The Science-Music Borderlands

Reckoning with the Past and Imagining the Future

Edited by: Elizabeth H. Margulis, Psyche Loui, Deirdre Loughridge

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3 Cross-Species Research in Biomusicality: Methods, Pitfalls, and Prospects

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> We need another and a wiser and perhaps a more mystical concept of animals. . . . We patronize them for their incompleteness, for their tragic fate of having taken form so far below ourselves. And therein we err, and greatly err. For the animal shall not be measured by man. In a world older and more complete than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained living by voices we shall never hear. They are not brethren, they are not underlings; they are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth.
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> —Henry Beston, *The Outermost House*, 1928

What Is Animal Musicality, and Why Should We Study It?

Musicality can be defined as a set of capacities that underlie music perception and production (Hoeschele et al., 2015). Fitch (2015) defines *biomusicology* as "the biological study of musicality in all its forms." Hoeschele et al. (2015) state that the origins of musicality can be investigated by searching for components of musicality in other species, thereby advocating for a comparative approach. What do we mean by *animal* in animal musicality? Many comparative papers begin by stating that *animals* refers to nonhuman animals. Here, although we adopt this meaning of *animals*, we want to emphasize the importance of considering humans as part of the animal category, not only in terms of the obvious biological classification but also in a conceptually non-anthropocentric sense (see Mundy, chapter 4 of this volume, for a complementary perspective). We consider human animals an integral part of the animal kingdom, so we use the terms *nonhuman animals* and *humans* (as an abbreviation of *human animals*).

Research on animal musicality serves a variety of purposes; one of these is to better understand the evolutionary history of musical abilities in our own species, in all its potential diversity. For a successful discipline of biomusicology, Fitch (2015) proposes to follow a pluralistic approach—including Tinbergen's (1963) method to address mechanistic (see Mundy, chapter 4), ontogenetic (see Kragness, Hannon, and Cirelli, chapter 8 of this volume), phylogenetic, and functional questions[1]—as animal communication systems provide us with information about the biology of human music, thereby underlining the importance of animal homologues or analogues. An example of a homologue (a trait shared by two species, both of which inherited it from a common ancestor) within the animal kingdom is bimanual drumming in apes, which provides us phylogenetic insight into drumming in our own species. An analogue (a trait shared by two different species, with the second species developing it independently from the first and not inheriting it from a common ancestor) can provide insight into similar evolutionary pressures; a good example is flight. Flight is a trait that evolved separately many times and in many animal classes, such as insects, birds, and mammals. To understand flight in bats, for instance, one would study not only bats but also other mammals that do not fly and other animals that have convergently evolved wings. Likewise, we argue, humans are only one data point to understand human traits, even those traits that look uniquely human at first. According to Fitch (2015), biomusicology can be divided into four core components: song, drumming, social synchronization, and dance. Dance is an almost inseparable part of biomusicality, with fascinating examples in the animal kingdom: chimpanzees (*Pan troglodytes*) rhythmically swinging to music (Hattori & Tomonaga, 2020, 2021); several bird species exhibiting impressive "dancing" skills, such as lyrebirds (*Menura novaehollandiae*) (Dalziell et al., 2013); or blue-capped cordon-bleus (*Uraeginthus cyanocephalus*), both sexes of which perform multicomponent and multimodal courtship displays, including singing, bobbing, and step dancing (Ota et al., 2015). This chapter, however, focuses on animal songs, drumming, and synchronization, leaving the less explored topic of dance for future work.

We start by discussing the anthropocentric versus biocentric approaches and critically review some examples among the plethora of past research, beginning with acoustic discrimination and categorization experiments from the twentieth century. We then discuss three aspects of biomusicality: song, instrumental music (percussion and drumming), and synchronization (entrainment, duets, and chorus). Finally, we examine the spectral and temporal parameters of music and relevant animal research and then discuss potential prospects and pitfalls in biomusicality.

Anthropocentric versus Biocentric Approach

The anthropocentric orientation places humans at the center of meaning, value, knowledge, and action (Weitzenfeld & Joy, 2014), while the biocentric perspective regards each species in its own evolutionary history (Bräuer et al., 2020). According to Shettleworth (2010), the anthropocentric approach dominates research, and Bräuer et al. (2020) report that research in animal cognition is often anthropocentric, driven by human cognition. This may seem obvious because, in (comparative) research, one species, the human animal, studies (and compares) several species, nonhuman animals. When trying to understand an animal's cognition, it is essential to consider its *Umwelt*, which is defined as a closed unit by von Uexküll (1934). The *Umwelt* consists of a *Merkwelt*, the perceptual world, and a *Wirkwelt*, the effector world. An animal's environment is determined by these two subunits, explaining how perception and production can be species specific. Naturally, immense phylogenetic contrasts exist in different species' sensory processing. Partan and Marler explained the concept nicely: "[It] is more complex than just sense organ physiology, embracing not only how animals sense and perceive their environments, both physical and social, but also what resources are proffered to the organism, how animals respond to their situation, and how those responses in turn modify both the environment and the organism's perceptions of the environment and of itself" (2002, p. 116). More recently, Bueno-Guerra (2018) suggested including another element, the *Sozialwelt*, when designing species-specific experimental setups. For example, would we expect a solitary species to succeed in a cognitive task—such as reaching a hidden food reward—that demands cooperation with conspecifics? Likely not. Although this will not provide information about the animal's cognition, it can provide information about its *Sozialwelt* as one sphere of its *Umwelt*. The same cognitive task may be successfully performed if approached in a species-tailored way, such as if it is solvable by one individual alone.

Prior to conducting cognitive studies on animals, both stimuli and responses should come naturally to the species—that is, the animal responds to the stimulus with a modality that lies within the ethogram (repertoire of capabilities) of the particular species (Bräuer et al., 2020; Bueno-Guerra, 2018; Cook, 1993). Therefore, the ecological background of the species of interest needs to be thoroughly considered, and experiments should be aligned species specifically. Bräuer et al. (2020) argue that the design of comparative studies must be ecologically valid; this is achieved by using naturalistic situations with relevant modalities and test settings that match naturally occurring contexts and by stressing the importance of both the tested skills and the experimental setup. We agree with this view: when animals are trained on unnatural skills that lie beyond the scope of their ethogram, this demonstrates cognitive flexibility but does not tell us much about their ecology. Having this in mind, we advocate inspecting musical traits in different species to elucidate the evolution of music, while pointing to the importance of homologies and analogies, and we support a biocentric approach. Cognitive capacities of species are often compared and measured according to whether and how much they match those of humans (Bräuer et al., 2020). Here, we aim to examine the evolution of music by taking a comparative perspective on biomusicality. Musicality is not a capacity unique to humans. Several statistical universals described by Savage et al. (2015) are found within the animal kingdom and provide a valuable opportunity to analyze the evolution of musicality. By tapping into homologues and analogues of musicality in other species, we may come a bit closer to understanding the nature of music.

Pioneer Studies and State of the Art

Porter and Neuringer (1984) introduced acoustic discrimination tasks when testing pigeons' ability to discriminate music by two different composers. Since then, discrimination for complex auditory stimuli has been probed in a variety of other animals. For example, Java sparrows (*Padda oryzivora*) were tested for their ability to discriminate among composers (Watanabe & Sato, 1999), koi carps (*Cyprinus carpio*) were tested for their ability to categorize blues and classical music (Chase, 2001), and rodents were tested for their ability to distinguish the Beatles' "Yesterday" from white noise, Mozart, and an altered version of "Yesterday" (Okaichi & Okaichi, 2001). Animals succeeded in most discrimination and categorization tasks. But what were the animals actually discriminating and categorizing?

