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Rhythmic Preferences in Budgerigars

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Abstract

Rhythm is one of the most widespread aspects of human music, and vocal-learning species have emerged as strong non-human models in the comparative study of rhythm-related processing. Earlier work in budgerigars (Melopsittacus undulatus), an advanced vocal-learning parrot, reported sex-specific preferences in a place-preference paradigm using artificial percussion stimuli: female birds spent more time near rhythmic than arrhythmic stimuli, while male birds showed the opposite pattern (Hoeschele & Bowling, 2016). The present study extended this work by using stimuli derived from natural budgerigar vocalisations, by adding a silent comparison condition to disambiguate attraction from avoidance, and by analysing visit duration and visit counts alongside listening time.

Thirteen budgerigars (6 females, 7 males) were tested in a three-perch apparatus across three two-hour sessions, with rhythmic (R), arrhythmic (A), and silent (S) perches counterbalanced within and across sessions. Listening time, visit counts, and visit duration were analysed using mixed-effects models, negative binomial GEE, and within-bird bootstrap on bird-level medians, respectively. Rhythmic-versus-arrhythmic contrasts were treated as confirmatory; silent-condition analyses as exploratory.

Listening time showed a session-dependent rhythmic preference, with rhythmic exceeding arrhythmic by Session 3. Visit counts produced a marginal rhythmic-by-sex interaction in the same direction as Hoeschele and Bowling (2016). Visit-duration analyses supported a positive R-versus-A contrast carried by female birds, and an overall silent-versus-arrhythmic contrast supported in both sexes; within males, the silent perch was also preferred over the rhythmic perch.

These findings indicate that budgerigars develop a rhythmic-versus-arrhythmic preference across sessions when given ecologically relevant vocal stimuli. The supported silent-over-arrhythmic contrast reframes the effect as one in which aversion to arrhythmic structure plays a substantial role alongside any attraction to rhythmic structure.

Kurzfassung

Rhythmus ist eines der am weitesten verbreiteten Merkmale menschlicher Musik, und stimmlernende Arten haben sich als starke nicht-menschliche Modelle in der vergleichenden Erforschung rhythmusbezogener Verarbeitung etabliert. Frühere Studien an Wellensittichen (*Melopsittacus undulatus*), einem fortgeschrittenen stimmlernenden Papagei, berichteten geschlechtsspezifische Präferenzen in einem Ortspräferenzparadigma mit künstlichen perkussionsbasierten Stimuli: Weibchen verbrachten mehr Zeit in der Nähe rhythmischer als arrhythmischer Stimuli, während Männchen das gegenteilige Muster zeigten (Hoeschele & Bowling, 2016). Die vorliegende Studie erweiterte diese Arbeit durch Stimuli aus natürlichen Wellensittich-Vokalisationen, eine stille Vergleichsbedingung zur Unterscheidung zwischen Anziehung und Vermeidung sowie durch die Analyse von Besuchsdauer und Besuchsanzahl zusätzlich zur Hörzeit.

Dreizehn Wellensittiche (6 Weibchen, 7 Männchen) wurden in einer Apparatur mit drei Sitzstangen über drei zweistündige Sitzungen getestet, wobei rhythmische (R), arrhythmische (A) und stille (S) Sitzstangen innerhalb und über Sitzungen hinweg ausbalanciert wurden. Hörzeit, Besuchsanzahl und Besuchsdauer wurden mit Mixed-Effects-Modellen, negativer binomialer GEE bzw. vogelinternem Bootstrap über vogelbezogene Mediane analysiert. Rhythmisch-versus-arrhythmische Kontraste galten als konfirmatorisch, Analysen mit der stillen Bedingung als explorativ.

Die Hörzeit zeigte eine sitzungsabhängige rhythmische Präferenz, wobei die rhythmische die arrhythmische Hörzeit bis Sitzung 3 überstieg. Die Besuchsanzahl ergab eine marginale Rhythmus-mal-Geschlecht-Interaktion in derselben Richtung wie bei Hoeschele und Bowling (2016). Die Besuchsdaueranalysen stützten einen positiven R-versus-A-Kontrast, getragen von den Weibchen, sowie einen still-versus-arrhythmischen Gesamtkontrast in beiden Geschlechtern; bei den Männchen wurde die stille Sitzstange zudem gegenüber der rhythmischen bevorzugt.

Diese Befunde zeigen, dass Wellensittiche bei ökologisch relevanten vokalen Stimuli eine rhythmisch-versus-arrhythmische Präferenz über Sitzungen hinweg entwickeln. Der gestützte still-über-arrhythmisch-Kontrast verändert die Interpretation des Effekts dahingehend, dass Aversion gegenüber arrhythmischer Struktur eine wesentliche Rolle neben einer möglichen Anziehung zu rhythmischer Struktur spielt.

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List of Abbreviations

A	Arrhythmic
BPMC	Beat Perception and Motor Coordination
bpm	Beats per minute
CI	Confidence interval
Cohen's d_z	Standardised mean of paired differences
dB	Decibel
GEE	Generalized Estimating Equations
Hz	Hertz
kHz	Kilohertz
LED	Light-Emitting Diode
MixedLM	Mixed Linear Model
ms	Millisecond
OLS	Ordinary Least Squares
P1, P2, P3	Physical perch locations 1, 2, 3
P(diff > 0)	Bootstrap probability that the contrast is positive
R	Rhythmic
S	Silent
SD	Standard deviation
SE	Standard error

Declaration on the use of AI tools

Claude (Anthropic), model Claude Opus 4.7, accessed via the Claude.ai web interface, was used during the preparation of this thesis in June 2026 for language editing, drafting and reviewing of Python analysis scripts, figure-design code, and translation assistance for the German abstract and summary. All experimental design, methodological decisions, statistical interpretation, and scientific conclusions are the author's own work, independently developed and verified. The author takes full responsibility for the content of this thesis.

1 Introduction

1.1 Rhythm

Rhythm can be understood, in the broadest sense, as the organization of sound events in time. In music, this organization operates on several dimensions at once. The timing of when sounds begin, how long they last, and how they are separated by silence creates the basic temporal scaffolding. On top of this, some events are marked as more prominent than others through accent or stress. Together, these features produce a temporal structure that listeners can perceive and, in many cases, anticipate.
It is useful to distinguish rhythm from related concepts such as pulse and meter. The pulse is the steady underlying beat a listener perceives in a piece of music, and meter is the recurring pattern of stronger and weaker beats that organises those pulses into groups. As Fitch (2013) explains, pulse perception involves extracting a regular pulse, or tactus, from a stream of events, whereas meter involves grouping those events into a hierarchical structure of stronger and weaker positions. These distinctions are important because rhythm is not just any sequence of sounds in time; it is the temporal structure that makes patterned sound intelligible and, often, predictable.
Rhythm is also one of the most widespread features of human music. Musical traditions differ greatly across cultures in melody, harmony, instrumentation, and social use, but temporal organization is consistently present. Importantly, the evidence does not suggest that there is one single rhythmic form shared by all musical cultures. Rather, Savage et al. (2015), in a large cross-cultural analysis of 304 recordings from around the world, found no absolute universals, but they did find strong statistical universals, including recurrent features of rhythm and temporal organization across all nine geographic regions in their sample. In this sense, rhythm is not a minor element of music, but one of the core ways in which music becomes structured, recognizable, and socially shared.

When sound unfolds in a temporally regular way, listeners can form expectations about when future events will occur, making rhythm a useful tool for prediction and coordination. Patel and Iversen (2014) emphasize that beat perception is fundamentally predictive: listeners do not simply react to each sound after it happens; they actively anticipate upcoming beats. This predictive quality is closely linked to movement. Repp (2005), in his review of sensorimotor synchronization research, defines this process as the rhythmic coordination of perception and action and shows that it is especially prominent in music and dance. Rhythm therefore matters in two ways: it structures what we hear and can direct anticipation. This anticipation can then be tied to action: it allows people to move together, coordinate, and participate in shared musical behavior.

Rhythm is not limited to music. It also plays an important role in speech production and comprehension. Poeppel and Assaneo (2020) argue that speech has a remarkably stable rhythmic structure at the relevant temporal scale, and that this rhythmicity is necessary for the construction of intelligible speech. In other words, one can think of speech as temporally organized material that listeners must segment and interpret over time instead of an unstructured stream of sounds. More specifically, rhythmic cues in speech help listeners identify boundaries, track prominence, and process sentence structure as an utterance unfolds. Roncaglia-Denissen et al. (2013) provide

experimental evidence for this by showing that regular speech rhythm improves comprehension of syntactically ambiguous sentences. Relatedly, Gordon et al. (2015) found that children who were better at discriminating musical rhythm also showed stronger grammar skills, suggesting that rhythm processing in music and language may draw on overlapping cognitive resources. Together, these findings suggest that rhythm is not just a feature of speech, but part of how listeners build linguistic structure in real time.

Although rhythm is especially central to human music and speech, temporal patterning is not unique to humans. Kotz et al. (2018) and Ravignani (2019) both note that rhythmic structure and synchrony appear prominently in animal movement and communication, where they can carry communicative relevance. Therefore, it can be inferred that sensitivity to temporal structure is biologically widespread. These results do not directly indicate the same level of sensitivity to rhythm across all species, nor do they quantify how this sensitivity affects perception or movement. Rather, they mark rhythm as a useful lens for studying cognition broadly.

1.2 Musicality

The term musicality is generally used to refer to the cognitive and biological capacities that make music possible. Honing (2018) describes musicality as the set of underlying traits that allow humans to perceive, appreciate, and produce music, while Honing et al. (2015) define it more specifically as a natural and spontaneously developing set of abilities that is constrained by biology and cognition. This distinction is important because music is a cultural product that varies greatly across time and place, whereas musicality refers to the underlying perceptual, cognitive, and affective capacities on which those cultural forms depend. Musicality is then best understood as a collection of component abilities rather than a single trait. Honing et al. (2015) and others have proposed that these components include sensitivity to rhythm, pitch, temporal grouping, melodic contour, and the emotional significance of sound.

Thinking in terms of musicality is useful because it allows music perception to be studied at the level of basic abilities rather than at the level of culturally specific musical systems. This is especially important in a field where musical forms are highly diverse. Trehub et al. (2015) emphasize that musical behaviours are universal across human populations, yet they differ widely in structure, function, and cultural meaning. Mehr et al. (Mehr, et al., 2019) likewise found that music appears in every one of 60 sampled societies, varying along a small number of dimensions but consistently associated with specific behavioural contexts such as infant care, dance, and healing. Together, these findings suggest that while musical traditions are shaped by culture, they are built on shared perceptual and cognitive foundations. Musicality therefore provides a way of talking about what humans broadly share, even when the music they create sounds very different across cultures.

Developmental evidence supports this framing. Hannon and Trehub (2005) showed that 6-month-old infants respond to musical rhythms in a relatively culture-general way, whereas by 12 months they already show more culture-specific rhythmic biases, demonstrating how early biological predispositions and later cultural experience interact in shaping music perception.

Rhythmic processing is also central because it connects perception to action and affect. Musicality is not only about detecting structure in sound, but also about responding to it in meaningful ways. Phillips-Silver and Trainor (2005) demonstrated that movement can influence how infants interpret an ambiguous rhythmic pattern, showing that rhythm perception is closely linked to bodily experience from very early on. In adults, this link between rhythm, movement, and positive affect is especially clear in studies of groove. Janata et al. (2012) define groove as a pleasurable urge to move in response to music, and their work shows that some rhythmic patterns are particularly effective at coupling temporal perception with motor engagement and enjoyment. Rhythm is therefore central to musicality not only because it helps listeners detect structure in sound, but because it turns that structure into embodied, often rewarding experience.

Although the term musicality is most often applied to humans, the capacities it refers to are not assumed to be exclusively human. Comparative work has increasingly argued that the most productive way to study the origins of musicality is not to ask whether other species have "music," but whether they share particular component abilities involved in music perception and production. Honing et al. (2015) therefore argue that the comparative study of musicality is most productive when it targets these constituent mechanisms, rather than asking whether other species possess music as a unified phenomenon. Hoeschele et al. (2015) similarly propose searching for components of musicality across species rather than treating music as a single all-or-nothing trait. This does not mean that all aspects of human musicality are widespread in animals, but it does support the idea that musicality refers to underlying perceptual and cognitive abilities, some of which may be shared more broadly across species.

