substantial body of research suggests that the two main functions of bird song are attracting a mate and defending a territory, and that these evolutionary pressures are what led to the stunning diversity that can be observed in the songs of different bird species throughout the world (Catchpole and Slater, 2008).

Birds have caught the interest of not only biologists and composers but also of music scholars, who study bird songs within an ethnomusicological or music theoretical framework (Martinelli, 2002, 2009; Taylor and Lestel, 2011). François-Bernard Mâche (1992), Dario Martinelli, and Hollis Taylor are three scholars who have been active in developing the recently established field of Zoomusicology, which aims to explore the "aesthetic use of sound communication among animals", while Patricia Gray (2001) and others explore similar topics under the more broadly defined field of "biomusic". However, the study of the aesthetic content of bird song predates any formal recognition of these disciplines, and there is a long line of authors who have appreciated bird song as music and described it as such. In the late 19th and early to mid 20th centuries, many naturalists and ornithologists considered bird song to have musical form. Among these were the German naturalists J. Oppel (1871), Bernhard Hoffmann (1908), and Jakob Graf (1962), the American naturalist and composer F. Schuyler Mathews (1906), ornithologist Wallace Craig (1943), and philosopher and amateur ornithologist Charles Hartshorne (1973), and British naturalist and musician Len (Gwendolen) Howard (1953). This view of birdsong as music was shared by the German composer Heinz Tiessen (1887-1971), as well as the better known French composer Olivier Messiaen (1908-1992).

To compare bird songs to human music, today's musicologists sometimes set them in staff notation, just as composers Tiessen and Messiaen, and the early naturalists did when listening to birds in the wild. In a second step, the notated bird song may be screened for elements that are commonly used in human music (Taylor, 2008). While this is useful for making comparisons with human music, musical transcriptions are not as informative as spectrograms from a modern scientific point of view (Dobson and Lemon, 1977; Marler, 2004). First, while standard musical notation deals primarily with discrete units of pitch and rhythm, spectrograms can depict all the physical characteristics of a sound, including timbre, amplitude, minute fluctuations of frequency, and complex, aperiodical rhythms. Second, Fast Fourier Transformations (on which spectrograms are based) are an objective quantification of the sound parameters, essential for valid scientific measurements. Finally, as Dobson and Lemon (1977) point out, using musical notation may lead one to overestimate the musical nature of bird song, because the song will need to be forced into the rhythms and pitches that can be notated this way. On the other hand, musical notation is more helpful than a spectrogram if one wishes to make an approximate reproduction of the pitch and rhythmic aspects of the song in the imagination or on instruments, to make immediately apparent the relationships between the song and human musical ideas, or to record how the song sounds to a particular human listener.

Both the scientific and the musicological approaches to bird song are thus informative in different ways, and we believe that the two combined can provide a more complete picture, in particular of how bird songs are perceived by humans. We are not the first to combine approaches. Hungarian musico-ornithologist Peter Szöke first wrote of combining musical notation and spectrograms as far back as 1969 (Szöke et al., 1969). British ornithologist Joan Hall-Craggs (1979), too, sought to create more informative means of representing bird songs by superimposing a musical staff on a logarithmic spectrogram. While both authors suggest useful ways of making bird song notation more informative, neither of their approaches goes much beyond simple representation of the sounds. With the modern tools of bioacoustics at hand, objective measurements of spectral and temporal parameters of bird song can be added to musical transcriptions and spectrograms. One can then use statistics as well as music theoretical and ethnomusicological approaches in analyzing the song. This integrated quantitative approach enables us to validate statistically whether the patterns we observe are significant – rather than the outcome of chance use of certain musical elements by some birds, or indeed the bias identified by Dobson and Lemon (1977)

In this paper, we examine the song of the musician wren (*Cyphorhinus arada*), also known as the organ wren, quadrille wren or, in its native South America, the uirapuru. We chose the musician wren because, as its name suggests, its song is regarded by human listeners as particularly beautiful or musical, and thus is well suited for such an interdisciplinary music-science study. The analysis of the song structure in terms of both statistical and music theoretical concepts in combination with sound perception experiments may help answer some of the questions about why humans find the musician wren's song so exceptionally musical. To this we also add an anthropological study of human representations of musician wren song in a variety of cultural contexts, to get a fuller picture of how the song functions in its environment, both natural and human.

We thus begin by investigating how uirapuru song is reflected in South American fables and folklore. Then we examine how composers, both South American and Western, use musician wren song in their pieces, and how their usage relates both to the sound of the song and to the perception of the bird. In the second part of this paper, we look into the natural history of the species. Finally, we report the results of an acoustic analysis of its song that was conducted using a combination of music theoretical, statistical, and computer-based bioacoustic methods.

Because musician wren song consists primarily of a linear succession of single pitches, our analysis focuses primarily on the analysis of melodic intervals, the frequency ratios between successive pitches. The use of intervals in bird song has already been considered more than a century ago by Bernhard Hoffmann, in his seminal book *Kunst und Vogelgesang in ihren wechselseitigen Beziehungen von naturwissenschaftlich-musikalischen Standpunkte beleuchtet* (*The interrelationships of art and bird song viewed from a scientific-musical perspective*) (1908). Hoffmann used examples from more than two dozen bird species to illustrate parallels between bird song and (Western) music. He reports that several individuals of common blackbirds (*Turdus merula*) and song thrushes (*Turdus philomelos*), for example, used intervals in their song repertoire that produced an astonishingly musical effect. Similarly, it might be that it is the use of particular intervals that makes the songs of musician wrens so exceptionally musical to a human listener. To test this idea, we ran an experiment in which human listeners were asked to compare the musicality of a melody that used pitches and durations taken from a musician wren song with a melody in which the contours and rhythms remained the same, but the intervals between successive notes were slightly altered. To corroborate our conclusions about what makes the uirapuru song so captivating, we also compare the structure of musician wren songs to those of its closest relatives, the chestnut-breasted wren (*Cyphorhinus thoracicus*) and the song wren (*Cyphorhinus phaeocephalus*).

Uirapuru

The musician wren is a small brown wren native to the Amazon Rainforest of Brazil, and the surrounding countries Guyana, Suriname, French Guiana, Bolivia, Peru, Ecuador, Colombia and Venezuela. At once a real bird and a mythological character, the uirapuru is an important subject of legend for the Tupi, Guarani and other indigenous people with which it shares territory. The bird is known especially for its beautiful song, and this figures prominently in a number of stories. One legend tells of a young Guarani warrior who fell in love with the wife of the chief of his tribe. The god Tupä turned him into a uirapuru so he might be able to sing to the woman he loved. However, the chief noticed the bird singing and tried to capture it. The uirapuru flew into the forest, and the chief became lost. The bird was then free to return to sing for the woman, hoping that one day she would notice him and reverse the spell (Lendas e Contos, accessed 2012). In another version of the legend, two women fell in love with the chief. He agreed to marry whoever of them was the better hunter. Both drew their bows, but only one hit her mark, and thus was able to marry the chief. The other cried so much that her tears became a stream. Tupä turned her into a bird so she could visit the chief. When she did, she saw that he truly loved the other woman, so she flew far away to the Amazon. Tupä gave her a beautiful song, so she might be able to sing to forget her sorrow (Fermino, 1969). According to some legends, the song is so beautiful that when the uirapuru sings, all the other animals fall silent (Cruls, 1976, 180). According to others, all the birds of the forest flock around to listen to it sing (da Câmara Cascudo, 1962: 757). Some believe that one only hears the uirapuru sing at the moment of death, while others hold that hearing the bird sing ensures successful hunting, or brings good luck for life.

Certain aspects of uirapuru folklore are unfortunate for the actual *Cyphorhinus arada*, such as the belief that killing the bird will bring love, or that possessing feathers, a piece of the nest (http://www.scribd.com/doc/34084142/Canto-Do-Uirapuru), or even a stuffed uirapuru will bring happiness and fortune (da Câmara Cascudo, 1962). It is common for storekeepers and tavern owners in and around the Amazon to bury a uirapuru at their door to attract customers. Because of the widespread popularity of the belief in a stuffed uirapuru as a luck charm, there is an extensive trade in dead uirapurus. Many other species are sold as uirapurus too, though it is said that these false uirapurus do not bring luck (da Câmara Cascudo, 1962). This leads to some popular confusion as to the appearance of the uirapuru, with many preferring to attribute the beautiful song to a more colorful bird than the plain, brown *Cyphorhinus arada*. In different regions, the word "uirapuru" has been applied to at least 17 species of birds, mostly of the Troglodytidae, Vireonidae, and Pipridae families (Cruls, 1976). In some cases, it seems that the different birds called uirapuru embody different aspects of the mythical uirapuru. Children of the Corbeua tribe, for example, were given the brains of both the *Cyphorhinus arada* and of a more colorful bird also known as "uirapuru" to eat, so they would learn to speak quickly and well, and be physically beautiful (Cruls, 1976). *Cyphorhinus arada* is sometimes known as uirapuru-verdadeiro, "true uirapuru", to distinguish it from the others.

Dramatizations of the uirapuru stories are commonly performed throughout the countries in which the musician wren lives, in the form of plays, puppet shows, short films, and musical compositions. One well-known musical retelling is Brazilian composer Heitor Villa-Lobos's 1917 symphonic poem *Uirapuru*, first performed as a ballet with choreography by Serge Lifar in 1935. Villa-Lobos's *Uirapuru* tells yet another variant of the uirapuru legend. According to Villa-Lobos:

> [the Uirapuru's] nightly song lured the Indians into the woods in search of the enchanting singer. In such a search, a merry group of young natives comes upon an ancient and ugly Indian seated in the forest playing upon his nose-flute. Resenting the invasion of their forest by this unsightly old man, the natives beat him mercilessly and drive him out. The continued search for the elusive Uirapurú by the natives is witnessed by all the members of the nocturnal animal and insect kingdoms — glow worms — crickets — owls — enchanted toads and bats — and crawling things.
>
> A beautiful maiden appears — also lured by the sweet song of Uirapurú. Armed with bow and arrow, she catches up with the Enchanted Bird, piercing its heart, whereupon the singing Bird is immediately transformed into a handsome youth. The Happy Huntress, who has thoroughly captivated the handsome youth, is about to leave the forest followed by the amazed natives when they are halted by the shrill, unpleasant notes of a distant nose-flute. Suspecting the arrival of the ugly Indian seeking revenge for the merciless beating they had administered, the natives hide in the dense woods.

> The unsuspecting youth boldly confronts the ugly Indian, who slays him with a perfectly placed arrow. As the Indian maidens tenderly carry the body to a nearby fountain, it is suddenly transformed into a beautiful Bird which flies, its sweet song diminishing, into the silence of the forest (Villa-Lobos, 1917).

Villa-Lobos was strongly influenced by the music as well as the stories of the Amazonian peoples. In addition to drawing inspiration from the rhythms and motives of the music of Amazonian tribes, he imitates the timbres of their music, as in his use of a violinophone (horn-violin) to imitate the nose-flute played by the old "Indian" in the story (Wright, 1992, 171). He captures the natural sounds of the Amazonian forest with percussion and fast woodwind passages which imitate the rustling of the "glow worms, crickets, owls, [and] enchanted toads and bats" of the forest, and flute in symbolic imitation of the uirapuru, even if it sounds little like the actual bird. Villa Lobos's younger contemporary, Camargo Guarnieri, named his Symphony #2 *Uirapuru* (1945), in homage to Villa Lobos' *Uirapuru* rather than to the bird itself.