Discrimination is the ability of differentiate sensory information, and categorization is the ability to put items into classes or groups. For instance, the mental representation of a chair includes any item with chair legs and a chair back; the color or material does not change the assumption that it's a chair. Removing the back, however, would turn the chair into a stool. To study perception, discrimination, or categorization abilities, researchers frequently use operant conditioning methods. In operant conditioning, animals are trained to respond to stimuli and are rewarded for correct answers (positive reinforcement) and unrewarded or punished for incorrect answers (negative reinforcement). In some studies, negative reinforcement is used to enhance learning, such as when a wrong answer is "punished" by a time-out and no new stimuli are presented (Hulse et al., 1995). In any of these tasks, if the subject has more correct answers than statistically expected by chance, it is assumed that it can reliably discriminate or categorize. Ideally, cognitive tasks should be designed so that animals can respond as naturally as possible, such as birds moving to a response perch (Watanabe et al., 2005) or monkeys touching a screen (Wright & Rivera, 2000). To study the categorization process of the animals, unrewarded generalization or transfer tests are performed: novel stimuli are presented, following the same categorical rule.

Porter and Neuringer (1984) pioneered these studies by testing the ability of pigeons (*Columba livia*) to discriminate music by two different composers. The birds were placed in a box with a response disk and a food dispenser. Excerpts of Bach served as the positive stimulus (S+, rewarded) and Hindemith as the negative stimulus (S–, unrewarded). The pieces were alternated, and the pigeons were rewarded only when they pecked during Bach. Both birds learned the task. They were then tested on excerpts of Bach and Stravinsky by means of a two-alternative forced choice (2AFC) paradigm and the addition of a second response disk. The 2AFC paradigm enables a choice between two options, in this case, excerpts by Bach or Stravinsky. Decisions can be tracked, and reaction times can be measured. Correct pecks (S+, Bach) were positively reinforced by food, and wrong pecks (S–, Stravinsky) were negatively reinforced by a time-out. After learning the task, the birds were introduced to novel excerpts and generalized consistently and independently of the instruments involved. A subsequent experiment purportedly tested whether the pigeons were discriminating musical categories. Excerpts of works from other composers were presented, that—according to human listeners—were more similar to either Bach or Stravinsky. The pigeons generalized between the different composers, except for one piece by Vivaldi that was "wrongly" attributed to Stravinsky (Porter & Neuringer, 1984). Subsequent studies had similar goals, featuring a variety of approaches and species. Chase (2001) showed that koi are capable of auditory discrimination. The overall goal of the study was to investigate whether these fish can reliably discriminate between stylistically different musical genres and whether they are capable of generalizing known musical stimuli to unfamiliar music from the same stylistic category. All koi learned to discriminate and categorize; they were also capable of discriminating melodies without timbre cues.

How do these studies vary from visual discrimination and categorization tasks, and how do they help us understand animal musicality? Crucially, in these studies, the animals likely used specific sonic features rather than the abstract concept of "music from Bach or Stravinsky" to achieve categorization. The ability to categorize such complex stimuli is remarkable, but the underlying discriminative cues remain unknown, thereby telling us little about biomusicality. However, such studies do aid in investigating the cues animals might use to discriminate or categorize complex auditory stimuli (Chase, 2001). Because the animals learned to discriminate despite an indistinguishable timbre, Chase (2001) concluded that timbre does not serve as a discriminative cue. Consequently, reducing features of complex auditory stimuli to identify discriminative cues is a fruitful approach to understanding animal cognition. Other studies approach cognition by providing valuable insight into specific components of music, such as pigeons demonstrating the ability to discriminate between chords (Brooks & Cook, 2010), or by examining the psychophysical aspects, such as the ability of bottlenose dolphins (*Tursiops truncatus*) to determine just-noticeable differences in tempo or frequency (Thompson & Herman, 1975; Yunker & Herman, 1974).

Care must be taken in interpreting these studies. For example, in the Java sparrow experiments, two of four birds preferred musical pieces by Bach over Schoenberg and by Vivaldi over Carter, while the others showed no preference; one bird preferred Bach over white noise (Watanabe & Nemoto, 1998). The authors argued that the birds seemed to prefer classical music over modern music and that their results demonstrated music by Bach had reinforcing properties on the birds. Such statements can be challenging and have misleading implications. These kinds of categorization studies cannot demonstrate musical preference because the animals are conditioned to a positive stimulus (e.g., a genre or a composer). Other musical preference studies take an importantly different approach. Mingle et al. (2014) examined whether captive chimpanzees preferred different musical styles selected from Ghana, North India, and Japan over one another or over silence. Instead of conditioning the animals to a certain stimulus, their preference behavior was investigated by observing and recording their position during playback of each musical genre. The chimpanzees' enclosure was divided into four zones, from closest to farthest from the speaker. When compared with the control condition (no music), the animals displayed a significant preference for the zone closest to the speaker when the Ghanaian or North Indian examples were played. This strongly indicates that chimpanzees preferred these sounds over silence (Mingle et al., 2014). The authors hypothesized that the chimpanzees may prefer such music because it lacks an obvious pulse, in contrast to the clear, percussive beats of the Japanese taiko drumming example used. Chimpanzees naturally demonstrate regular dominance displays by incorporating isochronous sounds, such as clapping or banging (Goodall, 1986), which suggests that they might perceive the pulsed pattern as threatening (Mingle et al., 2014). Another valuable approach is observing animals' engagement in spontaneous behavior, such as spontaneous drumming and tempo matching in some nonhuman primates (Dufour et al., 2015; Large & Gray, 2015). This provides a starting point to understand the purpose of a species' behavior. Other studies of nonhuman primate musical preference revealed that the animals preferred silence (or white noise) over Western or non-Western music, suggesting the importance of nonmusical control stimuli in music experiments (McDermott & Hauser, 2007; Ritvo & MacDonald, 2016).

A parallel strand of research uses music for animal welfare studies or, contentiously, to enrich animal production in commercial agriculture (de Jonge et al., 2008; Li et al., 2019; Piitulainen & Hirskyj-Douglas, 2020; Wallace et al., 2017). Most of these studies have shown little effect. De Jonge et al. (2008) examined the playing behavior of piglets after weaning when they were exposed to music and playtime before weaning.

Six piglets listened to music while given daily access to a playroom; a control group of six piglets had no access to the playroom but still experienced music. As expected, the playback of music facilitated play behavior post weaning, even without access to a playroom. The authors of the study correctly point to the conditioning nature of the experiment, where the animals connected a pleasant experience (playing) with a neutral one (music). Many other natural or human-produced sounds, we suggest, could have had the same effect as music. Interestingly, the control group showed an increase in play behavior when exposed to music post weaning. The authors suggest that the control group picked up on the excitement of the play group, which might have stimulated playing behavior (de Jonge et al., 2008).