1.3 Comparative Approach to Musicality

A comparative approach is one of the main ways researchers investigate the origins of musicality. Rather than asking whether other animals "have music" in the human sense, comparative work asks whether they share specific component abilities that underlie music perception and production, such as sensitivity to temporal regularity, grouping, pitch, rhythm, or auditory-motor coupling. Rhythmic behavior is prevalent in the animal kingdom: its forms varying significantly across species and contexts. Ravignani (2019) notes that rhythmic and synchronous behaviors occur in movement and communication across many taxa and Kotz et al. (2018) argue that comparing these behaviors across species and cognitive domains can clarify which mechanisms are shared and which are not.

Although rhythmic behaviors are widespread across taxa (Keehn & Iversen, 2019), human-like rhythmic abilities — particularly beat perception and motor coordination (BPMC) — are rare. BPMC refers to the capacity to extract a regular beat from an auditory rhythm and to align body movements to that beat in a manner that is anticipatory rather than merely reactive, and flexible across a range of tempi (Patel, 2014). Several taxa have shown behaviors consistent with rhythmic processing: parrots and elephants under naturalistic observation, and sea lions and chimpanzees as trained individuals (Patel, Iversen, Bregman, & Schulz, 2009; Hattori, Tomonaga, & Matsuzawa, 2013).

The strongest line of non-human evidence comes from parrots. The case that opened this field was Snowball, a sulphur-crested cockatoo: Patel et al. (2009) showed that he

did not merely move excitedly when music played but adjusted his movements to match changes in tempo, meeting one of the central criteria for beat perception and synchronization. Schachner et al. (2009) extended this work by surveying a large public video database for comparable cases across species and found suggestive evidence of entrainment in 14 parrot species, alongside one elephant species and humans, but not in the many vocal non-mimicking species also represented in the sample. This pattern implied that the tendency was distributed broadly within the parrot clade rather than belonging to one unusual individual, and that it tracked vocal learning ability across species. Parrots also combine several features that may matter for rhythmic entrainment: vocal learning, strong auditory-motor coupling, sociality, and a capacity for flexible, whole-body movement. Parrots are therefore often treated as the strongest non-human model for investigating how rhythm perception and movement can become linked in music-like ways (Patel, 2014).

Within parrots, budgerigars (Melopsittacus undulatus) have been particularly important because they move the field from anecdotal or video-based observation toward controlled experimental work, with demonstrated entrainment to audio-visual metronomes across a range of tempi (Hasegawa, Okanoya, Hasegawa, & Seki, 2011). The species is treated in detail in Section 1.4.

The evidence from other species is generally more limited or more qualified, but it remains informative.

In *elephants*, the evidence for beat synchronization is suggestive rather than as experimentally strong as in parrots. Schachner et al. (2009) found suggestive evidence of entrainment in one elephant species in their video survey, but the material was less controlled than the parrot case studies. Elephants nevertheless remain relevant because they are among the few mammals with clear vocal learning ability, as illustrated by Stoeger and de Silva's (2013) account of an Asian elephant capable of imitating Korean speech.

Sea lions complicate the picture in a different way. Cook et al. (2013) showed that a California sea lion could learn to bob its head in time with rhythmic auditory stimuli, transfer this behavior to novel tempos, and entrain to complex musical stimuli. Because sea lions are not generally treated as classic vocal mimics, this finding challenged a simple reading of the vocal learning hypothesis.

Chimpanzees provide evidence that is intriguing but narrower. Hattori et al. (2013) found that one chimpanzee spontaneously aligned her tapping with an isochronous auditory rhythm after being trained on a keyboard task. This showed some sensitivity to rhythmic alignment, but it remained much more limited than the flexible and tempo-matching behavior seen in parrots.

Across these cases, the picture that emerges is mixed: rhythmic abilities are not absent outside humans, but they also make clear that different species show different degrees and forms of rhythmic competence. One of the main theoretical frameworks used to interpret these findings is the vocal learning hypothesis. Patel (2006) proposed that human-like beat perception and synchronization may have emerged as a by-product of neural adaptations for complex vocal learning, especially strengthened auditory-motor connections. Patel (2014) later refined this argument, stressing that the hypothesis does not claim all vocal learners will necessarily synchronize to a beat, only that

advanced vocal learning may provide an important preadaptation for this kind of behavior. Patel (2021) later strengthened the claim, arguing that advanced vocal learning is not only a possible preadaptation but a specific one — for the precise, predictive, and tempo-flexible form of beat perception that distinguishes human musical behavior from simpler timing abilities. The comparative evidence fits this view only partly. Parrots strongly support it, especially because they show spontaneous and flexible movement to music. Sea lions are harder to accommodate, since they entrain convincingly without being classic vocal mimics. Chimpanzees suggest that limited rhythmic alignment may occur even outside the vocal learning category, though only with training and within narrow conditions.

The comparative approach therefore does not yield a simple answer. Rhythmic musicality appears to be a set of abilities that differ across species in strength, flexibility, and ecological relevance, with vocal learning consistently associated with the most music-like forms of entrainment. Comparative research is valuable precisely because it allows these distinctions to be drawn, separating general timing abilities from the rarer forms of beat-based perception that are most relevant to human musical behavior.

1.4 Budgerigars (*Melopsittacus undulatus*) as a Model Species

Among parrots, budgerigars (*Melopsittacus undulatus*) are especially useful as a model species for studying the biological foundations of musicality. They are small Australian parrots with a well-documented learned vocal repertoire, and they live in large, highly social flocks in which vocal interactions are frequent and dynamic (Moussaoui, Overcashier, Kohn, Araya-Salas, & Wright, 2023; Seki & Dooling , 2016). Additionally, Wilson and Cook (2016) showed that rhythmic and vocal behaviors in parrots are closely tied to social interaction and reward, suggesting that rhythm may play a role in communication and social bonding. Many questions about musicality concern how animals perceive, produce, and respond to structured acoustic signals in socially meaningful contexts. The combination of strong sociality and vocal learning makes budgerigars particularly well-suited to address them.

One of the main reasons budgerigars are such a useful model is the richness and flexibility of their vocal behavior. Tu et al. (2011) describe the species as having an “extraordinarily complex” learned vocal repertoire, including both the long rambling warble song of males and a range of shorter calls produced by both sexes. Contact calls are especially important in this system. These calls are socially learned, individually variable, and highly responsive to changes in social context. Farabaugh et al. (1994) showed that adult budgerigars can develop convergent contact calls through mutual vocal imitation, demonstrating that vocal learning in this species is not limited to early development. Hile and Striedter (2000) extended this by showing that, during pair formation, males imitate female contact calls and pairs develop shared calls, suggesting that vocal learning contributes directly to pair-bond formation and maintenance. This matters for the study of musicality because it shows that budgerigar vocal behavior is not a fixed output, but a flexible, socially embedded system shaped by life-long learning, interaction, and communication.

Budgerigars are also a particularly strong laboratory model because their vocal behavior can be brought under experimental control. Seki and Dooling (2016) note that

budgerigars can be trained to vocalize as a conditioned response and can even be trained to produce different vocalizations to different visual signals. Related work showed that birds could be trained to match specific call templates and alter the timing of their vocal responses, demonstrating a level of experimental tractability that is rare in non-human vocal learners (Manabe, Dooling , & Brittan-Powell, 2008). Budgerigars are also useful for studying how complex vocal sequences are perceived. Tu and Dooling (2012) found that budgerigars show species-specific advantages in detecting acoustic changes in natural warble sequences, and more recent work suggests that they are comparatively strong in auditory pattern discrimination and sequence perception (Fishbein, 2022). These features make budgerigars one of the most experimentally accessible vocal learners outside of humans.

These same qualities — vocal learning, experimental tractability, and sensitivity to acoustic structure — also make budgerigars valuable for rhythm research specifically. Hasegawa et al. (2011) showed that budgerigars could synchronize pecking responses to an audio-visual metronome across a range of tempi, making them one of the few species for which entrainment-like behavior has been demonstrated under controlled conditions. Importantly, this places budgerigars in a different position from species for which rhythmic ability has only been inferred from anecdotal observation. In addition, Hoeschele and Bowling (2016) used a place preference design to show that rhythmic structure is behaviourally meaningful to budgerigars in spontaneous free-choice settings, with sex-specific patterns of approach (discussed in detail in Section 1.6.1). These two studies establish budgerigars as a species in which rhythmic structure can be both behaviorally tracked under laboratory control and spontaneously preferred in free-choice settings. More recently, van der Aa et al. (2026) showed that budgerigar warble song itself contains nonrandom, music-like rhythmic structure, suggesting that temporal organisation is not only something budgerigars can detect under laboratory conditions, but also something they produce in their own natural vocal behaviour.

In summary, budgerigars are an unusually powerful model for studying rhythm and musicality. They combine several qualities that are rarely found together in one species: vocal learning that continues into adulthood, experimentally tractable vocal behavior, and demonstrated sensitivity to temporal structure. At the same time, they are small, widely studied, and relatively manageable in laboratory settings, which makes them especially practical for controlled behavioral research. Budgerigars therefore offer an important bridge between broader comparative questions about musicality and more specific questions about how rhythmic structure is perceived, learned, and potentially valued in a non-human vocal learner.

1.5 The Place Preference Paradigm

The place preference paradigm is a useful method for studying whether animals are spontaneously attracted to, indifferent to, or avoid particular stimuli. In its basic form, subjects are allowed to move freely within an environment in which different locations are associated with different sensory cues, and preference is inferred from the amount of time spent near each stimulus. In auditory studies, this usually means that different sounds are broadcast from different spatial locations and the animal's position is used as an index of attraction or avoidance. As Hoeschele and Bowling (2016) explain in their budgerigar rhythm study, this kind of design is especially useful because it does

not require explicit training, reinforced choice learning, or complex task instructions. Instead, it aims to capture relatively spontaneous responses to sound, which makes it well suited for questions about perceptual salience, attraction, and reward-like effects in both humans and non-human animals.

One of the strengths of the place preference paradigm is that it measures behavior in a way that is closer to natural approach and avoidance than many traditional discrimination tasks. In an operant paradigm, animals can learn to respond correctly for food or some other reinforcement, but this does not necessarily show that the stimulus itself is attractive or meaningful outside the task. By contrast, place preference procedures are designed to test which stimuli subjects choose to spend time near when no explicit reward is given for making a particular response. This is why the paradigm has been especially valuable in studies of auditory preference, where the main question is often not whether an animal can perceptually discriminate between two sounds, but whether one of those sounds has greater positive value. Hoeschele and Bowling (2016) make this distinction clearly when they frame time spent near a stimulus as a measure of preference rather than performance, and Wagner et al. (2020) use the same logic in their budgerigar consonance study, where exploration of the sound field serves as an index of spontaneous attraction.

This paradigm has already been applied successfully in a number of studies relevant to music and acoustic preference. McDermott and Hauser (2004) used a V-shaped maze to test cotton-top tamarins and found no preference for consonant over dissonant sounds, despite clear human preferences for consonance in comparable work. In contrast, Chiandetti and Vallortigara (2011) reported that newly hatched chicks spent more time near consonant than dissonant versions of the same melodies, suggesting that attraction to some kinds of acoustic structure may emerge even with very limited prior experience. These contrasting findings show how place preference methods can reveal species differences that would be difficult to interpret from discrimination tasks alone. The issue is not simply whether animals hear the difference between stimuli, but whether they orient toward one kind of sound over another, which is often the more relevant question when studying preference, salience, or potential reward value.