Some South American composers were influenced by the legend but not by the actual sound of the uirapuru. Waldemar Henrique's song *Uirapuru* (1934), for example, makes reference to uirapuru mythology, but not to the song. For others, the musician wren plays a similar role that the nightingale does for composers in Europe. Both birds may be used in music as a symbol of beauty, love and courage, with the actual sound of their song of secondary importance to its symbolic meaning. For South American and European composers, beautiful songs are sometimes attributed to the uirapuru or the Nightingale respectively, whether or not the songs bear any resemblance to those of the bird in question. For example, the fourth movement of Brazilian Percussionist and composer Ney Rosauro's *Mitos Brasilieros*, tells of "Uirapuru: The wonder of the forests and protector of the birds. When it sings, all birds, animals and humans are magically attracted by the beauty of its melody" (Rosauro). This piece includes the prominent use of a birdcall (instrument), but the birdcall used sounds nothing like an actual uirapuru.

Just as many Brazilian musicians, however, have been primarily inspired by the song itself. Hermeto Pascoal's *Quando As Aves Se Encontram, Nasce O Som*, for example, begins with a recording of a musician wren singing alone, followed by several looped passages of the musician wren's song supported rhythmically and harmonically with chordal keyboard accompaniment. Albery de Albuquerque's album *Amazônia Verde Fauna* contains six songs which highlight musician wren song, *Uirapuru Verdadeiro*, *Uirapuru Da Alvorada*, *Uirapurus, Uirapuruzinho, Uirapuru Dos Bosques*, and *O Uirapuru e Vialao*, as well as a number in which the song plays a lesser role. In many of these songs, like in the Pascoal, the pieces begin with a field recording of the musician wren, often with other birds and rainforest sounds in the background. This is typically joined by a guitar, which picks up on and develops the rhythms introduced by the bird. The musician wren song may later be musically developed or altered, as in *O Uirapuru e Vialao*, where the piece ends with an electronically filtered version of the musician wren song, which blends with delicate guitar harmonics. In *A Danca del Uirapuru* on the album *Boa Fonte - Caminho Para O Amazonas* by the Conversa duo, the musician wren song functions as an independent instrumental layer, cyclically intersecting with the other instruments.

In Villa-Lobos' *Uirapuru*, the musician wren song provides musical inspiration, but is so changed in the instrumental rendering that it is not immediately recognizable, even to those familiar with the song. In the pieces by Pascoal, Albuquerque, and the Conversa duo, however, the musician wren song takes on a more significant musical role, appearing both in recorded form and as a source of rhythmic, melodic, or harmonic ideas. These musician wren-derived motives may be developed by the instruments, but are treated as musically valid ideas in themselves rather than as something which can only be considered musical when transformed by human musicians. These pieces would sound significantly different if they were inspired by a different species, or even by a different individual musician wren.

Eduardo Kac, an artist born in Rio de Janeiro and now living in Chicago, most famous for his transgenic bio-art such as Alba, the fluorescent green rabbit, has created a less literal, more personal interpretation of the uirapuru legend. Kac's *Uirapuru* (1996/99) is multimedia installation in which the bird is reimagined as a flying fish that hovers above a forest in an art gallery, "singing and giving good fortune to forest inhabitants" (Kac). Kac was drawn to the uirapuru as "a symbol of rarefied beauty", and to its "dual status as real and legendary". The movement of Kac's flying fish uirapuru can be controlled both locally and virtually, and its movement increases the song behaviour of another of Kac's creations for the installation, the "pingbirds", "fantastic creatures whose melody, derived from the songs of various Amazonian birds, oscillates according to the rhythm of global network traffic." While Kac's *Uirapuru* represents a departure from the story of uirapuru as a bird, in some ways it may provide an experience that feels closer to being in forest with a uirapuru than the more literal realizations. The visitors to Kac's *Uirapuru* are both affected by and affect the behaviour of the uirapuru and the sounds of the forest in which they are immersed.

For those living in or near the Amazon region, the musician wren has always been a part of the sonic environment, but for those from outside of South America, encounters with the bird and its song have only happened within the past two centuries. Botanist Richard Spruce, who spent 15 years exploring the Amazon and Andes, from 1849 to 1865, is reported to be the first non-South-American to become familiar with the song of the musician wren. He was enchanted by its "clear, bell-like tones, as accurately modulated as those of a musical instrument" (Spruce, 1908), and he made a brief musical transcription of the song. Spruce wrote that "Simple as this music was, its coming from an unseen musician in the depths of that wild wood gave it a weird-like character, and it held me spellbound for near an hour."

A number of European and North American musicians encountering the song have been equally spellbound. Olivier Messiaen, strongly influenced both musically and spiritually by birdsong, used a musician wren in the third movement of his wind and percussion piece *Et Exspecto Resurrectionem Mortuorum* (1964), *L'heure vient où les morts entendront la voix du Fils de Dieu* ("The hour is coming, and now is, when the dead shall hear the voice of the Son of God.") Messiaen describes the uirapuru's song as "mysterious, fluted with a magic timbre. It surprises and bewitches the listener with the disjointed melodic jumps, color changes, and dynamic contrasts" (Mostel, 1988). He imitates the song in an angular, richly harmonized passage in the woodwinds, though perhaps in a form unrecognizable to those unused to his compositional voice. Just as important for Messiaen as the sound of the birdsong is the relationship between the symbolism of the uirapuru and his own Catholic mysticism. Here Messiaen connects the legend that one only hears the uirapuru sing at the moment of death with the belief that Christ's voice will wake the dead from sleep (Johnson, 1989, 171). According to Messiaen, "This voice is the symbol of the signal of resurrection: divine order, executed immediately… Here it is symbolized… [in] the song of the uirapuru..." (Mostel, 1988).

French acousmatic composer François Bayle's 1971 work *La preuve par le sens III: 10. Uirapuru*, part of his cycle *L'Experience Acoustique*, focuses more on the sound of the uirapuru than on its legend, using a recording of the musician wren song essentially as a "found object", accompanying it with sustained, pulsing electronically generated sounds. Bayle states he was attracted to the song partially because of its "caractère très intentionné, savamment organisé" (very intentional, wisely organized character) (Bayle, personal correspondence, Nov. 2, 2011). In 1972 Bayle reused this piece as part of his composition *Trois Rêves d'Oiseau*, written to accompany a choreography by Vittorio Biaggi. In the program notes for this work, he does refer to Brazilian folklore that the song announces a peaceful death.

American Jazz saxophonist and composer Paul Winter's *Uirapuru do Amazonas* builds on Brazilian musician Gaudencio Thiago de Mello and Daniel Wolffs' piece of the same name. While the original has no apparent musical influence from musician wren song, Paul Winter adds to his version a recording of the musician wren, along with other sounds which may suggest the Amazon Rainforest, such as a rainstick, shakers, and plaintive lute calls. Here the musician wren song serves primarily an evocative purpose, and the actual characteristics of the song are less important.

Australian/American composer Warren Burt uses the uirapuru as one of six bird voices in *The Bird is the Word* (2011), along with another Brazilian bird, the red-billed toucan, the Antarctic emperor penguin, and three Australian birds, the tawny frogmouth, Australian magpie, and rainbow lorikeet. (To these he adds the deeper voice of a synthesized, imagined dinosaur call, recorded at the Chicago Field Museum). All the bird songs are subject to a variety of electronic processes, but in some parts they remain recognizable. Burt's piece for 31-tone microtonal organ, invented by Dutch theorist and composer Adriaan Fokker in 1950, *Fokker Organ Wren* (2011), is based on DNA patterns of the uirapuru, rather than on the bird's song.

Dutch/Slovenian composer and artist Tao G. Vrhovec Sambolec's *A Tree is Dreaming of Uirapuru* creates an immersive experience for the listener, more reminiscent of Kac's multimedia installation than of the purely musical realizations. Inspired by both the legendary and actual beauty of the musician wren's song, Sambolec hung several sound modules, each consisting of a solar cell and a small cassette player, on the branches of a tree. As Sambolec describes it, "Each sound module plays back different fragments of uirapuru song, preceded and followed by silence. If all the sound modules would start at the same time, then one could hear the whole uirapuru song in its originality. The speed and loudness of playback are dependant on the voltage coming in from the solar cell (http://www.taogvs.org/UirapuruMain.html)." Only when the sun is in the right position will all the disembodied song parts be sounded together, so the complete musician wren song can be heard.

Cyphorhinus arada

Despite the attention paid by musicians and artists to both the legend and the song of the musician wren, the bird has until now largely been ignored by scientists. Almost no literature exists, beyond basic descriptions of appearance, behavior and habitat in various guides to birds of South America. The *Cyphorhinus arada* is small – about 12.5 cm long, and 18-24 grams – and brownish, with white markings depending on subspecies (Elliott et al, 2005). It spends most of its time foraging on the ground, but is wary and furtive, making it difficult to observe (Ridgley et al., 1989). Musician wrens raise their young one or two at a time in spherical nests which are made of leaves and grass, lined on the inside with feathers. These may be used as dormitories outside of breeding season (Buzzetti and Silva, 2005). The bird is briefly mentioned in a study of the "Social and Sleeping Habits of Central American Wrens" (Skutch, 1940), and a hybrid music staff-spectrogram of its song appears in the 1979 paper by Joan Hall-Craggs, but beyond this it seldom appears in the literature. Clearly much observational work remains to be done.

Beside widespread recognition of the beauty of musician wren song, almost nothing has been written either about singing behaviour or about the structure of the song itself. For example, little is known about the extent to which females sing, or whether the species sings duets (Hilty and De Schauensee, 2003; Buzzetti and Silva, 2005). Given the widespread use of female song and duetting in other tropical wrens, both seem a possibility. Also unknown is whether adjacent birds share song-types, or to what extent regional dialects may determine features of the song. While these are great areas for further study, the recordings available are already sufficient to begin understanding the way members of the species constructs their songs.[i]

Pitch and pattern in musician wren songs

We listened to recordings of about 50 musician wrens, made available courtesy of Jacques Vielliard, Karl Martius and the Xeno-Canto database.[ii] From these we chose 20 in which the musician wren song was clearly distinguishable from background sounds, and in which the bird seemed to be singing complete song-types (stereotyped sequences of elements, recognizable as song-types through repetition). The songs are notable for using primarily tonal, nearly pure-tone "notes", without much frequency modulation (Figs. 1 and 2). These notes sound much like human whistling, and show a similar result on a spectrogram, with a strong fundamental and much weaker or no harmonics. In 51% of the analyzed notes no harmonic partials could be detected. In the remaining notes only the first or the first and the second harmonic could be identified (the loudest harmonic was on average 39 dB below the peak amplitude of the fundamental frequency [range: -27 – -56 dB]). In addition to the notes, musician wrens use other types of sounds as well, including multi-band noises, clucks, knocks, hoots, purrs, trills and slides (collectively referred to as "noises"). The noises most often appeared as short series at the beginning of the song, or individually or in clusters of two or three between notes. However, discrete, measurable notes made up 57% to 90% of the elements of each song-type, and it is the analysis of these with which we are primarily concerned.