Animal Song

Savage et al. (2015) describe eighteen statistical universal features of music, which include pitch, rhythm, instrumentation, and social context. When it comes to animal song, various definitions exist. In a broad sense, song is regarded as a melodic, metrical composition; it can be instrumental or vocal, and it is subjectively perceived as having an aesthetic purpose. Human songs are defined by anthropogenic constraints, which are paradoxically applied to animal songs: in human music, songs are considered songs when they have predefined characteristics; however, animal songs are often labeled songs only when they display similarities to human song, such as whale or bird song, or exhibit certain predefined characteristics (cf. Fitch, 2006; Rohrmeier et al., 2015). These animal songs are often melodic and include a sophisticated structure or hierarchy, such as the songs of humpback whales. Another good example is the musician wren (*Cyphorhinus arada*): this species' song is perceived as so extraordinarily musical that its name is "musician." By measuring the melodic intervals between successive utterances emitted by this bird, most intervals were revealed to be consonant (Doolittle & Brumm, 2012). Consonance is perceived by the human listener as pleasant or restful, but this also seems to depend on culture (Carterette & Kendall, 1999). Some authors argue that only species that are vocal learners qualify as singers, while others include nonvocal learners in their definition of song (Fitch, 2015; Geissmann, 1999; Marler & Slabbekoorn, 2004). Here, we include nonvocal learners, as our overall goal is to provide an overview of animal musicality, which, in our opinion, includes complex vocalizations such as that of gibbons (likely not vocal learners; see Geissmann, 1984, 1993). Fitch (2015) generally categorizes songs as complex, learned vocalizations, while Torti et al. define songs in indris as "complex sequence[s] of utterances emitted by group members, males and females, adults and subadults, in a co-ordinated manner" (2013, p. 596). In birds, songs are most often considered in a territorial or courtship setting

(Odom et al., 2014). Further, nonhuman primate singing has been documented among certain species of gibbons (Clarke et al., 2006; Geissmann, 2000; Marler & Mitani, 1989). To leave them out would exclude many interesting species often considered musical, according to Hoeschele et al. (2015). Far from adding another definition of song here, we make a distinction between calls and songs. While songs are complex sequences of (likely) nonreferential vocalizations, calls usually have referential properties, such as the semantically meaningful alarm calls in vervet monkeys (*Cercopithecus aethiops*; Seyfarth et al., 1980) and the elaborate signature whistles in several dolphin species (Janik et al., 2006; Sayigh et al., 2007).

Birdsong

Within the animal kingdom, birdsongs are among the most well known and studied songs. According to Fitch (2006), there is more information on the biology and evolution of birdsong than on any other animal signaling system. Birds' vocalizations can be divided into two main types of vocalizations: calls and songs, forming a broad spectrum from simple calls to complex songs (Smotherman et al., 2016). According to Catchpole and Slater (2003), calls are marked by short and discrete vocalizations, uttered irregularly or in isolation, whereas songs are characterized by longer, more complex, stereotyped sequences. Birdsongs are frequently repeated and spontaneously follow discrete daily and seasonal patterns (Catchpole & Slater, 2003), and they are most often associated with courtship or territorial battles (Odom et al., 2014). However, the long-held assumption that only male birds sing is untrue (Morton, 1996; Odom et al., 2014; Slater & Mann, 2004). Female birds seem to sing a lot more frequently in tropical regions than in temperate regions (Morton, 1996), and both females and males may sing solos or duets (Fitch, 2006). Odom et al. (2014) revealed that female song is present in 71 percent of surveyed species. Several studies investigated the function of male birdsong, identifying its role in male-male competition or mate choice (Collins, 2004), while the songs of females are thought to display territoriality, pair-bonding, mate defense, and attraction (see Langmore, 1998, 2000, and references therein). Other hypotheses exist, such as songs working as group "passwords" (Feekes, 1982) or functioning to form bonds within the family (Ritchison, 1983). Singing improves communication over long distances, thereby reducing the costs associated with territorial defense, such as injury from physical confrontations, and it enhances reproductive success (Morton, 1986; Read & Weary, 1992). Duetting (the coordination of a song in time by two participants, resulting in a joint song) is a widespread feature in birds: it appears in more than 200 different bird species (Farabaugh, 1982). Functions of duetting include territory and mate defense (Logue, 2005; Logue & Gammon, 2004; Sonnenschein & Reyer, 1983).

There are differences in interspecific song output, composition, and complexity, correlating with metabolism, foraging ecology, mating systems, and migratory behaviors (Read & Weary, 1992). In almost every songbird species studied today, the young birds need to listen to adults to learn their own species-specific songs (Soha, 2020). Thus, birdsong is a great example of animal culture, and it has been studied extensively (see Otter et al., 2020, for a continent-scale study for two decades). These cultures range from extremely stable (Pipek et al., 2018) to shifting and varying from one year to the next (Garland & McGregor, 2020).

Bat Song

Bat calls and songs span an extensive range of frequencies, up to the ultrasonic. Singing bats were found in five families (Smotherman et al., 2016). Bat songs show analogues to birdsongs, including courtship functions (Behr & von Helversen, 2004) and syntactic organization, being composed of hierarchically structured syllables and phrases (Bohn et al., 2008, 2009, 2013). Most species of bats appear to sing in defense of foraging or roosting territories and in support of courtship behaviors (Smotherman et al., 2016). Bat song remains understudied, mainly due to technical constraints; however, newly developed tools allow the study of bat songs across time, habitats, and behaviors (Behr & von Helversen, 2004; Bohn et al., 2008; Smotherman et al., 2016). Smotherman et al. (2016) propose that bats sing like birds because they fly like birds, which is energetically expensive: one of the main benefits of singing is improved long-distance communication, thereby reducing the need to fly (Morton, 1986). The authors suggest that because singing mitigates the high costs of flying, this likely explains why singing is comparatively rare among mammals.

Whale Song

Cetaceans (whales and dolphins) comprise toothed whales (Odontocetes) and baleen whales (Mysticetes), which vary significantly in their ecology and vocal behavior. Odontocetes include the family of dolphins (Delphinidae), with vocal learning representatives such as bottlenose dolphins and orcas (*Orcinus orca*; Deecke et al., 2000; Janik, 2014; Reiss & McCowan, 1993). These species are highly vocal; however, some do not consider these vocalizations songs due to the lack of complexity (Fitch, 2006; Smotherman et al., 2016). The variety of vocalizations Odontocetes emit are termed calls, pulses, whistles, and codas (Bradbury & Vehrencamp, 2011; Janik et al., 2006; Reiss & McCowan, 1993). Mysticete species, such as the fin whale (*Balaenoptera physalus*), emit species-specific calls that, as songs sung by males, seem to function in breeding displays (Croll et al., 2002). Some Mysticete species emit long and highly complex vocalizations (Payne & McVay, 1971; Rekdahl et al., 2013; Risch et al., 2014; Watkins et al., 1987), especially bowhead whales (*Balaena mysticetus*) and humpback whales (*Megaptera novaeangliae*), which produce songs that feature mature hierarchical structures (Payne & McVay, 1971). Humpback whale songs display a variety of sophisticated features, including cultural transmission, an extensive musical hierarchy, and geographic variation (Garland et al., 2011; Payne & McVay, 1971; Winn & Winn, 1978). The hierarchical structure of humpback whale songs is elaborate, consisting of units that form subphrases and phrases, which create full themes (Cholewiak et al., 2013; Payne & McVay, 1971; Winn & Winn, 1978). Apparently, similar songs are sung by all the males in a population, where song structure gradually evolves over the season (Cholewiak et al., 2013). Humpback whales show remarkable song revolutions, whereby a population-wide shared song type is replaced by a novel type introduced by a neighboring population (Garland & McGregor, 2020, and references therein). This type of cultural transmission occurs extremely fast (within one breeding season) and is far-reaching (across ocean basins), exhibiting a geographic dimension rivaled only by humans (Garland & McGregor, 2020). Bowhead whales are considerably less studied than humpback whales, but current research gives rise to the assumption that their songs might be just as complex and sophisticated, with the sharing of songs between clusters of animals (Erbs et al., 2021; Johnson et al., 2015; Stafford et al., 2018). Stafford et al. (2018) revealed that, over a three-year period, some bowhead whales displayed 184 different song types.