Auditory preference work in birds further demonstrates this paradigm's value. In European starlings, Gentner and Hulse (2000) developed a method for directly assessing female preference for variation in male song and found that females preferred longer song bouts, a result that has been taken as evidence that natural acoustic variation can influence attraction and choice. Although that study used operant control of song playback rather than the exact free-exploration version of a place preference setup, it helped establish an important principle that also motivates place preference research: listening behavior and spatial association can be used as meaningful indices of what kinds of sounds animals prefer. Later work in budgerigars extended this logic more directly to spontaneous auditory exploration. Hoeschele and Bowling (2016) used a place preference design to test rhythmic versus arrhythmic stimuli and found sex-specific preferences, while Wagner et al. (2020) used a similar setup to test consonant versus dissonant melodies and found no overall preference, even when budgerigar-derived stimuli were used. Across these studies, the paradigm proves flexible enough to address different questions about auditory structure while relying on the same core measure: where animals choose to spend their time.

While the place preference paradigm has the advantage of separating spontaneous attraction from trained discrimination, it comes with interpretive challenges that need to be kept in mind. Time spent near a stimulus can reflect attraction, avoidance of the alternative, curiosity, or even location biases unrelated to the sound itself. This makes experimental design especially important. Hoeschele and Bowling (2016) note this issue directly in discussing rhythm preferences, since a forced contrast between two stimuli can make it difficult to know whether subjects are approaching one option or simply avoiding the other. For that reason, the paradigm is particularly informative when it includes appropriate controls and when the stimuli are designed carefully enough to isolate the feature of interest. Even with these limitations, place preference remains one of the most useful methods for studying whether acoustic patterns are behaviorally meaningful, because it captures a form of response that is immediate, minimally trained, and closely tied to natural orientation toward sound. The present study uses this paradigm to address questions left open by previous rhythm research in budgerigars.

1.6 Hypothesis and Rationale for the study

The present study is motivated by a broader question that runs through research on rhythm and musicality: when animals respond differently to structured and unstructured temporal patterns, what exactly does that response mean? In the case of budgerigars, earlier work has already suggested that rhythmic structure is behaviorally relevant, but the meaning of that relevance is still unclear. A preference for one stimulus over another could reflect attraction, avoidance, greater perceptual salience, greater familiarity, or some combination of these. For that reason, the rationale behind the current study is not simply to ask whether budgerigars can detect rhythmic differences, but to ask what kind of behavioral value those differences may have.

A second part of the rationale concerns stimulus type. Much of the strongest existing evidence for non-human rhythm-related behavior comes either from synchronization tasks, which involve training and repeated exposure, or from experiments using artificial stimuli such as metronomes or percussive sounds. These approaches are highly valuable because they establish what animals can do under controlled conditions. However, trained performance and spontaneous attraction are not the same. Likewise, artificial sounds can demonstrate sensitivity to abstract temporal regularity, but they do not always show whether similar preferences hold for sounds that are more naturalistic or behaviorally relevant to the species. The present study is therefore grounded in the idea that a fuller understanding of rhythm perception requires moving beyond trained synchronization and asking how animals respond spontaneously to temporal structure in a more ecologically meaningful context.

1.6.1 Previous Research

The most directly relevant previous study is Hoeschele and Bowling (2016), who used a place preference paradigm to compare responses to rhythmic and arrhythmic stimuli in both humans and budgerigars. Their human participants showed a clear overall preference for rhythmic stimuli, both in where they chose to spend time and in their post-test reports. Budgerigars, by contrast, did not show a simple overall group-level preference, but the results became more informative when sex was taken into account: females spent more time near rhythmic stimuli, whereas males spent more time near

arrhythmic stimuli. On this basis, the authors concluded that rhythmic information is behaviorally interesting to budgerigars, even if the pattern of response is more complex than in humans. This study is important because it moved the question of rhythm in budgerigars away from trained performance alone and toward spontaneous behavioral engagement with temporal structure. In other words, it suggested that rhythm may matter to budgerigars not only as something they can track in a task, but also as something that influences where they choose to be.

At the same time, that study leaves several interpretive questions open, and these unresolved questions form the immediate rationale for the current experiment. First, the birds in that design always had to choose between two competing acoustic options. This means that more time spent near one stimulus cannot automatically be read as positive attraction to that stimulus — it may instead reflect weaker avoidance, lower aversion, or simply a relative preference within a forced comparison. Hoeschele and Bowling themselves point toward this issue in discussing how their findings should be interpreted. If birds spend more time with rhythmic stimuli than arrhythmic stimuli, it is still unclear whether rhythm is positively attractive, whether arrhythmia is negatively valued, or whether the animals are simply choosing the easier or more familiar of two imperfect options. This ambiguity is not trivial. It changes the meaning of the result from "rhythm is rewarding" to the much more cautious claim that "rhythm is preferred relative to arrhythmia." The current study addresses that exact gap by including silence as an additional comparison condition, allowing attraction and avoidance to be disentangled more clearly than in a strict two-choice design.

Another limitation of previous work is ecological validity. Earlier place preference studies on rhythm and consonance in budgerigars used artificial acoustic material, which is useful for experimental control but not always ideal for asking whether a feature is meaningful to the species itself. Artificial percussion can show whether animals discriminate temporal structure, but it is less informative about whether that structure has relevance when carried by sounds that more closely resemble the animals' own acoustic world. Seki (2023) makes a related point in reviewing why budgerigars rarely show robust beat synchronization to human music despite being capable vocal learners: the tempos used in such studies often fall outside the range of natural budgerigar vocal behaviour, and the stimuli themselves carry little motivational relevance for the species. This adds further reason to ask whether rhythmic structure becomes more behaviourally meaningful when delivered through species-relevant acoustic material. This consideration may matter especially for budgerigars, whose social lives are strongly shaped by learned vocal communication, contact calls, and other dynamic acoustic interactions. If rhythm-related effects appear only with artificial sounds, that would suggest one kind of interpretation. If they also appear with ecologically relevant budgerigar song elements, that could suggest that temporal structure may matter in a more natural and species-relevant way. The rationale for the present study is therefore strengthened by the decision to use acoustically meaningful budgerigar-derived material, because that allows the question to shift from whether birds respond to abstract timing in principle to whether they respond to it in a context that is closer to their natural perceptual world.

1.6.2 Predictions and Goals of the Current Study

The three goals of the present study correspond directly to the limitations identified above: the meaning of preference in a forced two-choice design, the ecological validity of artificial stimuli, and the limited use of behavioural measures other than time spent.

The first goal of the current study is to test whether budgerigars show differential responses to rhythmic and arrhythmic temporal structure when the stimuli are based on ecologically relevant song elements. This is the most basic prediction, but it is still important to state clearly because it serves as the foundation for all the other questions. If budgerigars do not respond differently to these stimulus types, then the interpretation of earlier work becomes narrower: it would suggest that the previously observed effects depend heavily on the particular artificial stimuli used or on features not preserved in a more naturalistic design. If, however, budgerigars do respond differently even when the sounds are drawn from species-relevant vocal material, then the conclusion becomes stronger. In that case, temporal structure would appear to matter not only in abstract laboratory patterns, but also in sounds that are closer to the kinds of signals budgerigars encounter and produce naturally. This would lend support to the idea that rhythm-related processing in budgerigars is not an artifact of one particular task or stimulus set, but part of a more general sensitivity to how sound is organized in time.

The second goal is to determine whether any observed preference reflects true attraction to rhythmic structure or relative avoidance of arrhythmic structure. Including a silent condition allows this distinction to be drawn. A preference between two sounds always provides only relative information: one option is chosen over the other, but the absolute status of either option remains uncertain. Silence changes that logic. If birds prefer rhythmic stimuli over silence, that suggests that rhythmic structure has positive value, whether in the form of attraction, interest, or reward-like salience. If birds avoid arrhythmic stimuli and instead spend more time in silence, that suggests that the key effect lies in the negative status of arrhythmia rather than the positive status of rhythm. If both sound types are preferred over silence, but rhythm is still preferred over arrhythmia, then the interpretation shifts again: both may be engaging, but rhythm may be more attractive or more behaviorally meaningful. This is one of the most important inferential strengths of the present design. It moves the experiment beyond simple contrast and allows the results to speak more clearly to the direction of the birds' responses. The silent condition is not merely an additional control; it is central to the logic of the experiment itself.

The third goal is to assess the relationship between time spent with each stimulus and the number and duration of visits to the corresponding location. Previous studies have used time spent as the primary measure of preference, on the reasonable assumption that animals tend to avoid unpleasant places and stimuli. However, in a paradigm that allows free movement, behavior also includes the number of times an animal chooses to visit a location and how long it chooses to remain in each visit when there. The interpretation of visit count alone is harder: frequent visits could reflect preference, but also curiosity or restlessness, but considered alongside time spent and visit duration, visit count can strengthen or qualify inferences about preference. For example, the combination of long total time, moderate visit count, and long mean visit duration suggests sustained engagement: the birds settle near a stimulus and remain

there for substantial periods on each visit. Many visits paired with short visit duration and modest total time, by contrast, suggests exploratory or sampling behaviour, with each visit consisting of brief approaches that do not translate into prolonged occupancy. The three measures are mathematically interdependent — total time equals visit count multiplied by mean visit duration — but they are not interchangeable as indices of preference, because each captures a different aspect of how an animal allocates its behaviour. Reading the three together is therefore informative beyond what any single one provides. This is therefore a secondary goal of the study: to characterise approach behaviour along three dimensions rather than one.

In summary, the current study extends previous findings in three ways. First, we use acoustically and ecologically relevant budgerigar song elements, allowing us to test whether rhythmic preferences generalize beyond artificial stimuli. Second, we introduce a silent condition, enabling us to distinguish attraction from avoidance. Third, we examine visit counts and duration alongside listening time, allowing approach behavior to be characterized along three dimensions rather than one.

We predict that:

1. Budgerigars will show differential responses to rhythmic versus arrhythmic stimuli.
2. Observed preferences will clarify whether previously reported effects reflect true attraction or relative avoidance.
3. Visit counts and visit duration will, together with listening time, allow preference to be characterised along multiple dimensions, distinguishing sustained engagement from brief, repeated approaches.

The current study also contributes to broader debates about the evolutionary origins of musicality by asking whether temporal regularity in a vocal-learning species has spontaneous behavioral value beyond trained synchronization tasks. At the same time, the inferences drawn from a place preference design need to be framed carefully. A place preference result does not by itself prove that a stimulus is rewarding in the same sense as food, mating opportunity, or social contact. However, it can provide evidence that a stimulus is sufficiently attractive or behaviorally relevant to bias spontaneous spatial behavior. In the context of this study, that means any robust preference for rhythmic stimuli, particularly when expressed through sustained engagement rather than mere approach behaviour, would support the idea that temporal regularity has more than just perceptual detectability; it has enough behavioral salience to shape where and in what pattern birds choose to spend time. This is a meaningful result even if the exact mechanism remains open. It would suggest that rhythm is not merely something budgerigars can process under laboratory demand, but something that matters to them in a low-demand, spontaneous setting. Such finding hints at a possible motivational dimension of rhythmic structure, which has been a recurring theme in work on human rhythm and groove but is much less well understood in non-human animals.

2 Method

This experiment used a place preference paradigm to test whether budgerigars show differential approach behaviour to rhythmic versus arrhythmic acoustic stimuli derived from conspecific vocalisations, and whether silence reveals attraction or avoidance as the underlying mechanism. The following sections describe the participants, stimuli, apparatus, procedure, ethical approval, and statistical analyses.