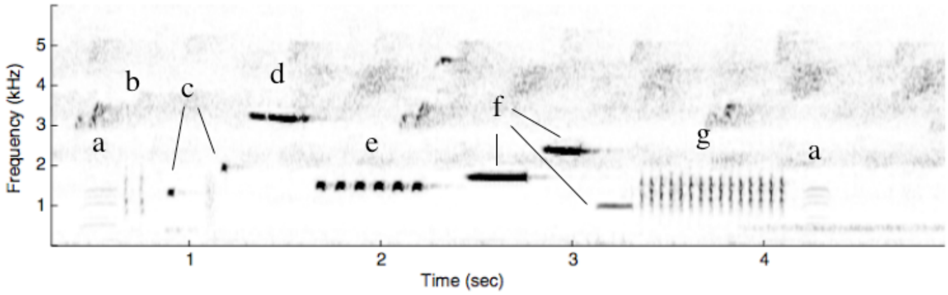


Figure 1. Some typical elements of a musician wren song: a) multi-band noise; b) knocks; c) short note; d) repeated long note (with a slight, downward frequency modulation); e) pulsed note; f) long note; g) ratchet.

The large difference in amplitude between the fundamental and the nearest harmonics, where they were present, suggests that the harmonics are unlikely to play a role in the perception of pitch or intervals for this species. Audiograms for musician wrens are not available, but auditory thresholds for other species of songbirds (Dooling et al., 2000) suggest that it is very unlikely that birds can hear such faint harmonics. This is especially likely to be true for the musician wren, because it is a rainforest bird and frequency-dependent sound attenuation in forests means that high frequencies are heavily attenuated by the environment (Brumm and Naguib, 2009). It thus seemed appropriate to limit our analysis of frequencies to the fundamental of each note.

On the basis of recordings available, it appears that each musician wren sings one to three song-types. It is possible that more extended recordings, or recordings of the same bird made at different times, would reveal more song-types. Song-types are repeated with little change, though they may sometimes be shortened from either end. Occasionally the last two or three elements are varied or, less often, a part of the song is repeated. Comparison of three renditions of the same song-type in bird MW1, for example, shows identical ordering of element types for the first 26 elements of each song, with variations only in the final one to three notes (Fig. 2). Corresponding tonal elements between the three versions of the song showed no more than 2% variation in the frequencies of the note elements.

By contrast, different song-types within a single bird are clearly distinguishable from each other, though may occasionally share some features (Fig. 3).

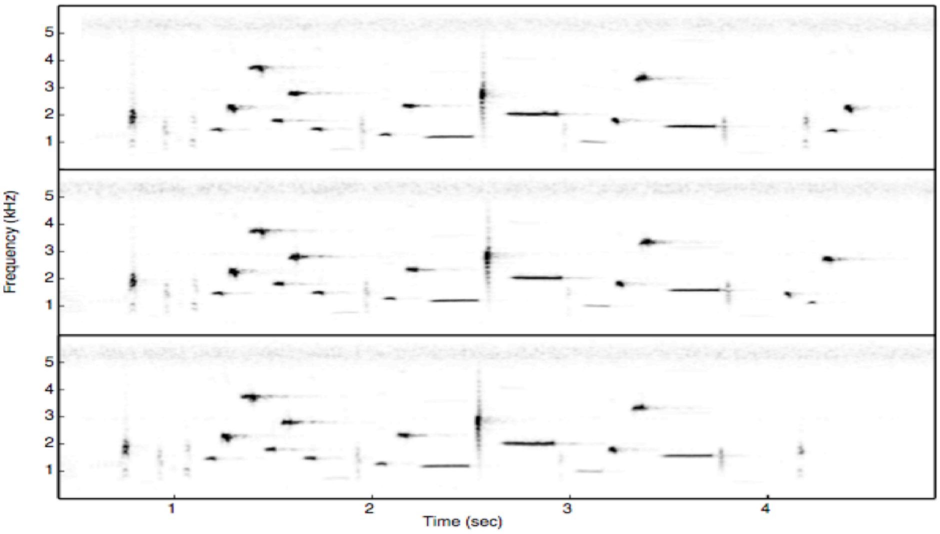


Figure 2. Three examples of the same song-type from bird MW1

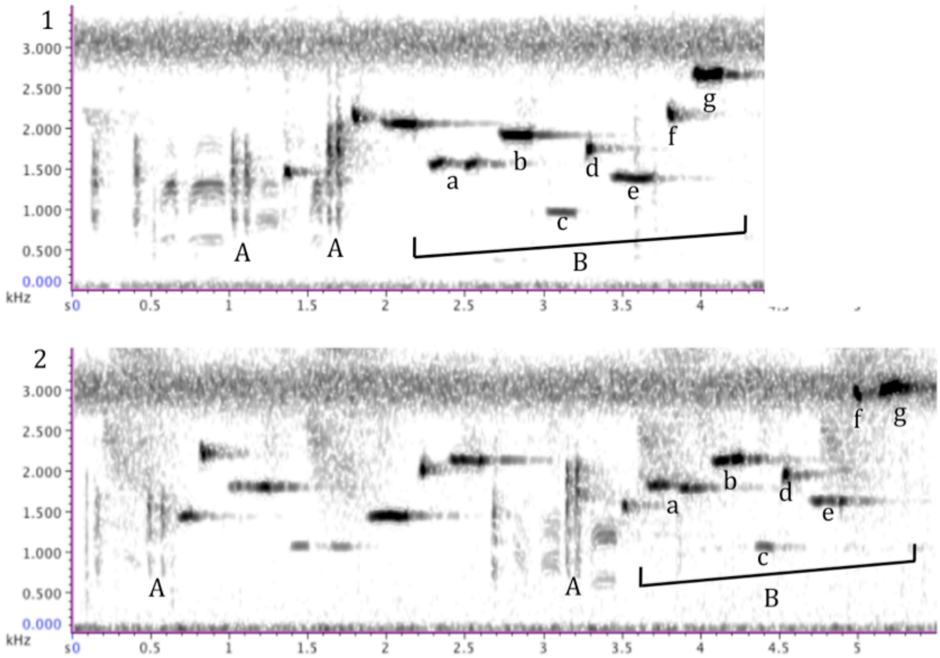


Figure 3. These two song-types, 1 and 2, from bird MW19, are clearly distinguished from each other in terms of duration, ordering of element types, and frequencies. Some features are nonetheless similar, such as the double knocking figure (labeled "A"), and the rhythmic and contoural "motive" labeled "B". The elements of B are as follows. a) short repeated note; b) longer, higher note; c) lower shorter/same length note; d) higher short note; e) lower long note; f) higher short note; g) higher longer note.

Our recordings indicate that musician wrens sing with eventual variety, that is, they typically repeat each song-type several times before switching to another song-type. Some birds repeated a song-type up to 10 times before switching, though considerably longer recordings would be necessary to determine the typical patterns of song-type change. Some birds occasionally sang hybrid songs, using the beginning of one song-type and the ending of another, particularly when transitioning from one song-type to the next.

Although many of the birds sang more than one song-type, we analyzed only one song-type from each bird to avoid biasing our sample by over-representing some birds. For each bird we chose the longest song-type available. (Because the recordings may not have included all of a bird's song-types, this may not have been the longest song-type in each bird's repertoire). Song-types ranged from 2.9 to 14.75 seconds long (average 5.92 seconds), and consisted of between 9 and 48 elements (average 27), of which 7 to 38 (20.6 ± 10.4) were notes. It is unknown whether this wide variation in length is because of regional characteristics (it has been suggested that birds from higher regions in Venezuela may sing less complex songs [Hilty and De Schauensee, 2003]), because not all of a bird's song types were recorded, because some may have been female songs, or simply because different individuals have different length songs.

Using the pitch-tracking function of RavenPro 1.4 (Bioacoustics Research Program, 2011), we measured the averaged centre frequency of each note for the 20 selected song-types, following established bioacoustics procedures (Zollinger et al 2012). The start and end of each note was determined from the waveform (Fig. 4).

The measured notes had an average duration of 151 ms (standard deviation: 103 ms). In a next step, we calculated the frequency ratio (interval) between successive notes in each song. Ratios were converted into "cents", a logarithmic unit of measure for musical intervals which describes the subjective perception of "distance" between musical notes. We represent descending intervals (going from a higher to a lower frequency) as a negative number, and ascending intervals as a positive number. Musician wren frequencies ranged from 619 Hz to 3765 Hz, roughly comparable to the range of a piccolo or a soprano recorder, and thus well within the range humans are used to hearing as music. Intervals between adjacent frequencies ranged from -2323 cents to 2406 cents, with 99% of the intervals falling between -1939 and 1692 cents.

In most modern (post-1750) Western classical music, the octave (a ratio of 2 to 1, the difference between the sound of a vibrating string or air column and one of half the length) is divided into 12 equally spaced semitones. Each semitone (the interval between any two most closely adjacent keys on the piano) is divided into 100 cents, and an octave is 1200 cents. The intervals found in Western classical music can be described in terms of scale steps – for example, a unison, major second, major third, and perfect fourth make up the first four steps of a major scale – or in terms of cents – in this case 0 cents, 200 cents, 400 cents, and 500 cents respectively, if in equal temperament. For describing smaller gradations of interval, cents are used. For example, an interval halfway (logarithmically) between a perfect fifth (700 cents) and a minor sixth (800 cents) cannot easily be expressed in standard modern Western musical notation or scale-step terminology, but is precisely described as 750 cents.

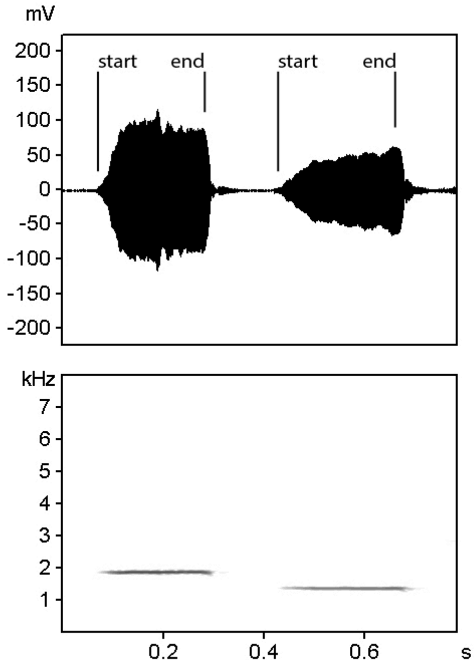


Figure 4. The start and end of the analyzed notes were determined from the envelope curve (upper panel). The measurement began immediately after the attack of the note (avoiding any noise associated with the attack), and ended as the note began to fade. Note that there is almost no frequency modulation within notes (lower panel).