Seal Song

Earless seals (Phocidae) constitute one of three families within the group of pinnipeds—the others being eared seals (Otariidae) and walruses (Odobenidae). All pinniped families are vocal; vocalizations constitute a large part of their social lives, depending on the species. Although odobenids and phocids display complex vocalizations sometimes categorized as song, eared seals' vocalizations consist mainly of less complex, sometimes repetitive calls (termed, e.g., barks and screams), depending on context and sex (Fitch, 2006; Gwilliam et al., 2008; Peterson & Bartholomew, 1969). Phocids exhibit a rich vocal repertoire and use vocal displays during mating, when male vocalizations are often individually distinctive (Boness et al., 2006; Van Parijs et al., 2000, 2003). Females usually vocalize only during mother-offspring interactions, but it depends on the species whether both female and pup call or only pups emit individually distinctive calls (Insley, 1992; Renouf, 1984; Van Opzeeland et al., 2012; Van Parijs et al., 2003). Ralls, Fiorelli, and Gish (1985) showed that harbor seals (*Phoca vitulina*) are capable of vocal imitation: two adult males mimicked English words, and one of them even imitated whole phrases and engaged in formant modulation. This seal became quite popular in the media, mimicking phrases such as "hello there" and "come over here" (Ralls et al., 1985). Stansbury and Janik (2019) reported remarkable vocal learning skills in the closely related gray seals (*Halichoerus grypus*): the animals were able to match modulations in peak frequency patterns of call sequences or whole melodies—which they achieved by modifying formants of their own calls (see also Torres Borda et al., 2021).

Instrumental Music

We start this section by considering the definition of musical instruments and drawing a parallel to the classic definition of tools. We then present some examples of animals using external means for sound production, showing that both animals and humans employ physical structures to create or enhance sound. In fact, we relate the use of physical phenomena in nonhuman animal sound production to the tools classically considered musical instruments. We adopt a broad concept of instrumental music and highlight the remarkable features of sound production across species when production is facilitated by using tool-like structures or piggybacking on physical phenomena.

Instrumental music can be defined as music production facilitated by the use of musical tools. Tool use has been considered a uniquely human trait for centuries. Jane Goodall's (1964) discovery that chimpanzees use tools provoked a tremendous reexamination of what makes us unique as a species. It might be time to acknowledge that every species is unique, instead of redefining our own uniqueness each time a discovery calls it into question. At present, 284 species have been shown to use tools (Bentley-Condit & Smith, 2010). A consistent feature of the definition of tool use is manipulation, or using an object detached from a substrate (see Bentley-Condit & Smith, 2010, for a concise history of tool definition in nonhuman animals). For example, Boswall (1977) identifies a true tool as an object manipulated by its user and not part of the substrate. However, whether something, such as a leaf, is part of the substrate may be subjective. Orangutans take leaves and place them in front of their mouths while vocalizing, whereas tree crickets place themselves in a hole they dig into a leaf while vibrating their wings (Mhatre et al., 2017; van Schaik, 2003). Both species use leaves for sound production, but orangutans can pick up a leaf, whereas tree crickets cannot. Following Boswall's classification, orangutans use a true tool, while the tree crickets do not. However, in several ways, tree crickets' use of leaves is more similar to human tool use than orangutan tool use: tree crickets pick the leaves they use for sound production based on size and modify them accordingly, whereas there is no sign that orangutans behave in such a way. Nevertheless, because orangutans hold the leaves in their hands and tree crickets do not, the former are considered to use a true tool (per the definition) and the latter are not. It may be time to abandon the idea that tool use requires specific motor functions, especially when a primate with an opposable thumb becomes comparable to an insect using a leaf considerably larger than itself. Boswall (1977) defines the leaf, when used by tree crickets, as a "borderline tool"—a tool that remains part of the substrate. The distinction between "true" and "borderline" establishes a hierarchy of value, but defining and refining the vocabulary we use for animals should keep in mind its main purpose: serving questions about concepts, not establishing a hierarchy of value.

A fascinating physical phenomenon, common across species, is the resonance effect in sound production. Most musical instruments make use of this; the body of a violin, flute, and saxophone, for instance, are all resonant objects. In every resonant object, some frequencies make the object vibrate at a greater amplitude than others, resulting in these frequencies being louder relative to others. This depends on many factors, including the dimension, shape, tension, and mass of the object. In this way, the conception and construction of musical instruments consider the desired frequencies of the user. Male mole crickets (Orthoptera: family Gryllotalpidae), for example, use the resonance effects of their burrow: They build horn-like holes in which they produce sounds by rubbing their forewings against specialized anatomical structures to attract females. They gradually restructure their burrows to bring its resonance closer to their call frequency, which is constrained mainly by body size, in order to boost sound amplitude. To some extent, mole crickets tune their burrows (Forrest & Green, 1991), and they seem to do so by trial and error, making short chirps during burrow building, after which they adjust its volume and shape (Bennet-Clark, 1987). This results in a louder signal with lower frequencies at a higher intensity, closer to pure tones (Bennet-Clark, 1987). In two different species of mole crickets, louder calls attract more females (Forrest & Green, 1991; Walker & Forrest, 1989), which indicates that sound amplification and modification provide an evolutionary benefit.

Quite similarly, the short-tailed cricket (*Anurogryllus muticus*) selects its call site and body position to optimize sound amplification (Erregger & Schmidt, 2018). It uses anthropogenic calling sites (e.g., walls of buildings or concrete stairs) to amplify signals, which presumably allows its calls to be heard twice as far (Erregger & Schmidt, 2018). Male sand gobies (*Pomatoschistus minutus*) are tiny fish that produce mating calls inside cavities underneath submerged objects like stones, shells, and artificial shelters. They cover these objects by piling sand onto them; the function of this behavior has been discussed for decades. It appears that the sand pile amplifies the signal and therefore aids in attracting females (Lugli, 2013). Male Mientien tree frogs (*Kurixalus idiootocus*) modify calling sites by using anthropogenic objects with high resonance properties

(Tan et al., 2014). Spix's disc-winged bats (*Thyroptera tricolor*) also use cavities to communicate by choosing roosting structures that resemble an acoustic horn (Chaverri & Gillam, 2013). In this case, the cavity amplifies both incoming and outgoing vocalizations. While some species select or adjust their burrows to match the cavity's resonant frequency to that of their calling frequency, tree-hole frogs (*Metaphrynella sundana*) do the reverse: they adjust their calling strategy and pitch to the shape and volume of the hole from which they call (Lardner & bin Lakim, 2002). In the rain forest, cavities can fill rapidly with water, altering their resonant frequency. When this happens, frogs adapt their frequency to consistently produce a loud signal.