2.1 Participants

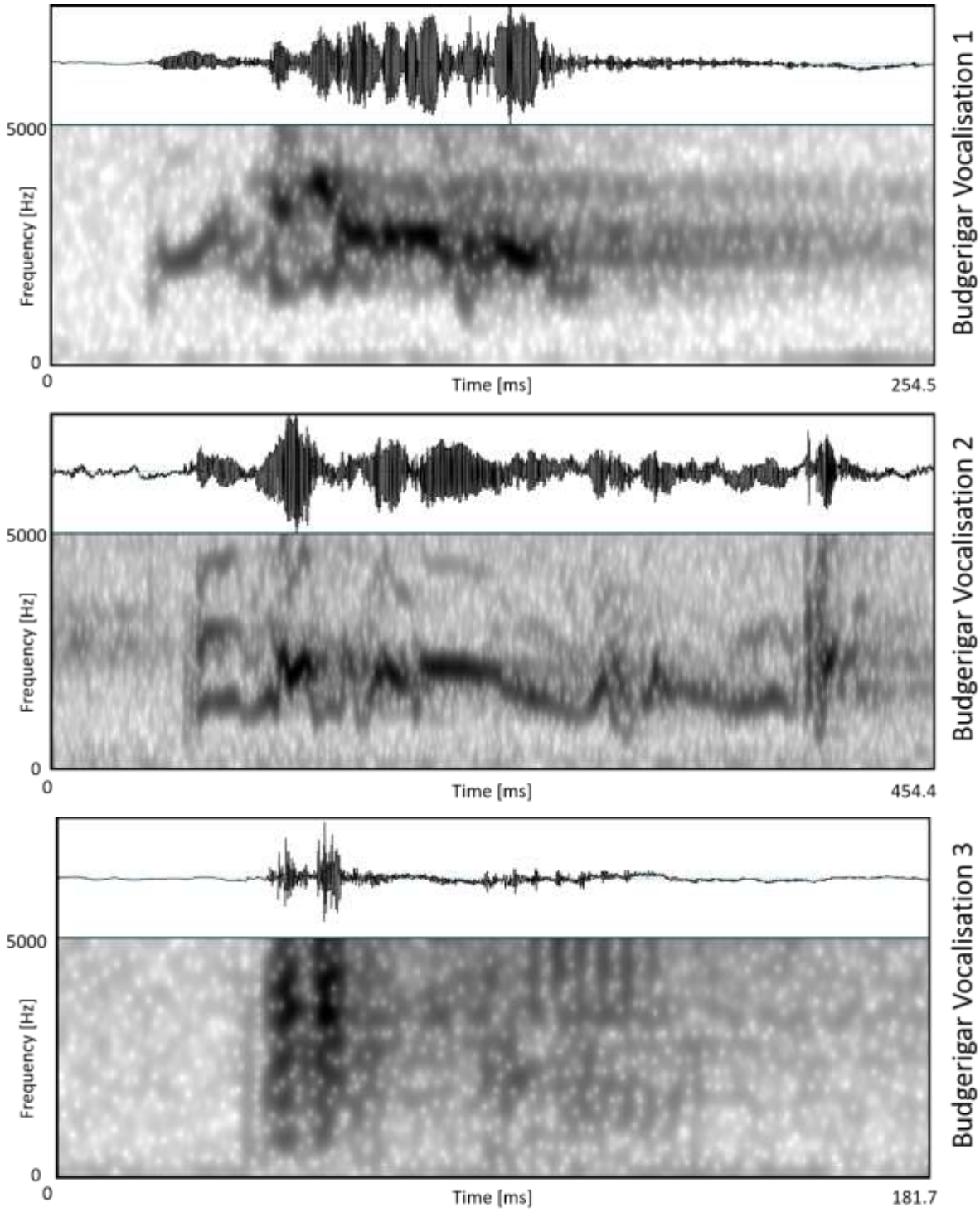
Thirteen budgerigars (Melopsittacus undulatus; 6 females and 7 males), aged between 2 and 5 years, participated in the experiment. The birds were housed socially in the same room in two separate aviaries.

2.2 Stimuli

The acoustic stimuli used in the experiment were constructed from budgerigar vocalisation samples arranged according to five rhythmic templates. This section describes the vocalisation samples used as sound sources, the rhythmic patterns on which the stimuli were based, and the generation of the final rhythmic and arrhythmic playback tracks.

2.2.1 Budgerigar Vocalisations as Sound Sources

Five budgerigar vocalisation samples were extracted from recordings of an adult male budgerigar unfamiliar to the participating birds. The source recording was made at a sampling rate of 48 kHz. The recording was segmented into multiple clips bounded by silence at the beginning and end. From these clips, five vocalisations were selected to maximise acoustic diversity based on their spectral composition and perceptual distinctiveness as judged by the experimenters. All selected clips were also normalised in amplitude. These five vocalisation samples (shown in Figure 2.1) were then used as the sound sources for stimulus generation.


5000
Frequency [Hz]
0
0
Time [ms]
254.5
Budgerigar Vocalisation 1
5000
Frequency [Hz]
0
0
Time [ms]
454.4
Budgerigar Vocalisation 2
5000
Frequency [Hz]
0
0
Time [ms]
181.7
Budgerigar Vocalisation 3

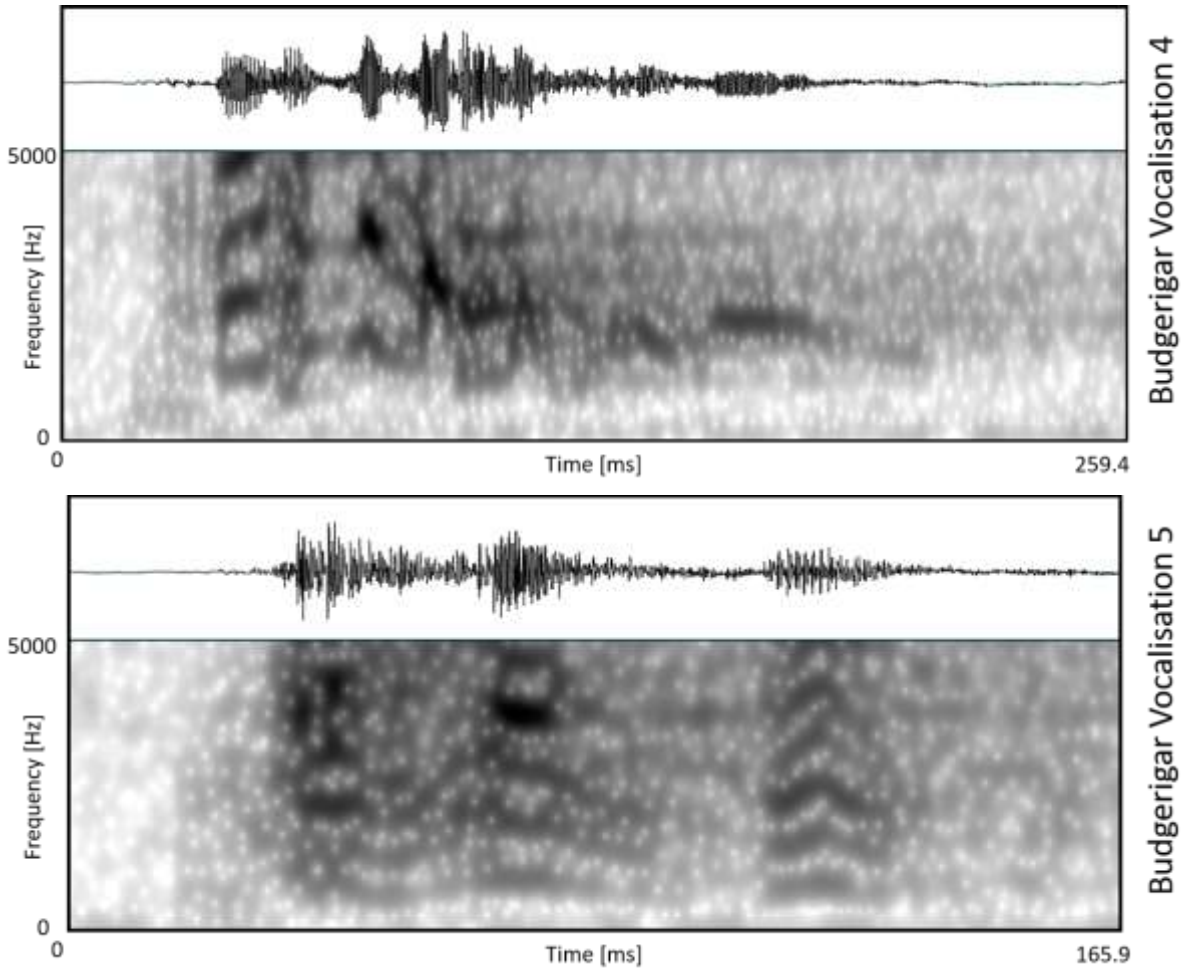


Figure 2.1: Budgerigar vocalisations used as sound sources

2.2.2 Rhythmic Patterns

Five rhythmic patterns were used to generate the stimuli. All patterns were produced at a tempo of 160 beats per minute (bpm), corresponding to 375 ms per beat. The shortest possible interval between successive onsets was 93.75 ms, corresponding to a sixteenth-note subdivision. Each pattern consisted of a single 4/4 bar lasting 1.5 s and containing 14 sound events. A schematic representation of the five rhythmic patterns is shown in Figure 2.2.

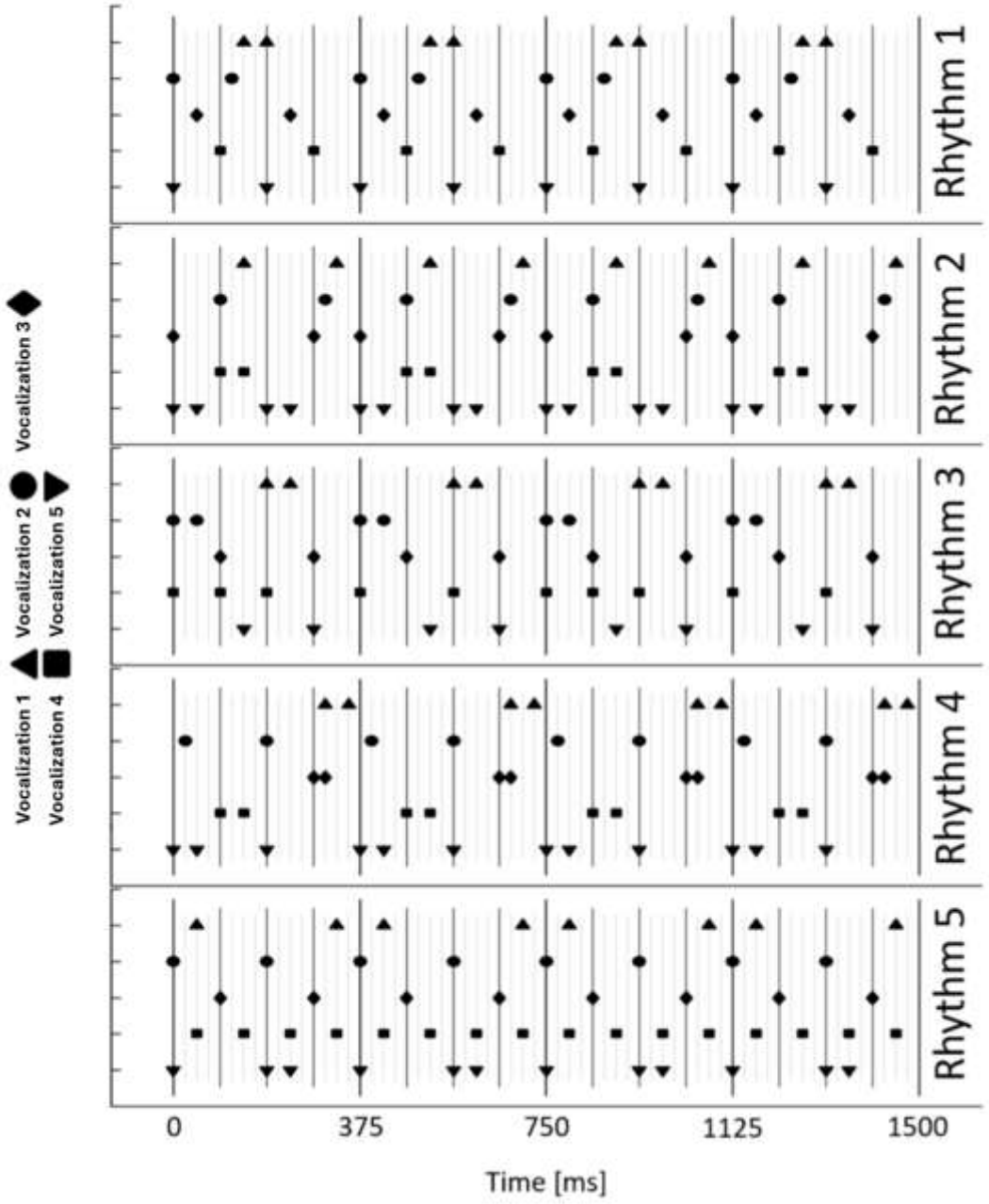


Figure 2.2: Rhythmic patterns used in creation of stimuli

2.2.3 Stimulus Generation

A total of 1,200 acoustic stimuli were generated for the experiment, comprising 600 rhythmic tracks and 600 corresponding arrhythmic tracks. Each rhythmic track was based on one of the five rhythmic patterns described above and was constructed using the five budgerigar vocalisation samples as sound sources. For each base pattern, 120 permutations were created by varying the assignment of vocalisation samples within the pattern.