The intervals of an equally tempered scale approximate those of the more "natural", small integer ratio-based intervals of justly tuned scales – those scales in which all intervals can be found between the harmonics in the harmonic series, or, in mathematical terms, in which the frequencies are related by ratios of small integers. Pythagorean tuning, which dates back at least as far as the Babylonian times, is a specific form of just intonation based on ratios using only multiples of 3 and 2. While some Pythagorean intervals, such as the 3 to 2 perfect fifth are used in most systems of just intonation, many Pythagorean intervals would occur much higher up in the overtone series. Other just systems may be based on ratios in which neither number has a prime factor larger than five ("five-limit") or seven ("seven-limit"). Before the modern era, just intonation tuning systems were favored in the West, and they continue to be the tuning system of choice in many musics outside of the Western classical system. While justly tuned intervals sound "purer", the exact size of the intervals varies depending on what scale degrees are involved, making modulation between keys difficult. For example, in equal temperament a major sixth is always 900 cents, no matter which two scale degrees it is between, or in which key. In just intonation, a major sixth could be 884 cents (a ratio of 5 to 3, in a five-limit system), 933 cents (12 to 7, in a seven-limit system), or 906 cents (27 to 16, the Pythagorean major sixth), depending on context and tuning choices. Equal temperament renders an almost perfectly in tune version of the most consonant (perceptually smooth) "perfect" intervals – those built on the ratios of 2 to 1 (a [perfect] octave), 3 to 2 (a perfect fifth), and 4 to 3 (a perfect fourth). The equal temperament values for the imperfect consonances (minor and major thirds and sixths) and dissonances (perceptually rough intervals – major and minor sevenths and "tritones" in a melodic [sequential] context, and sevenths, tritones and seconds in a harmonic [simultaneous] context) fall within the range for these intervals that may occur in just intonation systems, though discrepancies are audible (Table 1).

Table 1. A) Intervals labeled according to scale-step. B) Intervals labeled according to number of semitones. C and D) Note names and frequency (in Hz) of a chromatic scale starting on C 261.63 Hz. E) Size of intervals, in cents, in equal temperament. F and G) Some common sizes of intervals, in cents, in just intonation, and the ratios that would produce them. Intervals which also occur in Pythagorean tuning are labeled with a P.

A. Scale-Step Interval	**B. Semi-tones**	**C. Note Name**	**D. Freq. (Hz)**	**E. Equal Temp. (cents)**	**F. Just Int. (cents)**	**G. Ratio**
Unison (U)	0	C	261.63	0	0	1 to 1 (P)
Minor Second (m2)	1	C#/Db	277.18	100	71	25 to 24
					112	16 to 15
Major Second (M2)	2	D	293.67	200	182	10 to 9
					204	9 to 8 (P)
Minor Third (m3)	3	D#/Eb	311.13	300	298	19 to 16
					316	6 to 5
Major Third (M3)	4	E	329.63	400	386	5 to 4
					408	81 to 64
Perfect Fourth (P4)	5	F	349.23	500	498	4 to 3 (P)
Tritone (T)	6	F#/Gb	369.99	600	583	7 to 5
					617	10 to 7
Perfect Fifth (P5)	7	G	392	700	702	3 to 2 (P)
Minor Sixth (m6)	8	G#/Ab	415.3	800	782	11 to 7
					814	8 to 5
Major Sixth (M6)	9	A	440	900	884	5 to 3
					906	27 to 16 (P)
					933	12 to 7
Minor Seventh (m7)	10	A#/Bb	466.16	1000	969	7 to 4
					996	16 to 9 (P)
					1018	9 to 5
Major Seventh (M7)	11	B	493.88	1100	1088	15 to 8
Octave (P8)	12	C	523.25	1200	1200	2 to 1

We do not know how musician wrens select intervals, or whether the ratios that are important in so many human musical systems are relevant for them. Even for humans, the ratios of just intonation are often more theoretical than something that is realized in performance. While keyboards or other pre-tuned instruments can hold complicated tunings fairly exactly – at least until temperature or use causes them to go out of tune – sung music and music on instruments able to bend their pitch only approximates these tunings. For this research, we thus used cents (rather than integer ratios) to measure the musician wren intervals, and the intervals of the equally tempered scale as a point of comparison. Of course we do not mean to suggest that the bird shares a human music theoretical framework, or that it actually divides octaves into 12 equal semitones. These merely serve as a reference point, and as a beginning measure for understanding musician wren song. Future research may deal with finer gradations of pitch choice.

A preliminary analysis with different bin sizes confirmed that a bin size of ±50 cents seemed to most clearly delineate which intervals the musician wren favored or avoided. At the same time, this bin size seems to be the least arbitrary choice since we wanted to find out whether musician wrens sing consonant intervals as perceived by western listeners, and westerners typically perceive pitch categorically relative to the chromatic scale with a category width of ± 50 cents (Burns and Campbell 1994, Burns 1999).We thus considered intervals between 1150 and 1250 cents (those within a quarter tone of a perfectly in-tune octave) to be octaves, intervals between 1050 and 1150 cents to be major sevenths, and so forth. Though this allows considerable discrepancy in tuning, the range is in fact much narrower than that demonstrated by a trial of 10 human singers singing the same interval (in the context of the song *Happy Birthday*), in which attempted octaves ranged from 1122 to 1456 cents among all singers, and from 1156 to 1280 cents among the 4 singers in the group who had musical training (Doolittle et al., MS in prep 2013).

Intervals based on the smallest integer ratios, the "perfect" consonances, tend to be most structurally important in human music. One of the few human musical universals is that notes an octave (ratio of 2 to 1) apart, as when men and women sing together, are considered to be "the same". Octaves serve as a frame for many human musical scales, and repetition an octave higher or lower is often used as a way of reinforcing a structurally important note. Perfect fifths (3 to 2) were the first non-octave interval recognized as a consonance as Western music made the transition from monophonic (single voice) to polyphonic (multiple voice) in the middle ages, and they figure prominently outside of the Western musical world too. In Indian music, for example, the perfect fifth is often droned along with the tonic (Lavezzoli, 2007). The most common Chinese pentatonic scale is constructed out of five consecutive perfect fifths, brought into the range of an octave (corresponding approximately to the intervallic relationships between the black keys on the piano) (Trehub et al, 1997). Perfect fourths (4 to 3; in musical terms an "inversion" of a perfect fifth) framed the "tetrachords" out of which ancient Greek scales were built, and were the second consonance recognized in the middle ages.

In human vocal music, successive notes are likely to move by small intervals – seconds or thirds. These are easiest to sing, and create a feeling of connection within the musical line. The larger intervals such as perfect fourths, fifths, and octaves, are more likely to occur as "harmonic" intervals, between simultaneously sounding voices. When larger leaps do occur within a voice, however, they are likely to be these perfect intervals. A leap of an octave changes the register, but not the harmony, whereas a melodic leap of a fourth or fifth often signals a departure from or return to the “home” key. Leaps of a major or minor sixth, also consonances, occur too, often in the context of outlining a triad. Vocal leaps of dissonant intervals such as tritones, sevenths, and ninths are much less frequent (Fux, 1725/1971). Although most instruments can leap a dissonance as easily as a consonance, consonant leaps remain more prevalent both because of the harmonic implications and because vocal and instrumental styles tend to be closely intertwined.

Successive notes in the musician wrens’ songs tended to be separated by intervals of a fourth or more, rather than by the seconds and thirds that most often separate successive pitches in a human song. But the musician wrens, like the humans, preferentially sang perfect consonances for these leaps (Fig. 5). Octaves were the most frequently sung interval, making up an average of more than 12% of all interval types, followed by perfect fifths and perfect fourths (Fig. 5). The consonant major 6th was slightly favored as well. The relative lack of steps (seconds) and small leaps (thirds) that are so prevalent in human vocal music mean that the musician wren’s song may be more reminiscent of a human instrumental melody than a sung melody.

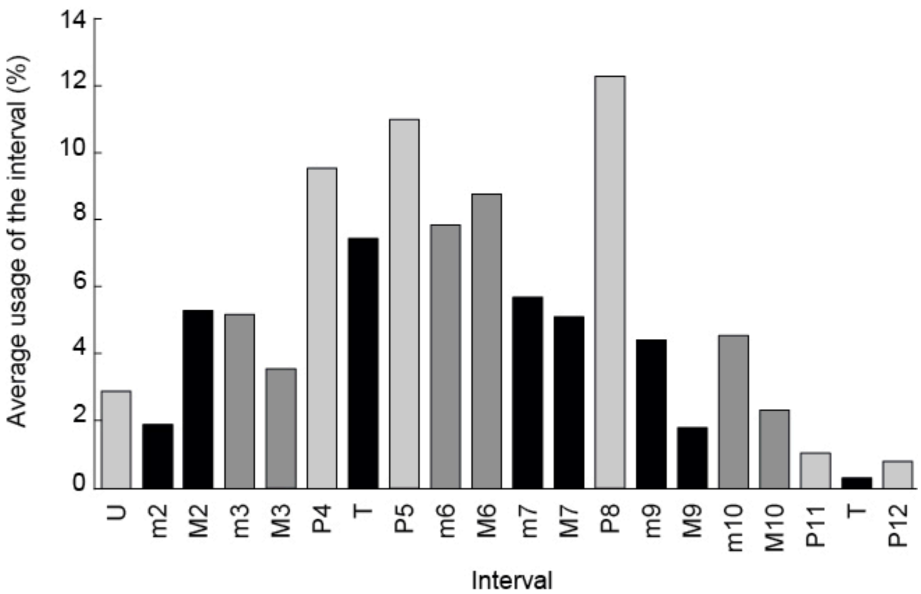


Figure 5. Usage of melodic intervals in musician wren song. Average values for all 20 analyzed birds are given for dissonant (black bars), imperfect consonant (dark grey bars) and perfect consonant intervals (light grey bars).

The averaged interval preference for all birds was similar to each individual bird’s preference. The three most favoured intervals, perfect octaves, perfect fifths, and perfect fourths were also the intervals sung by the largest number of birds (19, 16, and 16 respectively). The 11 musician wrens analyzed that showed a preference for one interval all favored a consonance (Table 2, binomial test: N = 20, p < 0.001). Four more birds favored two or more consonant intervals equally. Although five birds did not show a clear preference for just one interval and also had a dissonant interval as their most common pitch ratio, the analyzed musician wrens generally were more likely to sing consonant than dissonant dyads (Wilcoxon signed ranks test: z = 3.063, N = 20, p = 0.002).

Table 2. Melodic intervals used in musician wren song.