A second phenomenon often encountered in instrumental music is acoustic short-circuiting. Membrane vibration produces sound waves. When moving outward, one side of the membrane delivers positive pressure to the air, while the other delivers negative pressure. The converse happens when the membrane moves inward. The membrane therefore produces sound waves from each side that are out of phase. When these wavelengths meet, a destructive interference occurs and attenuates the produced sound. One way to reduce short-circuiting is delaying the confrontation of these two wavelengths by elongating the distance they travel before meeting. Many musical instruments are designed to reduce this acoustic short-circuiting by adjusting the structure, shape, or thickness of the instrument (Heller, 2013). Tree crickets (genus *Oecanthus*) deal with the same issue: They set their forewings, which are vibrating membranes, into resonant vibration while standing on leaves (Mhatre et al., 2017). Sometimes they cut a hole in the leaf, position themselves in the hole, and call. This strategy against short-circuiting is similar to the one used in loudspeakers: the leaf acts as a baffle, like a loudspeaker's membrane (Heller, 2013). The out-of-phase wavelengths must travel all over the leaf before they meet, which attenuates the destructive interference and amplifies the sound level. In decision-making experiments, crickets chose big leaves over small ones and tended to make the hole into the center of the leaf. This resulted in calls that were up to four times louder than when the cricket was standing on the edge of the leaf (Mhatre et al., 2017). Some populations of Bornean orangutans (*Pongo pygmaeus*) share a cultural trait of using vibrating membranes for sound production: they place leaves in front of their mouths while producing the so-called kiss-squeak vocalization, an agonistic signal produced in the face of a threat (Wich et al., 2008). The use of the leaves to produce sound seems analogous to that of humans using instruments such as the kazoo or mirliton (Wieczorkowska et al., 2007). Kiss-squeaks can be produced with or without leaves, but kiss-squeaks with leaves are louder and have a lower maximum call frequency than those produced using only the mouth (Hardus et al., 2009). This may be a sort of dishonest signaling: the maximum frequency of a sound provides information about its emitter, and a lower frequency indicates a larger individual (Charlton & Reby, 2016; Martin et al., 2017); therefore, lowering the frequency by using a tool may mislead the receiver about the emitter's size and potentially dissuade it from attacking.

The last element of instrumental music discussed here is the use of percussion (Savage et al., 2015). Drumming is a common behavior in a variety of nonhuman primates, such as bonobos (*Pan paniscus*) and chimpanzees (Arcadi et al., 1998; De Waal, 1988), but underlying regular beats have rarely been detected (Kugler & Savage Rumbaugh, 2002). Nonhuman primate drumming may be of particular importance when studying the origins of music due to the phylogenetic proximity to our own species (Bispham, 2006). General characteristics of drumming include structure and context (Dufour et al., 2015; Merker et al., 2009), and according to Arom (2000), these constitute intentionality, decontextualization, and formality. However, these characteristics do not appear solely in humans. Dufour et al. (2015) examined a spontaneous performance of a captive-born chimpanzee according to these characteristics: the chimpanzee's drumming seemed to be intentional (focused on drumming), was decontextualized (the animal was unaccompanied, so no social context), and displayed a formal quality (even intervals with regular beating). Chimpanzees drum with their hands and feet on tree buttresses, often accompanied by pant-hoot calls, a species-specific long-distance call (Reynolds, 2005). Babiszewska et al. (2015) suggest that chimpanzee drumming may serve to coordinate the movement and distribution of dispersed individuals within a community. Another study describes chimpanzees throwing stones against trees, mainly coupled with pant-hoot calls (Kühl et al., 2016). Male palm cockatoos (*Probosciger aterrimus*) shape tree twigs into drumsticks and use them to strike hollow tree limbs during vocal and visual displays (Heinsohn et al., 2017; Wood, 1984). This drumming is nonrandom and creates a regular pulse, and the birds have a wide range of tapping rates both within and between individuals (Heinsohn et al., 2017). Remarkably, each individual has its own consistent signature that differs significantly in intertap intervals. With the goal of identifying the significance of these differing beat rates, the authors considered other species' behavior and suggest that these drumming displays encode information about the drummer: the beat rate in palm cockatoos might be age related, as it is in humans, who produce a spontaneous regular beat rate from early childhood that decreases with age (Drake et al., 2000). Beat rate might be an identity cue, given that some bird species have recognizable songs, perhaps enabling the recognition of strangers over neighbors (Stoddard et al., 1991). Woodpeckers (Piciformes: family Picidesdrum) commonly drum by repeatedly striking their beaks against resonating surfaces. These displays seem to have a mating and territorial function (Williams, 2005) and can carry individual-level information (Budka et al., 2018). Woodpeckers also drum on anthropogenic constructions such as metallic drainpipes and gutters, likely choosing surfaces with high resonating properties (De Ernest, 2005).

These examples show parallels between the use of human musical instruments and nonhuman animal sound production. The main commonality lies in the use of external devices (tools or instruments) to manipulate sound when bodily structures (e.g., the vocal tract) fail to do so. This manipulation should constitute an improvement of the emitted sound, as it likely comes with a benefit, such as frequency-modulated kiss-squeaks to deter potential threats. Determining whether a trait constitutes an improvement is a thorny question. From a biological point of view, frequency modulation can be considered an improvement if it has a positive effect on reproductive success. In the foregoing examples, we tried to analyze as many elements as possible to assess this question of evolutionary function. When animals, such as mole crickets, adjust their sound production, probably due to auditory feedback, we are much more confident in calling the object they use a sound production tool, especially because auditory-sensorimotor integration is known to be crucial for musical performance (Bishop et al., 2014; Osmanski & Dooling, 2009). In other cases, determining whether an object used during sound production improves the signal may be less clear-cut. For example, the cohesion calls emitted by the Spix's disc-winged bat in a cavity are slightly louder with enhanced directionality, but because the signal receivers are flying conspecifics, it is debatable whether cavities constitute sound-producing tools. However, because the incoming calls are much louder, cavities might be considered hearing tools rather than sound-producing tools (Chaverri & Gillam, 2013).

The amplification of sound is crucial in the conception of many instruments, along with optimization of the resonance effect and reduction of acoustic short-circuiting (Heller, 2013). The importance of sound amplification shouldn't be underestimated in the evolution of human music: researchers found a positive correlation between the resonance properties of French caves and the number of prehistoric paintings and signs, suggesting an early and considerable interest in sound quality and resonance properties among prehistoric humans (Reznikoff, 2008). More recent examples include Greek and Roman amphitheaters, which have astonishing amplification properties evolving across time; some of the more ancient ruins date to approximatively 600 BC (Mourjopoulos, 2015).

Synchronization

Entrainment and Beat

Rhythmical entrainment is the ability to perceive a beat (i.e., the underlying musical pulse) and align one's body movements to it (Hoeschele et al., 2015; see also Witek, chapter 7 of this volume). Studies have demonstrated that entrainment is not, as previously thought, unique to humans. It may be linked to vocal production learning, although studies have proved that some animals that are unlikely to possess this ability can perceive a pulse in a regular stimulus or "keep the beat" (Cook et al., 2013; Patel et al., 2009). The vocal learning–beat perception and synchronization hypothesis states that vocal production learning, or vocal mimicry, is a species' prerequisite to perceiving a pulse in a periodic stimulus and synchronizing movements to it (Patel, 2006).

Sea lions (*Zalophus californianus*) are not considered vocal learners, but a four-year-old female sea lion named Ronan was tested on her entrainment abilities (Cook et al., 2013; Rouse et al., 2016). Cook et al. (2013) examined the sea lion's capabilities with respect to the three criteria stated in the vocal learning–beat perception and synchronization hypothesis (Patel, 2006): the ability to entrain to (1) rhythm multimodally, (2) a range of different tempos, and (3) a tempo embedded in joined rhythmic-melodic elements. These criteria were tested by six different experiments: (1) entrainment to a familiar stimulus, (2) transfer of entrainment to novel tempos, (3) assessment of beat-matching performance as a potential stimulus-response chain, (4) transfer of entrainment to complex musical stimuli, (5) entrainment to a novel complex musical stimulus, and (6) assessment of the capability for sustained entrainment. Ronan was trained to respond to a visual discrimination stimulus by bobbing her head and neck up and down. She was then trained to bob her head to auditory stimuli. She learned all six tasks, displaying the ability to entrain and synchronize motor behavior to an auditory beat. Remarkably, Ronan was able to transfer to novel tempos and stimuli, including complex settings. She kept the beat in musical pieces with both steady and unsteady tempos, meeting all three criteria of the vocal learning–beat perception and synchronization hypothesis (Patel et al., 2009). Thus, a California sea lion was the first nonhuman mammal to exhibit the ability to keep the beat (Cook et al., 2013).