Each bar lasted 1.5 s, and each track consisted of 40 repetitions of the same bar, resulting in a total track duration of 60 s. In the rhythmic tracks, the temporal structure was identical across all 40 repetitions, such that each event corresponded to the onset of one vocalisation sample at the same position in every repetition.

For each rhythmic track, a corresponding arrhythmic track was created by jittering the onset time of each event by a random value drawn from a uniform distribution between -200 ms and +200 ms. Jittering was applied independently within each repetition, such that successive repetitions of an arrhythmic track did not repeat the same temporal pattern. This procedure was intended to eliminate any discernible repeating rhythmic structure while preserving the overall acoustic content of the track. Figure 2.3 shows an example of a rhythmic track and its corresponding arrhythmic version.

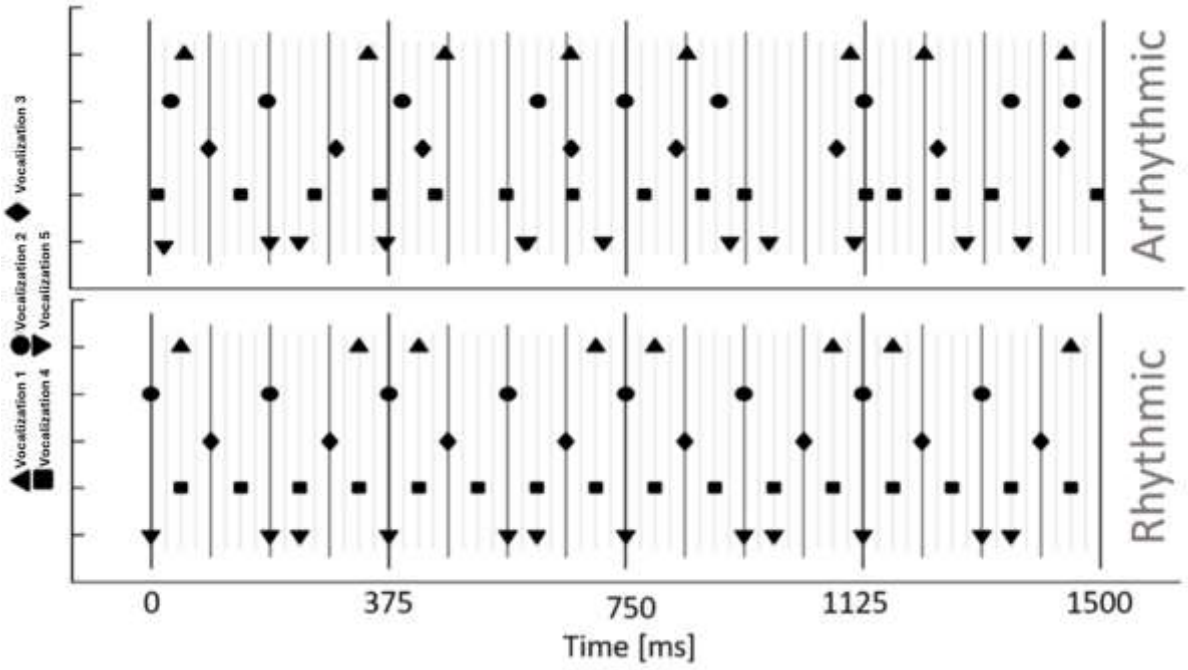


Figure 2.3: Example of a rhythmic track and its corresponding arrhythmic track for Pattern 5, repetition 1

Because one of the three speakers remained silent in each session, playback occurred from only two speakers at a time. To facilitate stimulus routing to the active speakers, all playback files were prepared as mono tracks and were presented through the relevant speaker according to the session configuration.

2.3 Apparatus

The experimental apparatus consisted of a hexagonal aviary with side lengths of 37 cm and a height of 110 cm. Three perches were mounted on alternating sides of the aviary, perpendicular to the side walls. Each perch had a length of 30 cm and a diameter of 1 cm. Three speakers (FE108 full-range speaker, Fostex, Tokyo, Japan; frequency range 200–16,000 Hz) were positioned on the sides aligned with the perches, facing inward toward the aviary. Each speaker was placed opposite the end of a perch such that the spatial relationship between perch and speaker was equivalent across all three locations. A schematic bird's-eye view of the apparatus is shown in Figure 2-4.

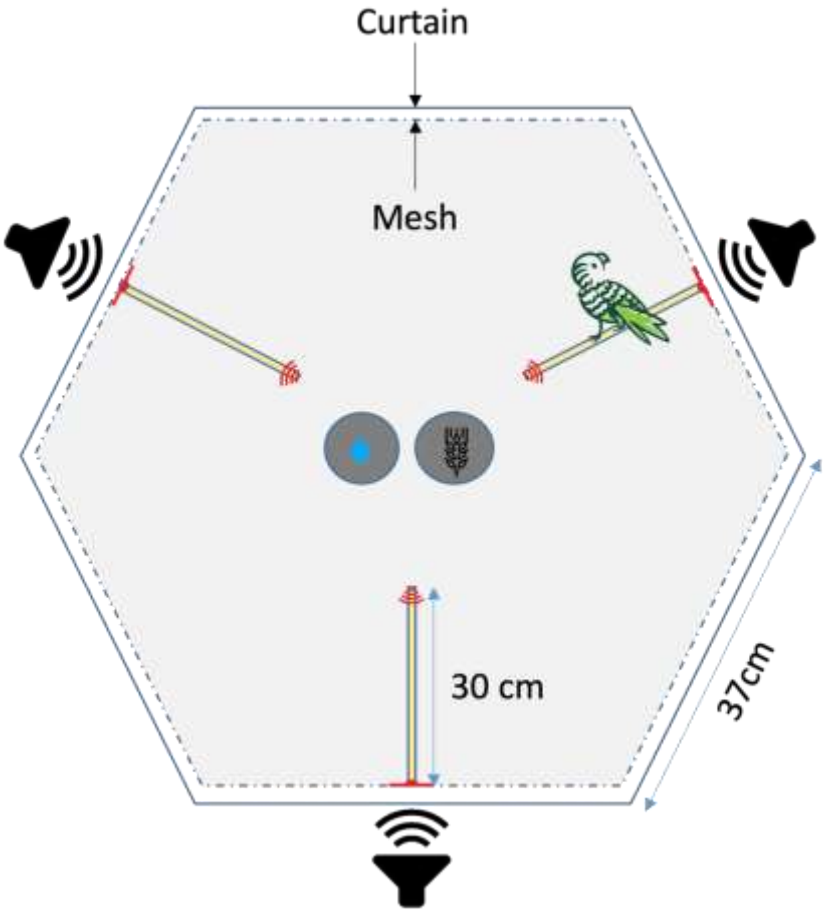


Figure 2.4: Bird's-eye view of the experimental apparatus

The aviary was enclosed by a thick curtain to reduce visual distraction from the surrounding room and to provide a visually sheltered environment for the birds. The ceiling was made of translucent material, allowing sufficient light to enter while maintaining a visually enclosed space.

Each perch was fitted with an infrared sensor (IR Break Beam Sensor, 3 mm LEDs, Adafruit Industries, New York, NY, USA). Each sensor consisted of two components positioned at opposite ends of the perch, producing a continuous infrared beam between them. When a bird landed on the perch, the beam was interrupted, and a signal was generated. These signals were transmitted via the sensor data wires to an Arduino Uno REV3 microcontroller (BCMI, Turin, Italy), which identified the active sensor and relayed the information to a Python-based application running on a laptop. The application-controlled stimulus playback and recorded behavioural events on the basis of the incoming sensor signals.

A separate speaker (M-Audio AV 40, Cumberland, RI, USA) was mounted on the ceiling above the centre of the aviary and continuously played a recording of ambient noise from the main aviary room in which the budgerigars were normally housed. This was intended to maintain a familiar acoustic background during testing. The full room setup is shown in Figure 2.5.

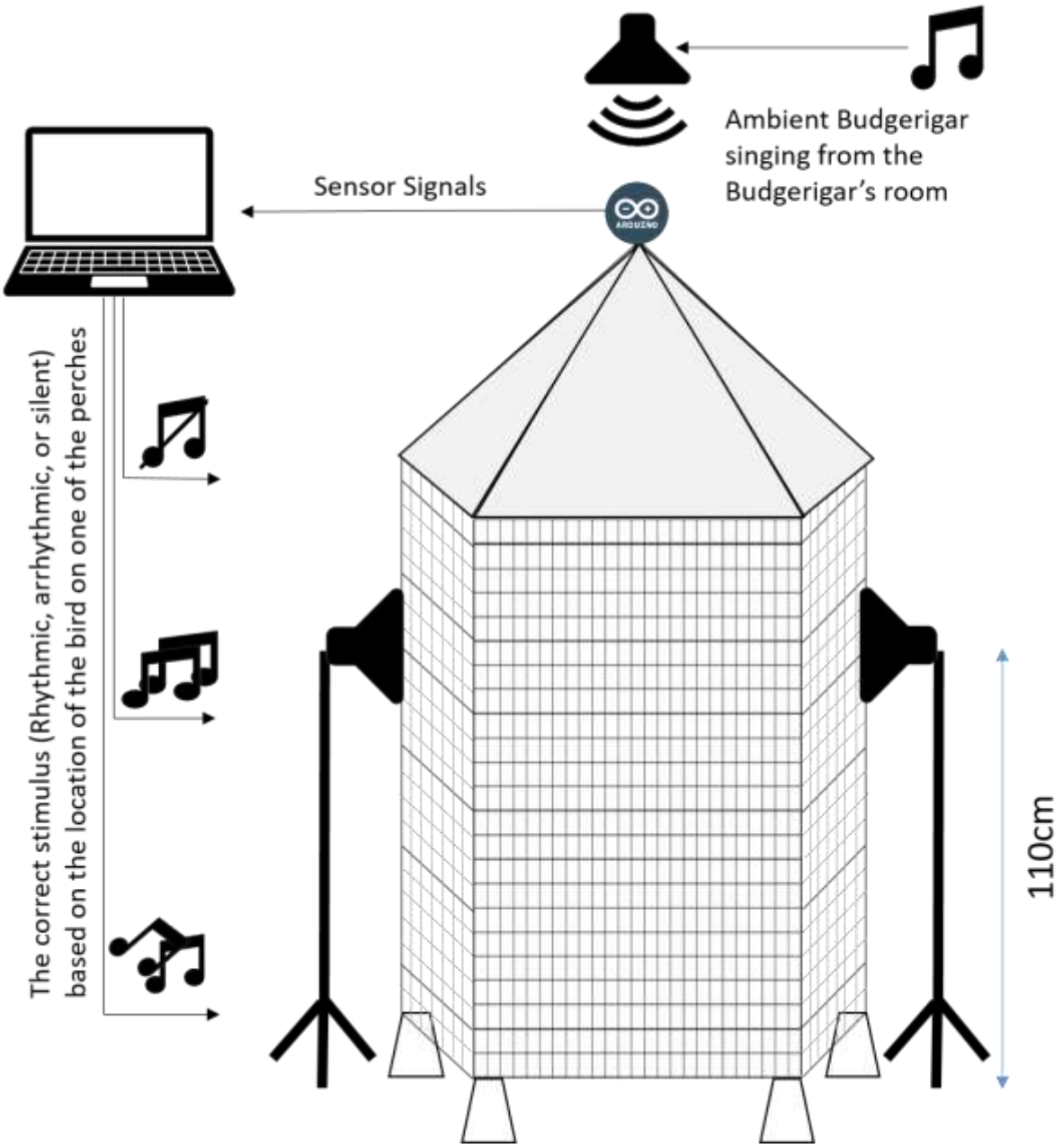


Figure 2.5: Experiment room set-up

Table 2.1 summarises the main equipment used in the experimental setup and its function.