Individual	**Total number of intervals**	**Number of different interval types**	**Most common interval(s) and percentage of usage of each of these intervals**
MW1	18	9	P8, M7, M6 (17%)
MW 2	34	15	P4 (15%)
MW 3	5	5	M9, m9, P8, m7, P4 (20%)
MW 4	6	6	m10, M9, P8, M6, P4, U (17%)
MW 5	48	16	M6, P5, P4 (13%)
MW 6	6	6	m10, m9, m6, P5, T, M2 (17%)
MW 7	15	9	P8 (20%)
MW 8	10	6	P8 (30%)
MW 9	20	12	P5 (20%)
MW 10	17	10	m3 (18%)
MW 11	17	12	P8, P5 (18%)
MW 12	30	13	m6 (23%)
MW 13	23	10	P5 (22%)
MW 14	24	12	M3 (16%)
MW 15	29	10	M6, m6, m3 (17%)
MW 16	11	8	P5, P4, U (18%)
MW 17	25	11	P4 (24%)
MW 18	17	10	P8 (18%)
MW 19	16	11	m3 (19%)
MW 20	17	12	P8, m6, P5, T, M2 (12%)

This is the first study we know of to show a performance preference for successive octaves, fifths and fourths in a non-human animal. The musician wren's preferential treatment of perfect intervals is in itself enough to make the songs begin to sound musical to us. Because we are used to hearing these intervals as frames or anchors, we may (consciously or unconsciously) interpret a perfect interval and one or more of the surrounding notes as part of a musical unit, and it is easy to hear the song in musical, sometimes even tonal sections, rather than as a series of disjunct notes. Regardless of whether the musician wrens themselves have or intend a sense of "key", these perfect interval frames strongly affect how we as human listeners experience the song.

The musician wrens also used the imperfect consonant major sixth (5 to 3 in simplest just intonation) almost as often as the perfect consonances, in about 9% of all dyads (Fig. 5). Interestingly, major and minor thirds – "simpler intervals", in that they occur between adjacent harmonics lower down on the harmonic series (5 to 4 and 6 to 5 respectively) – were less favored.

Musician wrens are not the first bird which has been demonstrated to prefer consonant over dissonant intervals. In 1972, William Thorpe, one of the pioneers of the scientific study of birdsong, conducted a similar study which showed that tropical boubou shrikes (*Laniarius aethiopicus major*) sing more consonant than dissonant intervals between successive notes in their duet songs (Thorpe et al., 1972). Unlike those of the musician wrens, tropical boubou shrikes' preferences are skewed towards smaller consonances, with their favored intervals being perfect fourths, major thirds, minor thirds, and perfect fifths in descending order of frequency. Other species who do not favor melodic (sequential) consonances in their own song may nonetheless be able to discriminate between consonance and dissonance. Java sparrows (*Padda oryzivora*) can be trained to discriminate between harmonic (simultaneous) presentations of consonance and dissonance, generalizing to novel consonances and dissonances, even though they do not favor melodic presentations of consonant intervals in their songs (Watanabe et al., 2005). Pigeons (*Columba livia domestica*) have been taught to distinguish between baroque and modern music. After four pigeons were trained to discriminate between Bach (1685-1750) and Stravinsky (1882-1971), they were able to generalize from Bach to Buxtehude (~1637-1707) and Scarlatti (1685-1757), on the one hand, and from Stravinsky to Carter (1908-2012) and Piston (1894-1976), on the other hand. It has been suggested that they may have done so by sensitivity to relative amounts of dissonance, both melodic and harmonic, in the given musical excerpts (Porter and Neuringer, 1984; Watanabe, 2013).

Likewise, Japanese macaques (*Macacca fuscata*) may use sensory dissonance to discriminate different chords (Izumi, 2000). Moreover, Wright et al. (2000) reported that two male rhesus macaques (*Macaca mulatta*) could be trained to show octave generalization in that the monkeys considered octave transposed melodies as similar. However, other studies failed to find evidence for octave generalization in rats and monkeys (D'Amato and Salmon, 1984) and birds (Dooling et al. 1987, Hulse and Cynx 1985, Cynx, 1993), and D'Amato (1988) concluded that animals are unlikely to produce harmonic intervals in successive notes if they cannot also perceive those intervals. We do not know whether and how musician wrens perceive musical intervals, but we found that they preferentially produce successive perfect octaves, perfect fifths, and perfect fourths. If perception of intervals is a prerequisite for their production, then this would mean that musician wrens can also perceive perfect consonances. The perception of intervals and other aspects of human music by non-human animals are of considerable relevance with regards to the origin of human music (e.g. Hulse et al 1992, Wallin et al 1999, Fitch 2006). In this context, the musician wren might prove to be an excellent candidate species for further studies on non-human animals, including investigations of octave generalization and other pitch relations.

Perception of musician wren song by human listeners

To test the hypothesis that the musician wren's interval choices are at least partially responsible for our perception of this bird as "musical", we extracted the frequencies and durations of the notes for seven of the musician wren songs that contained 16 or more notes. We divided the frequencies by three and multiplied the durations by six to bring the song into a range and tempo that was comfortable for human listeners, and generated a computer playback version of each song using the Max patch “Chirpie” (John Burrow, 2011). For each song, we also generated 14 unique altered versions, in which the intervals between successive pitches were each made 150 cents larger or smaller, with a random process determining in which intervals would be larger and which smaller in each altered song. To each of 91 human listeners that were recruited through the internet, we sent a pair of sound clips by email. One sound clip was one of the seven songs with the original intervals, and the other was one of the randomly altered versions of the same song. Each altered song was thus used only once. Half of the listeners received the original song as the first attachment of the email and the altered song as the second attachment, and half in the reverse order. We asked the listeners to answer the question “Which sound clip do you think would sound most like “music” to a typical attendee of a classical music concert?” and to categorize their musical experience as one of:

a) little or no experience studying music, singing, or playing an instrument

b) amateur/some experience studying music, singing, or playing an instrument

c) professional/extensive experience studying music, singing, or playing an instrument

Three listeners said they were unable to tell which of the two versions was more musical and these test persons were removed from the data set. 61 of the remaining 91 listeners (67%) said that the unaltered sound clip, with intervals taken from the original birdsong, “would sound most like “music” to a typical attendee of a classical music concert”. This ratio is statistically different from a chance distribution (binomial test: $p = 0.002$), indicating that the majority of the test persons perceived the original musician wren intervals as more musical than the altered versions. The results were similar for those describing themselves as “c) professional” or “b) amateur” musicians. Of the 34 self-described professionals, 25 (74%) chose the original birdsong, and 9 (26%) chose the altered song. Of the amateur group, 20 out of 27 (74%) chose the original birdsong and 7 (26%) the altered version. The group with “little or no experience” was less clear in their overall judgment, with 16 of the 30 (53%) choosing the original birdsong and 14 (47%) choosing the altered version. However, the musical experience had no statistically significant influence on the answers of the listeners (Wald test: $\chi^2 = 2.8481$, $df = 1$, $p = 0.091$). Taken together, the results of our perception tests suggest that the birds’ interval choices were, at least to some extent, responsible for the human perception of musician wren song as being “musical”.

Parallels with human music

The musician wren’s interval preferences overlap sufficiently with ours to lead to occasional sequences of notes which sound surprisingly like passages of music by human composers. The beginning of the song of MW5, for example, has a passage with a descending perfect fifth (-718 cents), rising minor third (299 cents), and descending major sixth (-917 cents), which can easily be heard as the fifth, root, and third of a (sharp) a-minor chord (or a [flat] Bb-minor chord). The following three notes can be heard as three of four notes of an f#-diminished-7th chord (also slightly sharp). The next three notes suggest the progression V – I in the key of G major. The overall series of notes can thus be heard as a ii – V°7 – V – I progression in the key of Ab or G (gradually flattening, but never so much that the sense of progression is lost). The same initial pattern of intervals (with the first note an octave lower and the last an octave higher) is the opening four notes of the second movement of Haydn's Symphony 103. The pattern is also reminiscent of the subject of Bach's fugue in A minor, WTC Book II, BWV 889 (Fig. 6).

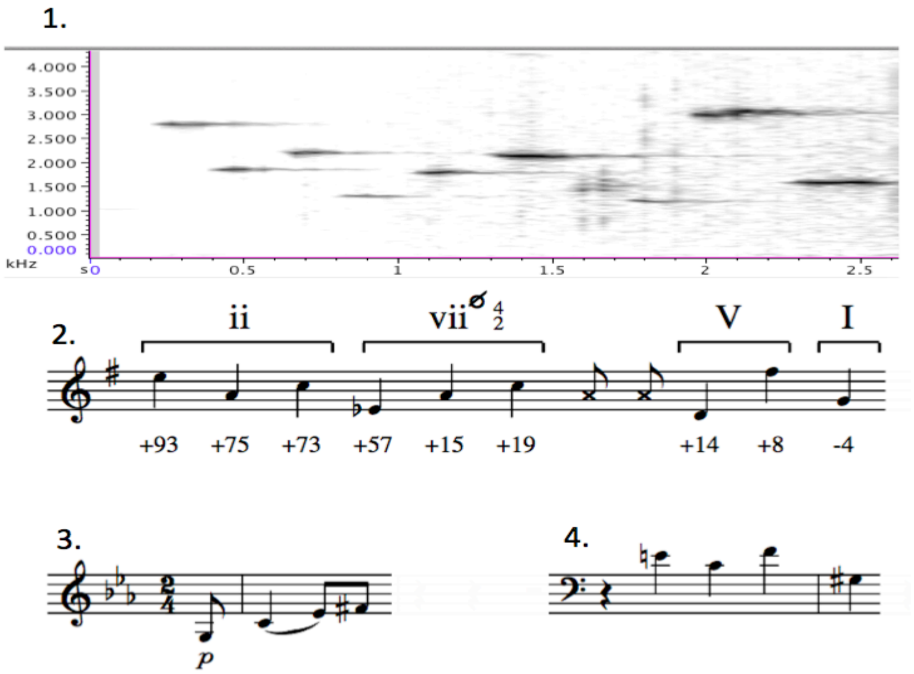


Figure 6. 1. Spectrogram of the beginning of MW5's song. 2. A transcription of the first nine notes of the song of MW5. 3. The opening melody of the 2nd movement of Haydn's Symphony #103. 4. The opening of Bach's fugue XX in A minor, WTC Book II, BWV 889.

Of course this does not mean the musician wren is singing in a key the way a human musician might. Rather, the bird's preference for consonances leads to occasional conjunctions of pitches which sound to human listeners like they are in a key. This contributes to our perception of the musician wrens as musical, even if it's not how the songs are structured from a musician wren perspective.

The song of MW19 overlaps even more surprisingly with human music. All except the final note can be analyzed as being (slightly sharp) in the key of F major (with raised fourth scale degrees), or in the mode of F Lydian. Not only do the notes fall within this key, but in most cases they are used in a way that would be appropriate in a Western tonal context. For example, the first time the B-natural (raised fourth scale degree) appears, it leads immediately to the C (fifth scale degree), as would be expected in Western tonal music (Fig. 7). As with the previous example, it is important to keep in mind that the bird is not really singing "in F" – the major and Lydian scales are constructs of a specific human musical culture – but it is remarkable that the musician wren's statistical preference for singing consonances rather than dissonances can lead to a passage that sounds so much like human music.