Duets and Choruses

Duetting and chorusing are remarkable capacities found in insects, anurans, birds, and primates. Interestingly, chorusing seems to involve males only, while duets include male-female pairs (Yoshida & Okanoya, 2005). A prerequisite of duetting is the ability to take turns, or send an acoustic signal after the preceding signal has ended (Yoshida & Okanoya, 2005). Duetting is not restricted to song-learning species. Gibbons provide a highly interesting subject, as all species of gibbons exhibit elaborate vocalizations; in most cases, mated pairs combine their songs to create coordinated duet songs (Geissmann, 1999). Duets may have several functions: territorial advertisement, mate attraction, and maintenance of pair and family bonds (Geissmann, 1986, 1999). By investigating the acoustic variation between daughters and mother-daughter resemblance, a more recent study suggested that in agile gibbons (*Hylobates agilis agilis*), mother-daughter duets may indicate socially mediated vocal flexibility in subadults and adults, as well as suggesting that mother-daughter co-singing may enhance vocal development (Koda, Lemasson, et al., 2013).

Parameters of Sound

As a first principle of biomusicology, Fitch (2015) established the importance of identifying and studying its multiple interacting components. Music is certainly more complex than the sum of its components. On the one hand, key to understanding complex sounds is the ability to isolate individual sound features in nonhuman animal production and perception. On the other hand, one can expect the interactions of different features to produce completely different results.

Sound comprises three nonexclusive components: amplitude (sound level), temporal features, and spectral features (parameters relative to pitch, frequencies). Here we provide an overview of the latter two, presenting how they are featured in the nonhuman animal kingdom. We discuss both fieldwork and lab studies to allow comprehensive conclusions regarding musical capacities. We share the views of Shofner (Plack et al., 2005) and Fay (1994) that cross-species research should ask this question: Are the stimulus features that influence perception and production the same in human listeners and in animals? Moreover, we want to go beyond these comparisons and be open to the possibility that nonhuman animals possess categorization abilities that might be utterly different from ours.

Temporal Parameters

Rhythm Rhythm can be defined as a nonrandom temporal auditory pattern (Hoeschele et al., 2015) and can be found in a variety of modalities and species (for a review, see de Reus et al., 2021; Ravignani, 2019a). Hagmann and Cook (2010) tested pigeons' ability to discriminate between different meters (the regular recurrence of stressed and unstressed beats), rhythms, and tempos and found that pigeons can time periodic auditory events. The birds readily discriminated 8/4 and 3/4 meters, fast and slow tempos of piano sound, and novel tempos. However, they were incapable of discriminating arrhythmic and rhythmic sound patterns.

Male northern elephant seals (*Mirounga angustirostris*) exhibit an extensive and highly competitive courtship display. Males of this species fight for status in the dominance hierarchy, where alpha males mate with and control female harems and beta males only occasionally mate with females (Le Bœuf & Petrinovich, 1974). Vocalizations play an elaborate role: mature male northern elephant seals produce a rhythmic series of pulses, where the call of each individual is characterized by tempo and timbre (Casey et al., 2015). Playback experiments showed that males memorize and recognize individual rhythmic and timbral features of other males' voices to identify their competitors (Mathevon et al., 2017). In another study, the calling of a harbor seal (*Phoca vitulina*) pup was investigated with respect to antisynchronous timing and its rhythmic capacities (Ravignani, 2018, 2019b). The wild-born, seven-day-old pup showed rhythmic call characteristics. Using playback experiments, Ravignani (2019b) demonstrated that the pup adapted the timing of her calling in response to conspecifics' calls. In detail, the calls' onset was adjusted to occur at a fraction of the playback tempo, thereby displaying a relative-phase antisynchrony. Interestingly, this species displays vocal learning in male adult individuals (Ralls et al., 1985) and a very vocal (Van Parijs et al., 1999) and vocally plastic (Torres Borda et al., 2021) puppyhood.

Isochrony vs. anisochrony Isochrony describes a series of events occurring at evenly spaced time intervals. Isochrony makes subsequent events predictable, and it facilitates entrainment (Arom, 2000; Dufour et al., 2015). The perception of isochronous patterns has been tested in several nonhuman species, including European starlings (*Sturnus vulgaris*; Hulse et al., 1984), an avian species with the ability to discriminate between rhythmic and arrhythmic patterns. Hulse, Humpal, and Cynx (1984) constructed an experiment with two different sound patterns: one according to a linear rule, in which tones and intertone intervals of equal duration alternated, and one according to a hierarchical rule, in which two subpatterns alternated. The arrhythmic pattern consisted of a tone and intertone interval, both of random duration. To receive a food reward, the birds were asked to peck on one key for a rhythmic pattern and on another key for an arrhythmic pattern. The birds learned the rhythmic-arrhythmic discrimination, and their discrimination accuracy was identical in both the linear and the hierarchical rhythmic structures. Transfer tests revealed that the birds reliably discriminated even if temporal structures were transformed logarithmically or additively, interchanged, or shifted an octave in pitch. However, performance deteriorated when patterns were degraded by holding tone duration constant while intertone duration varied randomly (or vice versa) (Hulse et al., 1984). In contrast to these findings in starlings, Hagmann and Cook (2010) found no evidence that pigeons could discriminate between rhythmic and arrhythmic structures.

Spectral Parameters

Pitch Rather than being a purely physical feature, *pitch* is a perceptual attribute related to a spectral feature—the fundamental frequency and its harmonics—that enables the perception of sounds as higher or lower (Hoeschele et al., 2015). In some papers, pitch is termed a *music note*. Actually, a note can be considered a particular pitch, depending on culture. For example, a sound with a pitch of 440 Hz, according to the current English convention, is termed an A note, while a sound with a pitch of 448.35 Hz does not have a note name in English. Two main categories of pitch perception and production can be distinguished: the *absolute pitch*, without an external referent, and the *relative pitch*, resulting from an external referent. For example, when listening to a succession of notes played on a keyboard, recognizing a melody or perceiving an ascending pattern results from relative frequency perception abilities. However, if this same succession of notes is perceived only as an x-note followed by a y-note, it means that mainly absolute pitch perception abilities are mobilized. Both *pitch height* and *pitch chroma* are components of absolute pitch. When we listen to music, these attributes interact, and some of them prevail. In humans, timbre can interact with pitch: in an experiment by Warrier and Zatorre (2002), subjects perceived a larger difference in pitch between two tones if their timbre was different.

Absolute pitch

PITCH HEIGHT Pitch height amounts to the fundamental frequency of a sound; for example, 10,000 Hz may be considered high-pitched and 100 Hz low-pitched. Different species have different sensitivities and discrimination abilities for pitch height. In that context, sensitivity refers to which frequencies and which minimum amplitudes can be perceived. Audiograms are common methods of measuring sound reception, based on behavioral or neural responses. Compared with humans, some species might need louder audio stimuli, such as yellow-bellied slider turtles (*Pseudemys scripta*; Patterson, 1966), or sounds with a different frequency range, such as house mice (*Mus musculus*) and some bat species (*Eptesicus fuscus*, *Rhinolophus ferrumequinum*; (Bohn et al., 2006; Heffner et al., 2001). Different species might present different sensitivity patterns: humans hear middle-range frequencies (400–4,000 Hz) best, and their sensitivity decreases for high-range and low-range frequencies. However, various bat species have two regions of enhanced sensitivity separated by a relatively insensitive region (Bohn et al., 2006). Coqui frogs (*Eleutherodactylus coqui*) even exhibit a different sensitivity pattern between females and males (Narins & Capranica, 1976).