Table 2.1: Summary of equipment used in the experimental setup

Equipment	Model	Remarks
Ambient-noise speaker	M-Audio AV 40, Cumberland, RI, USA	Playback of ambient room recording
Stimulus speakers (3)	FE108 full-range speaker, Fostex, Tokyo, Japan (frequency range: 200–16,000 Hz)	Playback of acoustic stimuli
iPad	Apple Inc., Cupertino, CA, USA	Playback of ambient-noise recording

Laptop	MacBook Pro, Apple Inc., Cupertino, CA, USA	Communication with Arduino, stimulus playback, and event logging
Infrared Sensors (3)	IR Break Beam Sensor, 3 mm LEDs, Adafruit Industries, New York, NY, USA	Detection of perch occupancy
Microcontroller	Arduino Uno REV3, BCMI, Turin, Italy	Sensor signal processing and relay to the control application

2.4 Procedure

During testing, the aviary contained three perch-activated positions, two of which were associated with acoustic playback and one of which remained silent. The birds were tested individually. When a bird landed on one of the two acoustic perches and remained there for longer than 300 ms, an acoustic stimulus was triggered (Gentner & Hulse, 2000). The third perch remained silent regardless of perch duration. The assignment of rhythmic, arrhythmic, and silent conditions to perch locations was counterbalanced across sessions for each bird to minimise the influence of spatial preference on stimulus choice. Food and water were available *ad libitum* throughout testing.

Throughout each session, a recording of ambient noise from the room in which the birds were normally housed was played continuously. This was intended to provide a familiar acoustic background and to facilitate habituation to the experimental apparatus. The ambient playback level inside the apparatus was maintained between 50 and 55 dB.

Each session lasted 2 h. Birds initially completed two sessions. If a bird did not meet the completion criteria after the second session, a third session was conducted. Completion criteria were defined as at least a single visit to all perches in each session, so that the bird could make an informed decision.

When a bird remained on an acoustic perch for at least 300 ms, playback of a stimulus track began. Once initiated, a track continued until its end unless the bird left the perch, in which case playback faded out immediately using a linear 5 ms fade. If the bird remained on the perch until the end of a track, a new track began automatically. Stimuli were selected pseudo-randomly: tracks were drawn from the five base rhythmic-pattern categories, and all pattern categories were sampled before a new stimulus from the same category could be repeated. No track was repeated within a session. If a bird left a perch before the end of a track, that partially heard track was not presented again within the same session.

The behavioural-control application continuously logged the identity of the perch visited, the associated condition (rhythmic, arrhythmic, or silent), the time of landing, the identity of any acoustic track played, and the time of departure. These records formed the basis of the subsequent analyses of occupancy time and visit frequency.

2.5 Ethical Statement

All procedures conducted in this study were in accordance with Austrian animal welfare and housing regulations and were approved by the ethical board of the

Behavioural Research Group, Faculty of Life Sciences, University of Vienna (Approval No. 2015-005). A copy of the approval document is provided in the Appendix (Section 6.1).

2.6 Analysis

All data handling, preprocessing, statistical modelling, and visualisation were conducted in Python. The analyses described in this section addressed three behavioural measures: listening time, visit count, and visit duration. Because the experiment yielded repeated observations from the same individuals across sessions and stimulus conditions, all analytic frameworks accounted for within-bird dependence.

Three analytic frameworks were used, one per measure. Listening time was analysed with mixed-effects models, with bird identity entered as a random intercept and a bird-by-session variance component to account for repeated measures within individuals. Listening times were log-transformed prior to analysis to address right-skew. Visit counts were analysed with Generalized Estimating Equations (GEE) using a negative binomial family, after an initial Poisson model showed substantial overdispersion. Visit durations, which were heavily right-skewed and contained extreme values, were analysed using a robust within-bird non-parametric bootstrap on bird-level median durations, which avoided distributional assumptions that the data would have violated.

The analyses are reported below in the order in which they appear in Chapter 3. For each measure, the rhythmic-versus-arrhythmic contrast is treated as the confirmatory analysis, and an exploratory analysis incorporating the silent condition is reported separately. The main reason for treating the R-vs-A contrast as confirmatory and the silent-condition analyses as exploratory was sample size. Models incorporating the silent condition include additional stimulus levels and stimulus-by-sex interaction terms, which would require larger effective per-cell samples than the present design provides. Limiting the confirmatory analyses to the two acoustic stimuli protects the main test against underpowering, while the exploratory analyses test silent-condition contrasts that the apparatus was designed to capture but cannot be tested with confirmatory rigour at this sample size.

Statistical tools, software details, and reporting conventions are described in Section 2.6.10.

2.6.1 Data restructuring and dependent variables

The raw data were reorganised into analysis-ready formats reflecting three behavioural measures: listening time, visit count, and visit duration. Listening-time variables captured the amount of time spent on each physical perch and, separately, the amount of time spent with each stimulus category. Visit-count variables captured the number of times a bird visited each physical perch and stimulus category in a given session. Visit-duration variables captured the elapsed time between perch landing and departure for each individual visit, computed per visit from the timestamped logs described in Section 2.4. For the stimulus-based analyses, the three conditions were rhythmic (R), arrhythmic (A), and silent (S). For the location-based analyses, the three physical perches were coded as P1, P2, and P3.

All birds other than Anabelle had three sessions, she only passed two of her sessions. Anabelle, Zora and Melanzani were excluded from visit duration analysis due to very few and short visits overall. Any sessions that lasted longer than 7200 seconds, was capped to only include the visits in the first 7200 seconds. Zero-duration visits were retained for visit-count analysis and excluded from visit-duration analysis.

Because listening times were strongly right-skewed, they were analysed after log-transformation using log(time + 1). Visit counts were retained on the count scale and analysed using a count-data model appropriate for overdispersion (see Section 2.6.6). Visit-duration distributions were also right-skewed but contained extreme values that made transformation alone inadequate; visit-duration analyses therefore used a robust non-parametric framework on bird-level median durations (see Section 2.6.8). Visit-level exclusion criteria specific to the visit-duration analyses are described in Section 2.6.8.

2.6.2 Perch-location preference

Before testing the main hypotheses concerning rhythmic preference, an initial analysis tested whether the birds showed a bias toward any physical perch location independent of the stimulus assigned to that location. The validity of the place-preference paradigm depends on the assumption that occupancy at a given perch reflects the acoustic content broadcast at that perch rather than a stable spatial bias.
The dependent variable was log-transformed time spent on each physical perch (P1, P2, P3). Fixed effects were perch identity, session number, and sex. The model was a linear mixed-effects model fitted using the maximum-likelihood implementation in statsmodels (Seabold & Perktold, 2010), an analytic framework that allows estimation of fixed effects and within-subject variance components simultaneously and is well-suited to repeated-measures designs (Pinheiro & Bates, 2000; Bates, Mächler, Bolker, & Walker, 2015). Bird identity was included as a random intercept, allowing each bird to have its own baseline level of perch occupancy, and a bird-by-session variance component was added to allow within-bird variability to differ across the three sessions. This model tested whether any perch location was associated with systematically greater time occupancy after accounting for session, sex, and within-bird repeated measures.

2.6.3 Rhythmic versus arrhythmic preference: session-level analysis (confirmatory)

The first confirmatory analysis tested Prediction 1 (Section 1.6.2): whether budgerigars showed differential listening-time responses to rhythmic and arrhythmic stimuli, and whether this contrast varied across the three sessions. Only rhythmic and arrhythmic observations were retained for this analysis; silent observations were excluded and were treated separately in Section 2.6.5.
The dependent variable was log-transformed listening time. Fixed effects were stimulus type (rhythmic versus arrhythmic), session number (Session 1 / 2 / 3), the stimulus-by-session interaction, and sex (female versus male). The stimulus-by-session interaction tested whether the rhythmic-versus-arrhythmic contrast varied across sessions. The model was a linear mixed-effects model with the random-effects structure described in Section 2.6.2: a bird random intercept and a bird-by-session variance component to account for repeated measurements within individuals across sessions.

2.6.4 Rhythmic versus arrhythmic preference: bird-level aggregate analysis (confirmatory)

A bird-level aggregate analysis tested Prediction 1 (Section 1.6.2) at the level of overall rhythmic preference, complementing the session-level analysis in Section 2.6.3 by collapsing across the three sessions to evaluate overall rhythmic preference independent of session progression.

Rhythmic and arrhythmic listening times were summed within each bird across the three sessions, producing one rhythmic total and one arrhythmic total per bird. These totals were log-transformed and analysed using paired within-bird comparisons. A paired-samples t-test on log-transformed totals assessed whether rhythmic totals exceeded arrhythmic totals on average. A Wilcoxon signed-rank test on the same totals was conducted as a non-parametric sensitivity check, given the small sample. To test whether overall rhythmic preference differed by sex, a bird-level difference score (computed as log(R + 1) minus log(A + 1)) was entered as the dependent variable in an ordinary least-squares regression with sex as the sole predictor. Effect-size reporting and statistical-tools conventions are described in Section 2.6.10.

2.6.5 Listening-time analysis: exploratory inclusion of the silent condition

The listening-time analysis was extended to include the silent condition to address Prediction 2 (Section 1.6.2): whether the silent condition would help disambiguate attraction to rhythmic structure from avoidance of arrhythmic structure. The analysis was treated as exploratory rather than confirmatory because it involved three stimulus categories and stimulus-by-sex interaction terms, drawing on a smaller effective per-cell sample than the two-stimulus comparisons in Sections 2.6.3 and 2.6.4. Statistical conclusions from this analysis were therefore framed cautiously, and findings from it were not used to test confirmatory predictions.

All three stimulus categories (A, R, S) were retained for this analysis. The dependent variable was log-transformed listening time. Fixed effects were stimulus category, session number, sex, and the stimulus-by-sex interactions (rhythmic-by-sex and silent-by-sex). The random-effects structure was as described in Section 2.6.2: a bird random intercept and a bird-by-session variance component.

2.6.6 Visit-count analysis: rhythmic versus arrhythmic (confirmatory)

A confirmatory analysis tested Prediction 3 (Section 1.6.2) using visit counts as the dependent variable. As stated in the chapter introduction, visit counts were analysed using Generalized Estimating Equations (GEE), an analytic framework that produces population-averaged regression estimates while accounting for within-cluster correlation in repeated-measures data (Liang & Zeger, 1986; Hardin & Hilbe, 2003). The negative binomial family was used to accommodate overdispersion in the count data, and an exchangeable correlation structure clustered observations within bird.
Only rhythmic and arrhythmic visit counts were retained for this analysis; silent visits were excluded and were treated separately in Section 2.6.7. Fixed effects were stimulus type (rhythmic versus arrhythmic), session number (Session 1 / 2 / 3), the stimulus-by-session interaction, and sex (female versus male). The stimulus-by-session interaction tested whether the rhythmic-versus-arrhythmic contrast in visit counts varied across sessions.

2.6.7 Visit-count analysis: exploratory inclusion of silent condition

The visit-count analysis was extended to include the silent condition to address Prediction 2 (Section 1.6.2). As with the corresponding listening-time exploratory analysis (Section 2.6.5), this analysis was treated as exploratory rather than confirmatory because it involved three stimulus categories and stimulus-by-sex interaction terms, drawing on a smaller effective per-cell sample than the two-stimulus comparison in Section 2.6.6. Statistical conclusions from this analysis were therefore framed cautiously, and findings from it were not used to test confirmatory predictions.

All three stimulus categories (A, R, S) were retained for this analysis. The analytic framework was the same as in Section 2.6.6: a negative binomial GEE with exchangeable correlation structure clustering observations within bird. Fixed effects were stimulus category, session number, sex, and the stimulus-by-sex interactions (rhythmic-by-sex and silent-by-sex).