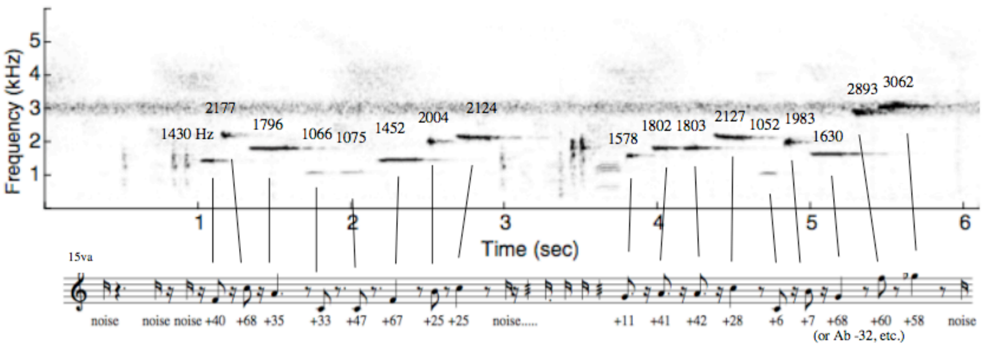
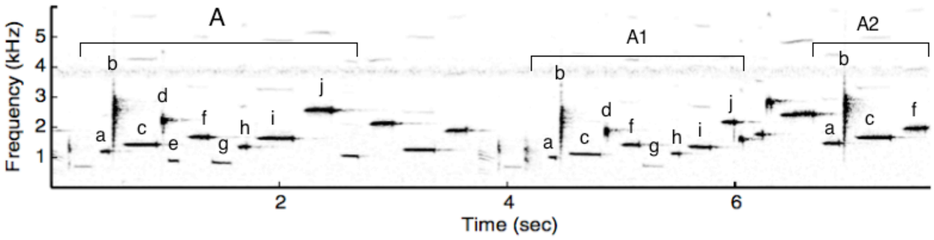


Figure 7. Sound spectrogram of MW19 (with frequencies, written in Hz), and musical transcription of the same song.

Perhaps even more remarkable than the similarities between musician wren and human pitch selection, and the conjunctions of pitches that result from these choices, is that the musician wren songs show striking structural similarities to human music as well. In human music a motive (or motif) is a short, recurring musical idea, which may consist of rhythmic, intervallic, harmonic, or timbral patterns, or some combination thereof. Motives are generally considered the smallest unit of musical construction, and can generate both small-scale musical ideas and larger-scale structures. Musician wrens appear to use motives similarly. We have defined a motive as a distinctive, repeated pattern of 2 or more elements in which some combination of contour, rhythm, and element type remain the same, but another aspect, such as the frequencies of the notes changes.

Bird MW15 makes use of a ten-element motive, which is repeated once in its entirety, and once in fragment (Fig. 8).

The element types and contours, with minor variation, remain the same, while the frequencies on which the patterns occur, and many of the intervals between them differ.



Element Type		a. short note	b. squawk	c. long note	d. hoot	e. short note	f. long note	g. long note	h. short note	i. long note	j.long note
Frequency (Hz)	A	1199		1422	2241	886	1671	825	1351	1629	2572
	A1	1000	n/a	1105	2279	n/a	1414	710	1129	1345	2178
	A2	1471		1660	n/a	n/a	1967	n/a	n/a	n/a	n/a
Interval from last note (cents)	A			295	787	-1607	-508	-1222	854	324	791
	A1	n/a	n/a	173	1253	n/a	-826	-1193	803	303	834
	A2			209	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Figure 8. Spectrogram of the song of MW15. Motives are bracketed. Frequencies of the note elements and intervals between successive notes are given in the table. Intervals which are similar in different iterations of the motive are colored in grey, while intervals that are substantially different are left white.

The bird MW9 uses a motive that is repeated at the same pitch, but with one note omitted the second time through (Fig. 9). This song-type is repeated exactly in our recording, suggesting that this repeated/varied motive is indeed characteristic of the song-type, rather than an instance of repetition of part of the song. This is quite similar to techniques used by human composers. For example, the fourth scene of Stravinsky's *The Rite of Spring* (1913), *Spring Rounds*, opens with a clarinet melody that adds and drops notes. The flute and viola melody at m. 51 of the same movement similarly adds and subtracts notes from a repeated melodic motive.

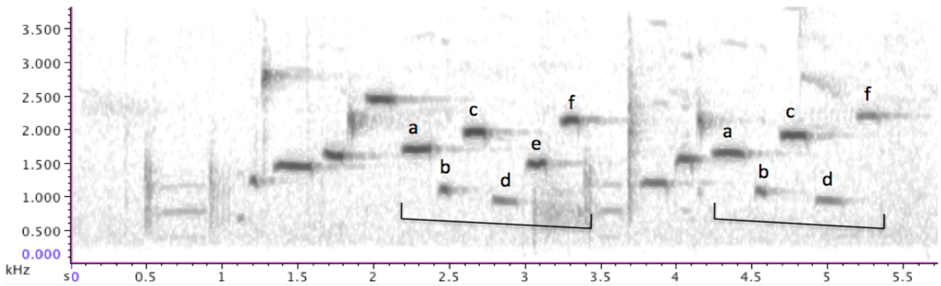


Figure 9. Element **e** is missing the second time this motive appears.

Bird MW3's song, though short (containing only 9 elements), has a somewhat more complex use of motivic construction, in which two interlocking versions of the motive frame almost the entire song (Fig. 10). The motive for this song consists of four or five elements (a) long low note, b) up to short high note, c) down to pulsed note [only in motive A1], d) down from high note to very long note, e) down to long note), in which the last element of motive A dovetails with the first element of motive A1.

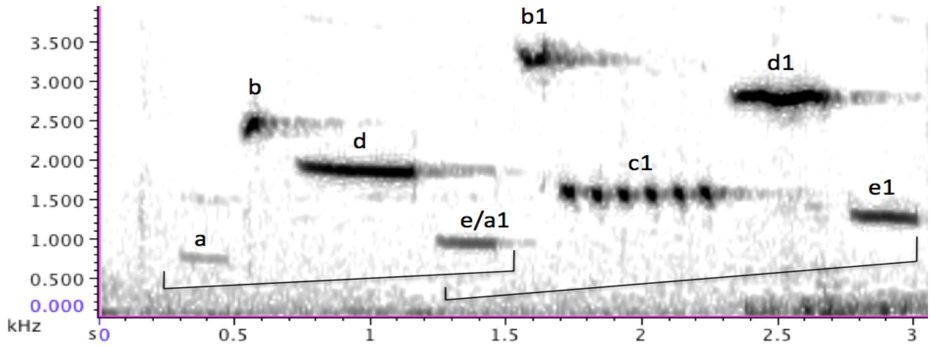


Figure 10. Interlocking "motives" in the song of MW3.

This use of a smaller motive to create a larger structure is very similar to some human music, especially from the Baroque period, where longer passages were often built out of "sequences" (series of transposed motives), and from the 20th-century twelve-tone and serial repertoire, in which interlocking, varied motives often provide the sense of structure that was provided by keys in earlier music.

While perception of motives is somewhat subjective (even when dealing with human music), and we have no way of knowing if or how the birds are perceiving these sequences as motives, we find it remarkable that motives which are distinctive to the authors are present in the songs of 14 of the 20 birds. None of the motives are shared between birds, suggesting that the exact characteristics of these motives are specific to the individual, or possibly to the region, rather than to the species.

Even the larger structure of a musician wren song session is not without parallels in human music. François-Bernard Mâche has written about similarities between the construction of a Blyth's Reed Warbler (*Acrocephalus dumetorum*) song and *The Rite of Sprin*g. Both Stravinsky and the Blyth's reed warbler, Mâche writes, juggle "with three sound objects of which one (A) is more frequently [used] than the others, reiterated several times in succession (Mâche, 1992, 117)." According to Mâche, this is not coincidental: Stravinsky wrote the Rite of Spring in Ustilug (Ukraine) on the river Bug, where marsh wrens are common. He suggests that this type of "block form", which seemed radically new when introduced by Stravinsky, is in fact no less natural than the melodic music more traditionally favored in Western classical music. One can hear a similar, if slightly less frantic, construction in the musician wren song, where the bird repeats a song-type up to ten times, cuts it off abruptly and moves to another song type, then to another, then back to the first.

Comparisons with congeneric species

There are two other species in the genus Cyphorhinus, the song wren (*Cyphorhinus phaeocephalus*), which is found in tropical and sub-tropical lowland evergreen forests in Honduras, Nicaragua, Costa Rica, Panama, western Columbia, and western Ecuador, and the chestnut-breasted wren (*Cyphorhinus thoracicus*), which lives in montane forests in the Columbian Andes, Ecuador, Peru, and western Bolivia. Both are considered to have pleasant songs, but neither is the subject of legend or musical tributes that the musician wren is. At one point the song wren was considered to be possibly the same species as the musician wren, but they now are considered distinct, in part because of the differences in their songs. From each of these other species we selected 20 song-types (each from a different individual) from the recordings available on Xeno-Canto and Avocet websites, and processed and analyzed them the same way as the musician wren songs.[iii]

The songs of both species shared some features with musician wren song, particularly the use of pure notes with steady pitch. However, the other features that make musician wren song seem musical to human listeners were mostly lacking in these two. Firstly, the songs of the three Cyphorhinus species differed in the number of tonal notes per song (Kruskal-Wallis test: Chi-Square = 40.139; df = 2; $p < 0.001$). On average, the song wrens only had 3.3 ± 1.3 (mean ± SD), notes per song, and the chestnut-sided wrens 4 ± 1.9. Thus, the musician wrens produced more notes per song than the song wrens (Mann-Whitney U test: N1 = N2 = 20, z = -5.446, $p < 0.001$) and the chestnut-breasted wrens (Mann-Whitney U test: N1 = N2 = 20, z = -5.326, $p < 0.001$), which enabled them to sing more complex melodies than their congeners (Fig. 11).

The song analysis of the two congeneric species also yielded a different picture regarding the usage of intervals. Although a slight majority of individuals of both the song wrens and the chestnut-breasted wrens used a consonance as their most frequent interval, this was not statistically significant (binomial tests, N = 20; song wrens: p = 0.126; chestnut-breasted wrens: p = 0.051). Moreover, we did not find any evidence that the examined chestnut-breasted wrens were more likely to sing a consonant or dissonant interval (Wilcoxon signed ranks tests: z = -0.688, N = 20, p = 0.491). In the song wrens, there was a marginal tendency to use consonant intervals more often than dissonant ones, but this was statistically not significant (Wilcoxon signed ranks tests: z = 1.874, N = 20, p = 0.061). Similar to our findings on the songs of the closest relatives of the musician wren, the ornithologist Marcelo Araya-Salas could not find a significant use of harmonic intervals in the songs of Northern nightingale wrens (*Microcerculus philomela*) (Araya-Salas, 2012), a species belonging to the same family as the three *Cyphorhinus* species studied here.