To identify such hearing thresholds, tones are played to animals in operant conditioning experiments, with some frequency ranges rewarded and alternated with unrewarded frequency ranges. For example, the rewarded frequency range might be 500 to 700 Hz and the unrewarded range 300 to 500 Hz. If a 550 Hz tone is played and the animal shows the correct response, it is reinforced. Some studies use three-pitch range tasks, while others use tasks up to a range of eight pitches. Like rats, humans perform

Table 3.1
Pitch height experiments

Species	Task	Results	Reference
Budgerigars (*Melopsittacus undulateus*)	Eight-pitch range	High accuracy	(Weisman et al., 2004)
White-throated sparrows (*Zonotrichia albicollis*)	Eight-pitch range	Medium accuracy	
Zebra finches (*Taeniopygia guttata*)	Eight-pitch range	High accuracy	(Lee et al., 2006)
Black-capped chickadees (*Poecile atricapillus*)	Eight-pitch range	High accuracy	
Mountain chickadees (*Poecile gambeli*)	Eight-pitch range	Medium accuracy	
Pigeons (*Columba livia*)	Eight-pitch-range	Low accuracy	(Friedrich et al., 2007)
Boreal chickadees (*Poecile hudsonicus*)	Eight-pitch range	Low accuracy	(Weisman et al., 2010)
Brown rats (*Rattus norvegicus*)	Three-pitch range	Success	(Weisman et al., 2012)
	Eight-pitch range	Fail	

poorly at these tasks, succeeding in a three-pitch range but not an eight-pitch range (Friedrich et al., 2007; Weisman et al., 2012). In a cross-species review by Weisman et al. (2012), bird species succeeded more easily than mammals. However, some birds were more accurate than others. The authors hypothesized that birds with more developed vocal learning abilities performed better.

Pitch Chroma Pitch chroma concerns the names of notes and their overlapping partial harmonics. A 440 Hz tone has the same pitch chroma as an 880 Hz one, and they are both A notes. Depending on the experimental conditions, humans are more likely to categorize different tones as similar when they have the same pitch chroma (Hoeschele, 2017; Hoeschele, Weisman, et al., 2012). This phenomenon is called *octave generalization*.

In nonhuman animals, Blackwell and Schlosberg (1943) concluded that rats exhibit octave equivalence. They trained rats to react only when 10 kHz pure tones were played; however, the rats also reacted to previously unrewarded tones that were one octave lower than the reinforced stimulus (i.e., 5 kHz), indicating octave equivalence. This study was criticized because the stimuli might have included harmonic distortion, which could have provided octave information (Burns, 1999). Octave equivalence was later tested successfully in rhesus monkeys (*Macaca mulatta*; Wright & Rivera, 2000) and bottlenose dolphins (Richards et al., 1984). Cynx (1993) failed to show octave

Table 3.2
Pitch chroma experiments

Species	Octave equivalence	Reference
Brown rats	Successful Contested	(Blackwell & Schlosberg, 1943)
Bottlenose dolphins	Successful	(Richards et al., 1984)
European starlings	Failed Contested	(Cynx, 1993)
Rhesus monkeys	Successful	(Wright & Rivera, 2000)
Black-capped chickadees	Failed	(Hoang, 2015; Hoeschele et al., 2013)
Budgerigars	Failed	(Wagner et al., 2019)

equivalence in European starlings, but this study was criticized because it did not control for pitch height. Hoeschele, Weisman, and Sturdy (2012) made their point by replicating Cynx's experiment with humans. Participants were trained to react to a pure tone and then exposed to entirely new tones, including one having an octave interval with the probe tone. This procedure failed to prove octave equivalence in humans, despite its presence. In similar procedures, tests for octave generalization in black-capped chickadees (Hoang, 2015; Hoeschele et al., 2013) and budgerigars (Wagner et al., 2019) likewise failed. This beautifully demonstrates the importance of fine-tuned experimental design in cognitive testing.

Relative pitch Relative pitch information can be divided into the pitch contour and the frequency ratio processing (Deutsch, 2013).

PITCH CONTOUR The pitch contour refers to the directional change of frequency (e.g., is this tone higher-pitched than the previous one?). A rising intonation can change the meaning of a word in tonal languages like Mandarin or Tikuna and change a statement into a question in more than 70 percent of the world's languages (Bolinger et al., 1978; Murphy, 2013). Some species exhibit significant discrimination between rising and falling tones and can successfully generalize over new frequencies, including ferrets (*Mustela furo*; Yin et al., 2010), bottlenose dolphins (Ralston & Herman, 1995), and European starlings (Page et al., 1989). Other species, such as capuchin monkeys (*Cebus apella*; D'Amato & Colombo, 1988), cowbirds (*Molothrus ater*), and mockingbirds (*Mimus polyglottos*), fail to do so (Hulse & Cynx, 1985).

FREQUENCY RATIO Frequency ratio processing is one of the fundamentals of tonal music. In music theory, the ratio between two tones is called the *interval*. When playing a song, regardless of the tone played first, if the interval between each successive note is conserved, the song is easily recognized. The melody will be *transposed*. Some researchers trained animals to discriminate tone sequences (melodies, chords, or simple tones) with a consistent ratio, performing a generalization task with new pitch height. European starlings (Hulse et al., 1995), pigeons (Brooks & Cook, 2010), and black-capped chickadees (Hoeschele, Cook, et al., 2012) succeeded in tests of relative pitch discrimination and generalization. A complementary approach focuses on animal acoustic production and finds consistent patterns in the frequency ratios of vocalizations. Veeries (*Catharus fuscescens*), black-capped chickadees, Carolina chickadees (*Poecile carolinensis*), and white-throated sparrows exhibit consistency in their pitch ratios between vocalizations of the exact phrase, despite variability in each vocalization's absolute pitch (Hurly et al., 1991; Lohr et al., 1991; Weary et al., 1991; Weisman & Ratcliffe, 2004).

Consonance and dissonance Frequency ratios may influence human affective perception (Virtala & Tervaniemi, 2017). Consonant intervals are considered pleasant and restful, whereas dissonant intervals are considered unpleasant and tense. Nevertheless, the interval's effect depends on culture, period, and musical training (Carterette & Kendall, 1999). McDermott et al. (2016) argued that consonance could be a creation of Western culture. They asked Tsimane' participants from lowland Bolivia to rate the pleasantness of consonant and dissonant chords. Although the Tsimane' did not exhibit any variation in preferences, Bolivian and American citizens did. Bowling et al. (2017) criticized this work, highlighting both the avoidance of the most consonant interval across cultures (the octave) and the exclusion of highly dissonant tone combinations that are usually avoided but not unthinkable in music. They summarized, "These restrictions diminish the contrast between stimuli and would obscure their differentiation, especially by naive listeners" (Bowling et al., 2017, p. 119). They argued that McDermott's group did not discuss the similarity of tonal organization across musical cultures, with the most frequently used intervals (the octave, perfect fifths and fourths) corresponding to those considered the most consonant by culturally diverse listeners (Bowling & Purves, 2015; Burns, 1999).