2.6.8 Visit-duration analysis: rhythmic versus arrhythmic (confirmatory)

A confirmatory analysis tested Prediction 3 (Section 1.6.2) using visit duration as the dependent variable. As stated in the chapter introduction, visit durations were heavily right-skewed and contained extreme values; the analysis therefore used a robust within-bird approach based on bird-level median visit durations and non-parametric bootstrap inference (Efron & Tibshirani, 1993). The bootstrap is a resampling-based method that estimates the sampling distribution of a statistic by repeatedly drawing samples (with replacement) from the observed data, allowing inference without distributional assumptions and without requiring large-sample approximations.

For each bird, all individual visit durations to the rhythmic perch and all individual visit durations to the arrhythmic perch were pooled, and the median visit duration was computed separately for each stimulus category. A bird-level difference score was computed as median(R) − median(A), with positive values indicating longer median visit duration on the rhythmic perch. The rhythmic-versus-arrhythmic contrast was evaluated overall (across all birds and sessions), separately by sex, and separately by session number. Inference was based on bootstrap resampling across birds, generating 95% confidence intervals and directional probabilities P(diff > 0) for the bird-level difference scores.

Prior to analysis, individual visits were excluded under the following criteria: visits with missing or non-numeric duration values, visits with duration ≤ 0 (reflecting sensor artefacts). For this confirmatory analysis, silent visits were also excluded; silent visits were retained for the exploratory analysis described in Section 2.6.9. Because not every bird produced visits in every session-stimulus combination, the bootstrap analyses were conducted on the subset of birds with non-empty data in the relevant condition, with the exact number of birds contributing to each contrast reported in the corresponding results table.

2.6.9 Visit-duration analysis: exploratory inclusion of silent condition

The visit-duration analysis was extended to include the silent condition to address Prediction 2 (Section 1.6.2). As with the corresponding listening-time and visit-count exploratory analyses (Sections 2.6.5 and 2.6.7), this analysis was treated as exploratory rather than confirmatory because it involved three stimulus categories and pairwise

contrasts that drew on a smaller effective per-bird sample than the two-stimulus comparison in Section 2.6.8. Statistical conclusions from this analysis were therefore framed cautiously, and findings from it were not used to test confirmatory predictions.

The analytic framework was the same as in Section 2.6.8: bird-level median visit durations summarised the right-skewed distributions, and inference was based on non-parametric bootstrap resampling across birds. All three stimulus categories (A, R, S) were retained for this analysis. For each bird, the median visit duration was computed separately for arrhythmic, rhythmic, and silent visits. Three bird-level pairwise difference scores were then computed: R – A, S – A, and R – S. Each contrast was evaluated overall, separately by sex, and separately by session number, generating 95% confidence intervals and directional probabilities P(diff > 0) for each contrast.

The exclusion criteria described in Section 2.6.8 also applied to this analysis, with one exception: silent visits were retained. Visits with missing or non-numeric duration values, visits with duration ≤ 0, and visits where the bird's sex was not recorded were excluded. Because not every bird produced visits in every session-stimulus combination, the bootstrap analyses were conducted on the subset of birds with non-empty data in the relevant condition, with the exact number of birds contributing to each contrast reported in the corresponding results table.

2.6.10 Statistical tools and reporting

All analyses were conducted in Python, using the statistical modelling implementations in statsmodels (Seabold & Perktold, 2010) for both mixed-effects models (MixedLM) and Generalized Estimating Equations (GEE). Bootstrap resampling for the visit-duration analyses was implemented using NumPy (Harris, 2020). Visualisation used matplotlib (Hunter, 2007) and seaborn (Waskom, 2021).

Reporting conventions were uniform across analyses. For each model, point estimates, standard errors, test statistics (z for GEE and mixed-effects models; t for paired t-tests), 95% confidence intervals, and exact p-values are reported. Listening-time results are presented on the original (seconds) scale for descriptive statistics and on the log scale within model tables, reflecting the log(time + 1) transformation applied prior to mixed-effects modelling. Visit-count results are presented on the count scale for descriptive statistics and on the log-count scale within model tables, reflecting the log link of the negative binomial GEE. For the bird-level aggregate analysis (Section 2.6.4), an effect size was reported alongside the paired t-test: Cohen's d_z, the standardised mean of paired differences, computed as the mean within-bird difference divided by the standard deviation of those differences. For the visit-duration bootstrap analyses (Sections 2.6.8 and 2.6.9), the mean bootstrap difference, 95% confidence interval, and directional probability P(diff > 0) are reported for each contrast; P(diff > 0) is the proportion of bootstrap samples in which the bird-level difference score was positive.

As stated in the beginning of the chapter, the analysis distinguished between confirmatory and exploratory analyses throughout. Confirmatory analyses tested the predictions specified in Section 1.6.2: the rhythmic-versus-arrhythmic contrasts in listening time (Sections 2.6.3 and 2.6.4), in visit counts (Section 2.6.6), and in visit duration (Section 2.6.8). Analyses involving the silent condition were treated as

exploratory (Sections 2.6.5, 2.6.7, and 2.6.9). Statistical conclusions from exploratory analyses were framed cautiously and were not used to test confirmatory predictions.

3 Results

This chapter reports the analyses described in Section 2.6, applied to the behavioural data collected from the eleven budgerigars retained for analysis. The chapter is organised around three analytic concerns. Section 3.1 reports a preliminary analysis of physical perch-location bias, which is logically prior to all other analyses because the validity of the place-preference paradigm depends on the absence of stable spatial preference for any particular perch independent of the stimulus assigned to it. Sections 3.2 and 3.3 report the main confirmatory analyses of rhythmic versus arrhythmic listening time, first at the session level using mixed-effects modelling and then at the bird level using paired comparisons of aggregated totals. Section 3.4 reports an exploratory mixed-effects analysis that incorporates the silent condition into the listening-time analysis. Section 3.5 reports the main confirmatory visit-count analysis using generalized estimating equations, and Section 3.6 reports the corresponding exploratory visit-count analysis with the silent condition included. Section 3.7 reports the main confirmatory visit-duration analysis using a robust within-bird non-parametric bootstrap, and Section 3.8 reports the corresponding exploratory visit-duration analysis with the silent condition included. Section 3.9 summarises the key findings.[1]

Confirmatory analyses tested the predictions stated in Section 1.6.2: that budgerigars would show differential responses to rhythmic versus arrhythmic stimuli, that any observed preference would be informative about whether rhythm is positively attractive or arrhythmia negatively avoided, and that visit counts and visit duration would, together with listening time, characterise preference along multiple dimensions. The first and third of these predictions correspond to direct two-way contrasts between rhythmic and arrhythmic stimuli: in listening time (Sections 3.2 and 3.3), in visit counts (Section 3.5), and in visit duration (Section 3.7). The second prediction depends on the silent condition, which provides an absolute reference point absent from a strict two-stimulus comparison. Because the silent condition entered analyses that involved three stimulus types and at least one interaction term, and because the resulting models drew on a smaller effective per-cell sample than the two-stimulus comparisons, the silent-condition analyses are reported as exploratory rather than confirmatory, in Sections 3.4, 3.6, and 3.8. Statistical conclusions in those sections are framed cautiously, and findings from them are not used to test confirmatory predictions.

Throughout the chapter, point estimates, standard errors, confidence intervals, and exact p-values are reported in model tables, with descriptive statistics for each contrast presented separately. For the visit-duration bootstrap analyses (Sections 3.7 and 3.8), the mean bootstrap difference, 95% confidence interval, and directional probability P(diff > 0) are reported for each contrast.

[1] A subset of the results presented in this chapter contributed to a co-authored manuscript (Haiduk, et al., 2025), currently in the second round of peer review at Annals of the New York Academy of Sciences.

3.1 Perch-location preference

A preliminary analysis examined whether birds showed stable spatial preference for any physical perch location, independent of the acoustic stimulus assigned to that location, as described in Section 2.6.2. This analysis was logically prior to all subsequent stimulus-preference analyses, because the validity of the place-preference design depends on the assumption that occupancy at a given perch reflects the acoustic content broadcast there rather than a fixed bias toward one position in the apparatus.

Descriptively, mean and median occupancy times were broadly similar across the three perches, with P1 marginally highest (*M = 2015,4 s, Mdn = 1080,0 s*), P2 intermediate (*M = 1915,1 s, Mdn = 1057,0 s*), and P3 marginally lowest (*M = 1776,5 s, Mdn = 749,0 s*). The standard deviations on the three perches were also similar (*P1 = 2269,2 s, P2 = 2259,5 s, P3 = 2253,1 s),* suggesting comparable between-bird variability across positions.

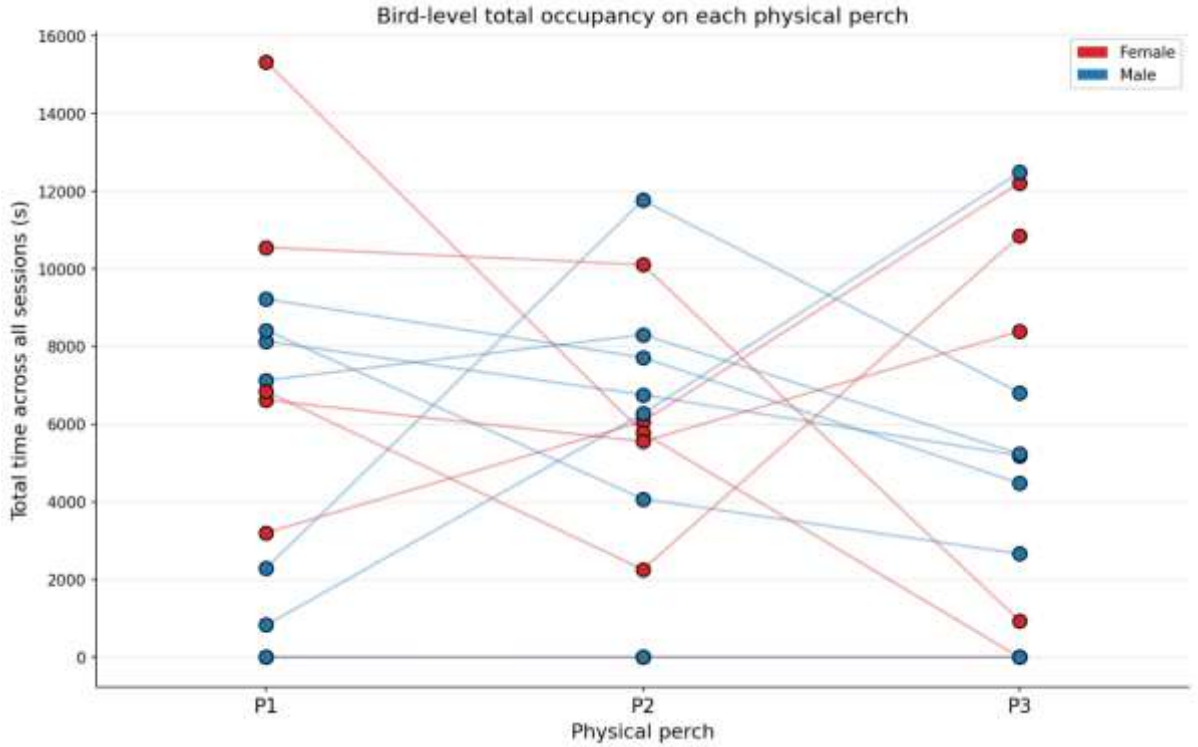


Figure 3.1: Bird-level total occupancy on each of the three physical perches (P1, P2, P3), summed across all stimulus conditions and all three sessions. Each line represents one bird's pattern across the three perches; dots mark that bird's total time on each perch in seconds. Lines and dots are coloured by sex (red = female, blue = male). N = 13 birds (6 female, 7 male).

As shown in Figure 3.1, no single bird produced occupancy values substantially distinct from the rest of the sample, and the lines connecting each bird's three perch totals criss-crossed without any consistent direction across birds. The absence of a structured pattern across perches is itself evidence against a stable spatial bias. Descriptive statistics are reported in Table 3.1.