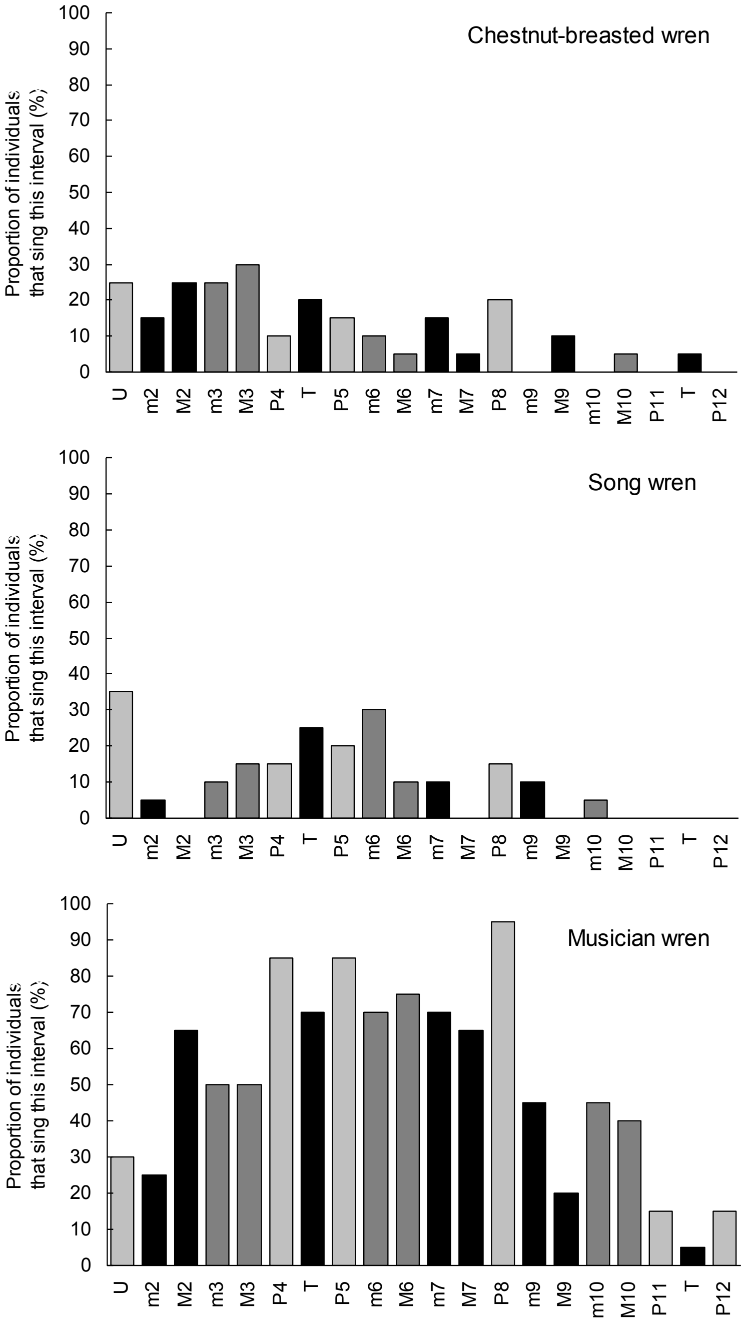


Figure 11. Occurrence of musical intervals in *Cyphorhinus* songs. Dissonant (black bars), imperfect consonant (dark grey bars) and perfect consonant intervals (light grey bars) are shown for the songs from 20 birds of each species.

Conclusions

We discovered that musician wrens favored consonant rather than dissonant intervals in their songs, with a clear preference for perfect rather than imperfect consonances. Octaves were the most frequently sung interval, followed by perfect fifths and perfect fourths. Because human listeners from a variety of musical cultures are used to hearing these intervals as frames or anchors, we are likely to perceive many passages of musician wren songs not as series of disjunct notes but as musical units. Sometimes these perfect interval frames even give the impression that the song is structured around a central pitch. A listener trained in western music may perceive the song as being in a key. This unusual usage of melodic intervals, combined with several other factors, such as the flute-like tone, the predominance of notes rather than noises, and the apparent use of motives, makes the songs seem strikingly musical to human listeners from diverse backgrounds.

However, our findings allow no insight into how the birds perceive songs or whether they have any concept of consonance, key or motive. The striking effect of key does not necessarily reflect a sense of higher order structuring in the bird itself. Instead, the birds' preference for consonances, and particularly for perfect consonances, may lead by chance to occasional conjunctions of pitches which sound to the human listener as if they were in a key. Moreover, one cannot generalize from musician wren song to a broader comparison between "birdsong" and music. There are about 4000 species of songbirds, and each has its own patterns of song construction. Even other birds that humans consider musical overlap with human music in different ways. The pied butcherbird, for example, uses music-like methods of motivic development and song structure (Taylor, 2008), but does not show a preference for perfect consonant intervals. Given the stunning number of different species, it is not surprising that some happen to have songs that resemble music, even if the parallels are as astounding as in the musician wren. Overall, this means that these particular examples of bird song are not necessarily music per se but, as we showed in this paper, are likely to be perceived as musical by human listeners.

Our study demonstrated that our interdisciplinary approach, using methods taken from both the humanities and the natural sciences to analyze bird songs, can be very informative. By combining quantitative analysis with concepts and methods of music theory and ethnomusicology, we were able to provide a more complete picture of how bird songs are perceived. In particular, we used the tools of bioacoustics to take objective measurements of frequency parameters which were then utilized to investigate pitch ratios in terms melodic intervals. This method is a considerable advance over previous studies that relied on the subjective hearing of the observer to transcribe bird songs directly into musical staff notation, which is prone to overestimate of the musical nature of the songs (Dobson and Lemon, 1977). Finally, our quantitative approach enabled us to validate statistically that the observed patterns occurred above chance level, that is, there was indeed a general pattern in our sample of 20 individuals. The use of statistical methods should become common practice in this kind of research because it prevents jumping to conclusions based on the observation of just one or a few selected individuals that happen to use musical elements.

We consider this research a beginning, not an ending. Even with just one species, the musician wren, many aspects remain to be explored. We have analyzed broad interval categories, but perhaps analysis of finer gradations of interval would yield new insight. Analysis of timbre, rhythm, patterns of song construction, and singing behavior might also be fruitful. And of course there are the thousands of other species of songbirds whose songs might also be better understood by combining musical and scientific approaches.

Acknowledgements

The authors would like to thank Ana Paz Martins for translating the Portuguese sources, John Burrow for writing the Max patch Chirpie (2011), Mathias Ritschard for help with the statistics, and Jarrad Powell for discussion of tuning. We also thank Sue Anne Zollinger for feedback on our research and editorial help with the manuscript. She, as well as Ford Doolittle, Richard Parncutt, Graham Hair, and an anonymous reviewer gave helpful comments on an earlier draft of the manuscript. E.D. would like to thank the Max Planck Society, the Erik Stokes Foundation, the Cornish College Faculty Development Fund, and the Culture and Animals Foundation. H.B. thanks Stefan Maul for pointing out the bird call text in the Sultantepe tablets, and the German Research Foundation for funding.

References

Araya-Salas, Marcelo. "Is birdsong music? Evaluating harmonic intervals in songs of a Neotropical songbird." *Animal Behavior* 84 (2012): 309-313.

Bioacoustics Research Program. Raven Pro: Interactive Sound Analysis Software (Version 1.4) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology, 2011. Available from http://www.birds.cornell.edu/raven.

Burns, Edward M. " Intervals, scales, and tuning." In *The Psychology of Music*, 2nd ed., edited by Diana Deutsch, 215–264. San Diego: Academic Press, 1999.

Burns, Edward M., and Shari L. Campbell. "Frequency and frequency-ratio resolution by possessors of absolute and relative pitch: Examples of categorical perception." *Journal of the Acoustical Society of America* 96 (1994): 2704–2719.

Brumm, Henrik. "Biomusic and Popular Culture: The Use of Animal Sounds in the Music of the Beatles." *Journal of Popular Music Studies* 24, no. 1 (2012): 25–38.

Brumm, Henrik, and Marc Naguib. "Environmental Acoustics and the Evolution of Bird Song." In *Advances in the Study of Behavior*, Volume 40:1–33. Oxford, UK: Academic Press, 2009.

Buzzetti, Dante, and Silvestre Silva. *Nurturing New Life-nests of Brazilian Birds*. Sao Paulo, Brazil: Editora Terceiro Nome, 2005.

da Câmara Cascudo, Luís. *Dicionário Do Folclore Brasileiro*. Vol. 1. Rio de Janeiro, Brazil: Ed. do Instituto Nacional do Livro, 1962.

Catchpole, Clive K., and Peter J. B. Slater. *Bird Song: Biological Themes and Variations*. Cambridge, UK: Cambridge University Press, 2008.

Craig, Wallace. *The Song of the Wood Pewee, Myiochanes Virens Linnaeus: a Study of Bird Music*. Albany, NY: The University of the State of New York, 1943.

Cruls, Gastáo. *Hiléia Amazônica: Aspectos Da Flora, Fauna, Arqueologia e Etnografia Indígenas*. Rio de Janeiro, Brazil: Livraria J. Olympio Editora, 1976.

Cynx, Jeffrey. "Auditory Frequency Generalization and a Failure to Find Octave Generalization in a Songbird, the European Starling (*Sturnus vulgaris*)." *Journal of Comparative Psychology* 107, no. 2 (1993): 140-146.

D'Amato, M. R. "A search for tonal pattern perception in Cebus monkeys: Why monkeys can't hum a tune." *Music Perception* 5, no. 4 (1988): 453–480.

D'Amato, M. R., and David P. Salmon. "Processing of complex auditory stimuli (tunes) by rats and monkeys (*Cebus apella*)."Animal Learning and Behavior 12, no. 2 (1984): 184-194.

Dobson, Charles W., and Robert E. Lemon. "Bird Song as Music." *Journal of the Acoustical Society of America* 61 (1977): 888–890.

Dooling, Robert, Bernard Lohr, and Micheal L. Dent. "Hearing in birds and reptiles." In *Comparative Hearing: Birds and Reptiles*, edited by Robert J. Dooling, R. R. Fay, and Arthur N. Popper, 308-359. New York: Springer, 2000.

Dooling, Robert J., Susan D. Brown, Thomas J. Park, Kazuo Okanoya, and Sigfrid D. Soli. "Perceptual Organization of Acoustic Stimuli by Budgerigars (*Melopsittacus undulatus*): I. Pure Tones." *Journal of Comparative Psychology* 10, no. 2 (1987): 139-149.

Doolittle, Emily. "Crickets in the Concert Hall: A History of Animals in Western Music." *TRANS Revista Transcultural De Música* 12 (2008): article 9.

Elliott, Andrew, David A Christie, and Josep del Hoyo. *Handbook of the Birds of the World*. Vol. 10. Barcelona: Lynx Edicions, 2005.

Fermino, Maria de Lourdes Mucci. *Contando Histórias da História*. Vol. VIII. "História Popular do Brasil." São Paulo: Iracema, 1969: 145.

Fitch, W. Tecumseh. "On the Biology and Evolution of Music." *Music Perception* 24, no. 1 (2006): 85–88.

Fux, Johann Joseph. *The Study of Counterpoint*. Translated by Alfred Mann. New York: W. W. Norton and Company, 1971. Originally published as *Gradus Ad Parnassum*, 1725.

Gil, Diego, and Manfred Gahr. "The Honesty of Bird Song: Multiple Constraints for Multiple Traits." *Trends in Ecology and Evolution* 17, no. 3 (2002): 133–141.