The interplay of biology and culture in consonance remains controversial. Helmholtz (1912) argues that dissonance corresponds to a physical phenomenon: a slow periodic fluctuation in the amplitude of the sound wave leads to perceived roughness, for example, by slight frequency differences in fundamental frequencies or overtones of simultaneously played sounds. Bowling, Purves, and Gill defend the vocal similarity theory: "consonance of chords is predicted by their relative similarity to voiced speech sounds" (2018, p. 216). This controversy becomes even more complex when considering that the more tones included in a chord, the rougher it is, whereas the consonant perception does not necessarily decrease (Bowling & Purves, 2015).

Some studies look at the different processing of consonant versus dissonant intervals in nonhuman animals (for a review, see Toro & Crespo-Bojorque, 2017). Java sparrows (Watanabe et al., 2005), black-capped chickadees, European starlings, and Japanese monkeys (Izumi, 2000) successfully discriminated consonant over dissonant intervals and generalized them toward new frequencies. Pigeons and rats were capable of discrimination but not generalization. Other studies looked at preferences: the only species with a preference for consonant over dissonant melodies were domestic chicks (*Gallus gallus*) and a single infant chimpanzee (Sugimoto et al., 2010). Recently, budgerigars were tested with the same stimuli as the chicks but showed no preference (Wagner et al., 2020). Other primate species were tested with isolated chords but showed no preference, including Campbell's monkeys (*Cercopithecus campbelli*; Koda, Basile, et al., 2013) and cotton-top tamarins (*Saguinus oedipus*; McDermott & Hauser, 2004). A study of tungara frogs (*Physalaemus pustulosus*) tested the attractiveness of artificial mating calls with manipulated ratios, which did not influence female preference (Akre et al., 2014). In addition to the difficulty of experimentally proving preferences in nonhuman animals, the use of consonant intervals in such studies may be questioned. First, only Western intervals were used, and second, consonance is not always associated with pleasantness in humans, so one might wonder why it would be for nonhuman animals. Third, some studies used equal temperament as a tuning system to build their chords and melodies, which was developed during the seventeenth century for Western musicians. Obviously, human musical composition should not be unproblematically transferred to nonhuman animal experiments, given that recent instrumental adjustments (e.g., equal temperament) are unlikely to have biological significance. With this in mind, just intonation (which favors interval purity) should be the preferred tuning system for comparative research (Doolittle & Brumm, 2012; Richner, 2016). Nevertheless, consonance does result from particular frequency ratios. Some studies have concluded that nonhuman animals successfully generalized a consonance-dissonance rule over new chords (Toro & Crespo-Bojorque, 2017). However, some intervals were identical to the training intervals. Therefore, the animals might have memorized and integrated relative pitch without considering consonant or dissonant quality (Toro & Crespo-Bojorque, 2017).

Timbre and spectral shape Spectral shape is the overall pattern of spectral amplitudes across particular frequency bands. Timbre includes the spectral shape, the amplitude envelope, and how both change over time. Only a few studies provide information on timbre perception in nonhuman animals, surely because of the difficulty of working with complex sounds. However, timbre should be investigated in comparative studies due to its possible interaction with pitch perception. In humans, this effect is well documented (McLachlan, 2016). It has also been detected in other species, such as black-capped chickadees (Hoeschele et al., 2014), zebra finches, and budgerigars (Lohr & Dooling, 1998). Timbre may well be a salient cue for several species: Northern elephant seals memorize their rivals' unique timbre to adjust their behavior (Mathevon et al., 2017), starlings categorize tone sequences based on spectral shape (Bregman et al., 2016), and some bird species (zebra finches and budgerigars) are highly accurate in perceiving variations in timbre, much more so than humans (Lohr & Dooling, 1998; Amagai et al., 1999).

Conclusions, Pitfalls, and Prospects

We aimed in this chapter to provide an overview of studies on animal musical cognition and biomusicality, advocating the assessment of human musicality by adopting a comparative approach. We highlighted why comparative questions should be addressed species specifically using appropriate modalities, such as designing cognitive tasks in a way that allows animals to respond naturally (Bräuer et al., 2020). We also pointed out that presenting identical tasks to different species might lead to an underestimation of their cognitive abilities if the task is not equally relevant to each species. Psychophysical experiments may reveal cognitive abilities in animals, providing insight into music subcomponents, but it is crucial to not consider these in isolation. Holistic experiments are a valuable approach to gain insights into biomusicality (see Williams and Sachs, chapter 11 in this volume, for a parallel). Much of the reviewed research used unnatural sounds or musical instruments, which calls to mind the experiments of Bregman, Patel, and Gentner (2012) to test relative pitch perception in starlings. The birds failed to recognize artificial pitch-shifted melodies but succeeded in recognizing pitch-shifted songs of conspecifics. Marler (1982) suggests considering that animals possess species-specific hierarchies of attentional preferences for perceptual cues and hypothesizes that the relative position of stimulus features in each hierarchy may be task dependent. In the study by Hulse and Cynx (1985), starlings were able to generalize pitch contour, but not independently of absolute pitch. When transposed to an octave away from the training frequency range, the birds failed to distinguish the falling phrases from the rising ones. However, they succeeded when the transposition was just one semitone apart. Later, Page, Hulse, and Cynx (1989) showed that starlings use both absolute and relative pitch information during a pitch contour task (for a review, see Patel, 2017). Moreover, starlings use primarily spectral shape to recognize a tone sequence, rather than relative and absolute pitch (Bregman et al., 2016). This is a key difference from humans, who tend to consider pitch over spectral shape information to recognize tone sequences (Patel, 2017). Humans are likely to recognize a piece of well-known music regardless of whether it is played on a guitar or a piano. These results should inspire us to consider distinctive discriminative strategies or hierarchies in other species. Though this might not be easily achievable, the design of cognitive experiments should not be inspired solely by our own species' cognition. Rather, they should be broadened to encompass the wide variety of cognitive capacities present in the field of comparative research. We also suggest the investigation of additional features of sound; for example, starlings discriminate sound sequences with different amplitude (loudness) patterns (Bernard & Hulse, 1992), but discrimination over loudness has barely been investigated in nonhuman animals.

We recognize the benefits of combining field studies and laboratory work: observing natural, spontaneous behavior is particularly important to gain insight into a species' ecology, even though underlying mechanisms can be revealed only in controlled cognitive experiments. Both are needed for many reasons, but just as an example: a very well trained animal can trick us into believing that the trained behavior is within the animal's natural repertoire (Bräuer et al., 2020). We advocate a rethinking of animal categories: there is a plethora of definitions of *songs* or *tools* in nonhuman animals, yet giving a (human) definition to a nonhuman animal song seems somewhat paradoxical, and the same applies to tool use or instrumental music. Therefore, we try to avoid current definitions and prefer to highlight the abundance of interesting features found in nonhuman animal sound production, such as innovation, optimization, and active modification of the natural habitat, and we hope to find this broader perspective in more research. We understand that categorization is both an involuntary (instinctive in human and nonhuman animal cognition) and a necessary part of understanding, but we would like to consider more gray areas. By complementing black and white categories with shades of gray, we aim to avoid overlooking musical capacities that might provide us with valuable insights into ultimate and proximate explanations of the evolution of biomusicality.

Note

1. Fitch (2015) also adds glossogeny, the study of cultural transmission, to Tinbergen's classic four questions. While we acknowledge the importance of cultural transmission and culture-biology coevolution in biomusicology, a comprehensive overview of this literature is beyond the scope of this chapter (but see Patel, chapter 1 of this volume; Tomlinson, chapter 2 of this volume).

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