Graf, Jakob, Martha Wehner, and Agathe Graf. *Vogelstimmen in Natur und Kunst*. Munich: Lehmann, 1962.

Gray, Patricia et al. "The Music of Nature and the Nature of Music" *Science* 291, no. 5501 (2001): 52-54.

Griffiths, Paul. *Olivier Messiaen and the Music of Time*. Ithaca, New York: Cornell University Press, 1985.

Hall-Craggs, Joan. "Sound Spectrographic Analysis: Suggestions for Facilitating Auditory Imagery." *The Condor* 81, no. 2 (1979): 185–192.

Hartshorne, Charles. *Born to Sing: An Interpretation and World Survey of Bird Song*. Bloomington, IN: Indiana University Press, 1973.

Hilty, Steven L., and Rodolphe Meyer De Schauensee. *Birds of Venezuela*. Princeton University Press, 2003.

Hoffmann, Bernhard. *Kunst und Vogelgesang in ihren wechselseitigen Beziehungen vom naturwissenschaftlich-musikalischen Standpunkte*. Leipzig: Quelle und Meyer, 1908.

Howard, Len. *Birds as Individuals*. New York: Doubleday, 1953.

Hulse, Stewart. H., and Jeffrey Cynx. "Relative pitch perception is constrained by absolute pitch in songbirds (Mimus, Molothrus, and Sturnus)." *Journal of Comparative Psychology* 99, (1985): 176–196.

Hulse, Stewart H., Annie H. Takeuchi, and Richard F. Braaten. "Perceptual Invariances in the Comparative Psychology of Music." *Music Perception* 10, no. 2 (1992): 151-184.

Izumi, Akihiro. "Japanese monkeys perceive sensory consonance of chords." *Journal of the Acoustical Society of America* 108, no. 6 (2000): 3073-3078.

Johnson, Robert Sherlaw. *Messiaen*. Berkeley, CA: University of California Press, 1989.

Kac, Eduardo. http://www.ekac.org/uirapuru.html, accessed July 14, 2012.
Lambert, W. G. "The Sultantepe Tablets: IX. The Birdcall Text." *Anatolian Studies* 20 (1970): 111–117.
Lendas e Contos. http://casadecha.wordpress.com/, accessed August 16, 2012.
Lavezzoli, Peter. *The Dawn of Indian Music in the West*. New York: Continuum, 2007.
Mâche, François Bernard. *Music, myth, and nature, or, The Dolphins of Arion*. Philadelphia: Harwood Academic Publishers, 1992.
Marler, Peter. "Science and Birdsong: The Good Old Days." In *Nature's Music: The Science of Birdsong*., 1–38. London: Elsevier, 2004.
Martinelli, Dario. *Of Birds, Whales, and Other Musicians: An Introduction to Zoomusicology*. Vol. 3. Scranton, Pennsylvania: University of Scranton Press, 2009.
Martinelli, Dario. *How Musical Is a Whale?: Towards a Theory of Zoömusicology*. Vol. 3. Helsinki: International Semiotics Institute at Imatra, Semiotic Society of Finland, 2002.
Mathews, F. Schuyler. *Field Book of Wild Birds and Their Music;* New York: G. P. Putnam's Sons, 1904.
Mostel, Ralph. "The Medium Is Doing Better Than the Message." *New York Times*, December 11, 1988, sec. Music.
Oppel, J. J. "Der Kukuksruf in akustischer Beziehung." *Annalen der Physik* 220, no. 10 (1871): 307–309.
Plomp, R, and W. J. Levelt. "Tonal consonance and critical bandwidth." *The Journal of the Acoustical Society of America* 38, no. 4 (1965): 548–60.
Porter, Debra, and Allen Neuringer. "Music Discriminations by Pigeons." *Journal of Experimental Psychology: Animal Behavior Processes* 10, no. 2 (1984): 138–148.
Ridgely, Robert S., Guy Tudor, and William L. Brown. *The Birds of South America: The Oscine Passerines*. Vol. 1. Austin, TX: University of Texas Press, 1989.
Rosauro, Ney. http://www.neyrosauro.com/composition.asp?wid=47, accessed July 15, 2012.
Sambolec, Tao G. Vrhovec, http://www.taogvs.org/UirapuruMain.html, accessed July 15, 2012.
Searcy, William, and M. Anderson. "Sexual Selection and the Evolution of Song." *Annual Review of Ecological Systems* 17 (1986): 507–533.
Skutch, Alexander. "Social and Sleeping Habits of Central American Wrens. Hábitos Sociales y Para Dormir De Los Soterrés Centroamericanos." *The Auk*. 57, no. 3 (1940): 293–312.
Slater, Peter J. B. "Fifty Years of Bird Song Research: a Case Study in Animal Behaviour." *Animal Behaviour* 65, no. 4 (2003): 633–639.
Spruce, Richard. *Notes of a Botanist on the Amazon & Andes*. New York: Johnson Reprint Corporation, 1970. http://www.getcited.org/pub/101904918.
Szöke, P., W. W. H. Gunn, and M. Filip. "The Musical Microcosm of the Hermit Thrush: From Athanasius Kircher's Naïve Experiments of Musical Transcription of Bird Voice to Sound Microscopy and the Scientific Musical Representation of Bird Song." *Studia Musicologica Academiae Scientiarum Hungaricae* 11, no. 1 (1969): 423–438.
Taylor, Hollis. "Decoding the Song of the Pied Butcherbird: An Initial Survey." *TRANS Revista Transcultural De Música* 12 (2008): article 9.
Taylor, Hollis, and Dominique Lestel. "The Australian Pied Butcherbird and the Natureculture Continuum." *Journal of Interdisciplinary Music Studies* 5, no. 1 (2011): 57–83.
Thorpe, William. H., J. Hall-Craggs, B. Hooker, T. Hooker, and R. Hutchison. "Duetting and Antiphonal Song in Birds: Its Extent and Significance." *Behaviour. Supplement*, no. 18 (1972).
Trehub, Sandra, E. Glenn Schellenberg, and David S. Hill. "The origins of music perception and cognition: A developmental perspective." In *Perception and Cognition of Music*, edited by Irene Deliege and John A. Sloboda, 103-128. Hove, England: Psychology Press, 1997.

Villa-Lobos, Heitor, Program notes for *Uirapurú* (1917), cited and translated by Richard E. Rodda. Program notes, Grant Park Music Festival, Chicago, IL: Jay Pritzker Pavillion, June 24 and 25, 2011.

Wallin, Nils L., Björn Merker, and Steven Brown. *The Origins of Music*. Cambridge, MA: MIT Press, 1999.

Watanabe, S. "Animal Aesthetics from the Perspective of Comparative Cognition." In *Emotions of Animals and Humans: Comparative Perspectives*, edited by S. Watanabe and S. Kuczaj, New York: Springer, 2013.

Watanabe, S., M. Uozumi, and N. Tanaka. "Discrimination of Consonance and Dissonance in Java Sparrows." *Behavioural Processes* 70, no. 2 (2005): 203–208.

Wright, Anthony A., Jacquelyne J. Rivera, Stewart H. Hulse, Melissa Shyan, and Julie J. Neiworth. "Music Perception and Octave Generalization in Rhesus Monkeys." *Journal of Experimental Psychology* 129, no. 3 (2000): 291-307.

Wright, Simon. *Villa-Lobos*. New York: Oxford University Press, USA, 1992.

Zollinger, Sue Anne, Jeffrey Podos, Erwin Nemeth, Franz Goller, and Henrik Brumm. "On the relationship between, and measurement of, amplitude and frequency in bird song." *Animal Behaviour* 84 (2012): e1–e9.

---

[i] It has been suggested that what sounds like a single song may actually be a tightly interlocking duet, with one bird singing primarily quieter low noises, and the other, higher purer tones. The authors find this unlikely given that there is almost no variation in the way the elements of the songs align, we never heard any overlapping elements, and we did not hear anything that sounded like one bird's portion of a duet. However, even if further study does reveal these songs to be duets, this would not affect our analysis of the frequencies and intervals used in the songs. Some of the recordings we studied do suggest antiphonal alternation of complete song-types (rather than of elements within a song) between two spatially separated birds, but more recordings and observation would be necessary for a detailed study of this aspect of musician wren song.

[ii] Thanks to Allen T. Chartier, Thiago V. V. Costa, Bradley Davis, Otte Ottema, Eduardo Patrial, Alexander Less, Sjoerd Mayer, Nick Athanas, David Geale, David Edwards, Andrew Spencer, Andrew Renaudier, Taylor Brooks, Galo Real, Daniel Lane, Leonardo Ordóñez-Delgado, Bob Planqué, F. Schmitt, Patrick Ingremeau, Joseph Tobias, Nathalie Seddon, Oswaldo Cortes, Chris Parrish, and Joe Klaiber for making their musician wren recordings available (under a Creative Commons license) on Xeno-Canto (www.xeno-canto.org).

[iii] Thanks to Ken Allaire, Todd Mark, Wouter Halfwerk, Allen T. Chartier, Don Jones, Daniel Lane, Andrew Spencer, William Adsett, Manuel Sanchez, David Bradley, Nick Athanas, Joseph Tobias, Nathalie Seddon, Thore Noernberg, Robin Carter, Mike Nelson, and Tom Stevens for their recordings of the song wren, and to Roger Ahlman, Todd Mark, David Edwards, Nick Athanas, Andrew Spencer, David Geale, Ottavio Janni, Herman Arias, Niels Krabbe, Louis Boon, Sofia Tello, Richard C. Hoyer, Frank Lambert, Fabrice Schmitt, Adrian Eisen Rupp, Fernando Angulo, Herman van Oosten, Bernabe Lopez-Lanus, Joseph Tobias, Nathalie Seddon, Galo Real, Diego Calderon, Sebastian K. Herzog, Roger Ahlman, Charlie Vogt, Niels Poul Dreyer, Oswaldo Cortes, and Joe Klaiber for their recordings of the chestnut-breasted wren. Thanks to www.xeno-canto.org for making these recordings available under the Creative Commons 3.0 license.

Biographies

Emily Doolittle is a composer and zoomusicologist, and is an associate professor of music composition and theory at Cornish College of the Arts in Seattle. She received her PhD from Princeton University in 2007, where she explored the question of whether some animal songs can be considered music in her dissertation “Other Species’ Counterpoint”. In 2011 she was composer-in-residence at the Max Planck Institute for Ornithology, where she researched musician wren song, wrote a set of pieces based on the songs of duetting birds, and presented a concert of her birdsong-related music, performed by members of the Bavarian State Opera.

Henrik Brumm heads a research group at the Max Planck Institute for Ornithology in Seewiesen, Germany. He received his PhD from Freie Universität Berlin in 2003, where he studied the behavioural biology of nightingale songs. In 2005, he was appointed as a fellow at the Institute for Advanced Study Berlin. He is an Associate Editor of the scientific journal *Behavioral Ecology and Sociobiolgy*, and a Consulting Editor of *Animal Behaviour*. His research focuses on the communication and social behavior of animals, and the relationships between animal sounds and music. He has written, broadcast and researched on bird song for more than 12 years and published over 40 articles in academic journals.