Table 3.1: Descriptive statistics for physical perch occupancy time

Perch	Mean time	Median time	SD	n
P1	2015,436	1080	2269,185	39
P2	1915,103	1057	2259,526	39
P3	1776,487	749	2253,085	39

Note. Time is the raw session-level time spent on each physical perch. n = bird-session observations (13 birds × 3 sessions = 39 per perch).

The mixed-effects model formally tested whether perch identity predicted log-transformed occupancy time after accounting for session, sex, and within-bird repeated measures (Table 3.2). No significant effect of perch identity emerged: P2 did not differ from P1 (*b = -0,482, p = ,441*), and P3 did not differ from P1 (*b = -0,708, p = ,257*). There were also no significant effects of session number (*Session 2 vs. Session 1, p = ,319; Session 3 vs. Session 1, p = ,444*) or sex (*b = 0,687, p = ,619*). The bird-level random intercept variance was estimated at 5,31, indicating substantial between-bird variability in baseline occupancy that the model absorbed but that did not differ systematically across the three perches.

Table 3.2: Mixed-effects model of perch-location preference

Term	Estimate	SE	z	p	95% CI
Intercept	4,903	1,134	4,323	0	[2,68, 7,126]
P2 (vs P1)	-0,482	0,625	-0,77	0,441	[-1,707, 0,744]
P3 (vs P1)	-0,708	0,625	-1,133	0,2571	[-1,934, 0,517]
Session 2 (vs 1)	0,623	0,625	0,997	0,319	[-0,602, 1,848]
Session 3 (vs 1)	0,479	0,625	0,766	0,4436	[-0,746, 1,704]
Male (vs female)	0,687	1,381	0,498	0,6187	[-2,019, 3,393]

Random effects / model information. Reference category = P1, Session 1, female. N = 117 observations from 13 birds (annabelle's missing Session 3 zero-padded). Bird identity included as random intercept (variance = 5,31); bird-by-session variance component estimated at 0,00. Model converged.

These results indicate that birds did not preferentially occupy any one physical perch in the apparatus. The counterbalancing of stimulus-perch assignments across sessions was therefore effective in removing spatial bias as a confound, and any stimulus-preference effects reported in the following sections cannot be attributed to a stable preference for a particular perch location.

3.2 Session-level rhythmic versus arrhythmic listening-time preference

The first confirmatory analysis tested Prediction 1 (Section 1.6.2) that expects budgerigars showing differential listening-time responses to rhythmic and arrhythmic stimuli, and tests whether this contrast varied across sessions. The mixed-effects model is described in Section 2.6.3.

Table 3.3: Descriptive statistics for rhythmic and arrhythmic listening time by session

Session	Stimulus	Mean time	Median time	SD	n
1	A	2177,077	913	2615,651	13
	R	2196	1058	2553,565	13
2	A	1897,231	1611	2177,243	13
	R	2252,538	1549	2321,565	13
3	A	750,308	428	1277,877	13
	R	3126,154	1898	2708,102	13

Note. Time in seconds. n = bird-session observations per cell. Annabelle's Session 3 is treated as 0 s for purposes of cell composition. Overall means across the three sessions: A = 1608,2 s, R = 2524,9 s.

At the descriptive level, mean listening time was higher overall on rhythmic perches (*M = 2524,9 s, SD = 2502,6*) than on arrhythmic perches (*M = 1608,2 s, SD = 2136,4*). The contrast varied across sessions (Table 3.3). In Session 1, mean listening times were nearly identical (*R = 2196,0 s; A = 2177,1 s*). In Session 2, the rhythmic mean exceeded the arrhythmic mean by approximately 19% (*R = 2252,5 s; A = 1897,2 s*). In Session 3, the rhythmic mean was approximately four times higher than the arrhythmic mean (*R = 3126,2 s; A = 750,3 s)*. Across the three sessions, mean rhythmic listening time increased by approximately 42% (*from 2196,0 s in Session 1 to 3126,2 s in Session 3*), while mean arrhythmic listening time decreased by approximately 66% (*from 2177,1 s to 750,3 s*). Relative to the available 7200-second session window, rhythmic occupancy accounted for approximately 31% of session time in Session 1 and 43% in Session 3; arrhythmic occupancy accounted for approximately 30% in Session 1 and 10% in Session 3. The session-level trajectories of mean listening time are shown in Figure 3.2.

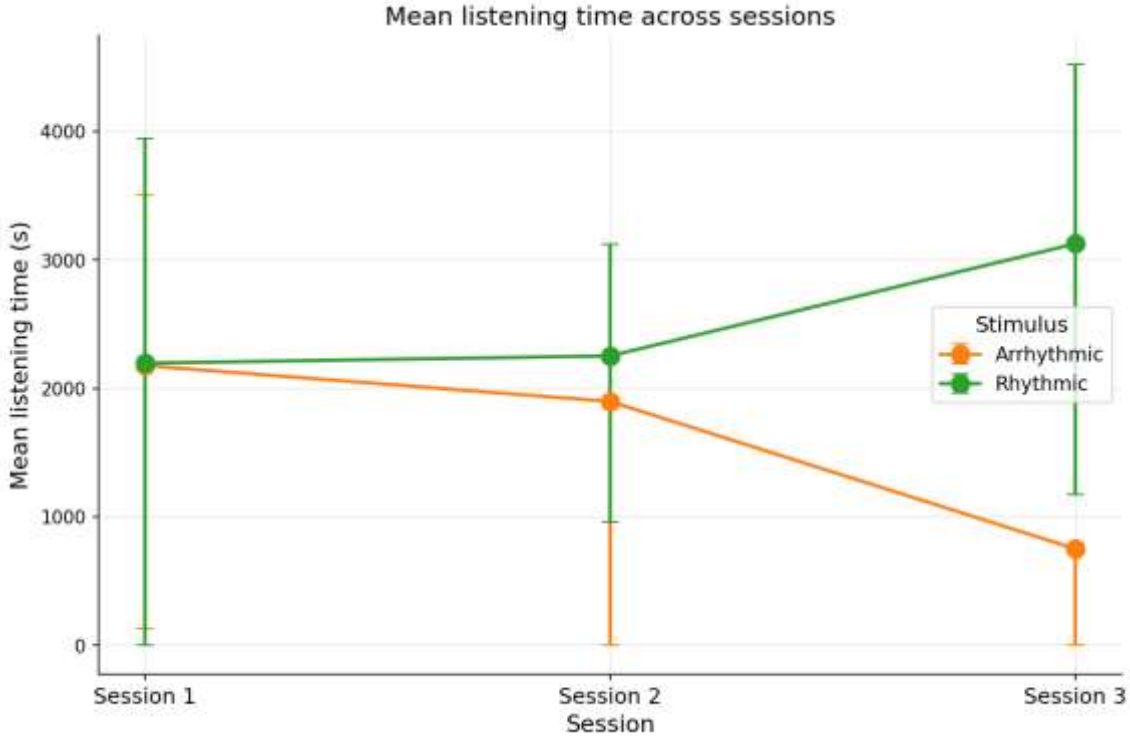


Figure 3.2: Mean listening time (in seconds) on rhythmic and arrhythmic perches across the three sessions. Points represent the mean across all thirteen birds; error bars show the 25th–75th percentile range, reflecting between-bird variability at each session. Lines connect session means within stimulus type to indicate the session-level trajectory. The compressed upper error bar for the arrhythmic Session 3 cell reflects strong right-skew in the data, with the 75th percentile (761 s) sitting just above the mean (750 s); a few birds with comparatively higher arrhythmic occupancy pull the mean up while the bulk of the distribution lies below.

The mixed-effects model (Table 3.4) tested the effect of stimulus type, session number, sex, and the stimulus-by-session interaction on log-transformed listening time. The reference category was arrhythmic stimuli in Session 1, with female as the reference sex. The contrast between rhythmic and arrhythmic listening time was not significant in Session 1 (*b = -0,725, SE = 0,995, p = ,466*), and the rhythmic-by-Session 2 interaction was also non-significant (*b = 1,541, SE = 1,407, p = ,274*). The rhythmic-by-Session 3 interaction was positive and statistically significant (*b = 3,150, SE = 1,407, z = 2,238, p = ,025, 95% CI [0,392, 5,909]*). Neither of the main effects of session reached significance (*Session 2 vs. Session 1: b = -0,666, p = ,503; Session 3 vs. Session 1: b = -1,538, p = ,122*), and the main effect of sex was not significant (*b = 0,222, p =*

,872). The bird-by-session variance component was estimated near zero, indicating that variability across sessions within birds was largely absorbed by the bird random intercept.

Table 3.4: Mixed-effects model of session-level rhythmic versus arrhythmic listening time (dependent variable: log time + 1)

Term	Estimate	SE	z	p	95% CI
Intercept	5,787	1,196	4,839	0	[3,443, 8,13]
Session 2 (vs 1)	-0,666	0,995	-0,67	0,5031	[-2,617, 1,284]
Session 3 (vs 1)	-1,538	0,995	-1,545	0,1223	[-3,488, 0,413]
Male (vs female)	0,222	1,374	0,162	0,8715	[-2,471, 2,916]
R vs A (session 1)	-0,725	0,995	-0,728	0,4664	[-2,676, 1,226]
R × Session 2	1,541	1,407	1,095	0,2736	[-1,218, 4,299]
R × Session 3	3,15	1,407	2,238	0,0252	[0,392, 5,909]

Random effects / model information: Reference category = arrhythmic stimulus, Session 1, female. N = 78 observations from 13 birds. Bird identity included as random intercept (variance = 5,03); bird-by-session variance component estimated at 0,00. Model converged.

In summary, the rhythmic-versus-arrhythmic listening-time contrast was not present in Session 1, was not statistically supported in Session 2, and was significant in Session 3.

3.3 Bird-level aggregate rhythmic versus arrhythmic listening-time preference

The bird-level aggregate analysis tested Prediction 1 (Section 1.6.2) at the level of overall rhythmic preference, complementing the session-level analysis in Section 3.2 by asking whether each bird's total listening time on rhythmic perches differed from its total listening time on arrhythmic perches across the three sessions combined. The analytic plan is described in Section 2.6.4.

Table 3.5: Bird-level total listening time across sessions by stimulus

Stimulus	Mean total	Median total	SD
A	4824,615	5023	3384,036
R	7574,692	8440	4849,849
S	4721,769	3469	4793,965

Notes. Totals aggregated across the sessions each bird completed and summarised across the 13 birds. The silent condition (S) is reported here for descriptive completeness; inferential analyses involving the silent condition are reported in Section 3.4. Annabelle (Sessions 1 and 2 only) contributes whatever data she has; her missing Session 3 is treated as 0 s.

Bird-level totals are reported in Table 3.5. Aggregated across sessions, mean total time on rhythmic perches (*M = 7574,7 s, SD = 4849,8*) substantially exceeded mean total time on arrhythmic perches (*M = 4824,6 s, SD = 3384,0*). Bird-level totals on the silent perch are reported in Table 3.5 for descriptive completeness; analyses involving the silent condition are presented in Section 3.4.

Table 3.6: Bird-level total listening time across sessions by sex

Sex	A mean	R mean	S mean
Female	5868,5	9359,5	2229,5
Male	3929,857	6044,857	6858

Notes. Mean and median total time (in seconds) summed across the sessions each bird completed, separated by sex. n = 6 female birds, 7 male birds. The silent condition (S) is reported here for descriptive completeness; inferential analyses involving the silent condition are reported in Section 3.4.

Bird-level totals separated by sex are reported in Table 3.6. Female birds had higher mean totals on rhythmic perches (*M = 9359,5 s*) than male birds (*M = 6044,9 s*), and a similar female-higher direction was observed for arrhythmic totals (*female M = 5868,5 s; male M = 3929,9 s*). Female birds had substantially lower totals on the silent perch (*M = 2229,5 s*) than male birds (*M = 6858,0 s*). Per-bird rhythmic and arrhythmic totals are shown in Figure 3.3.

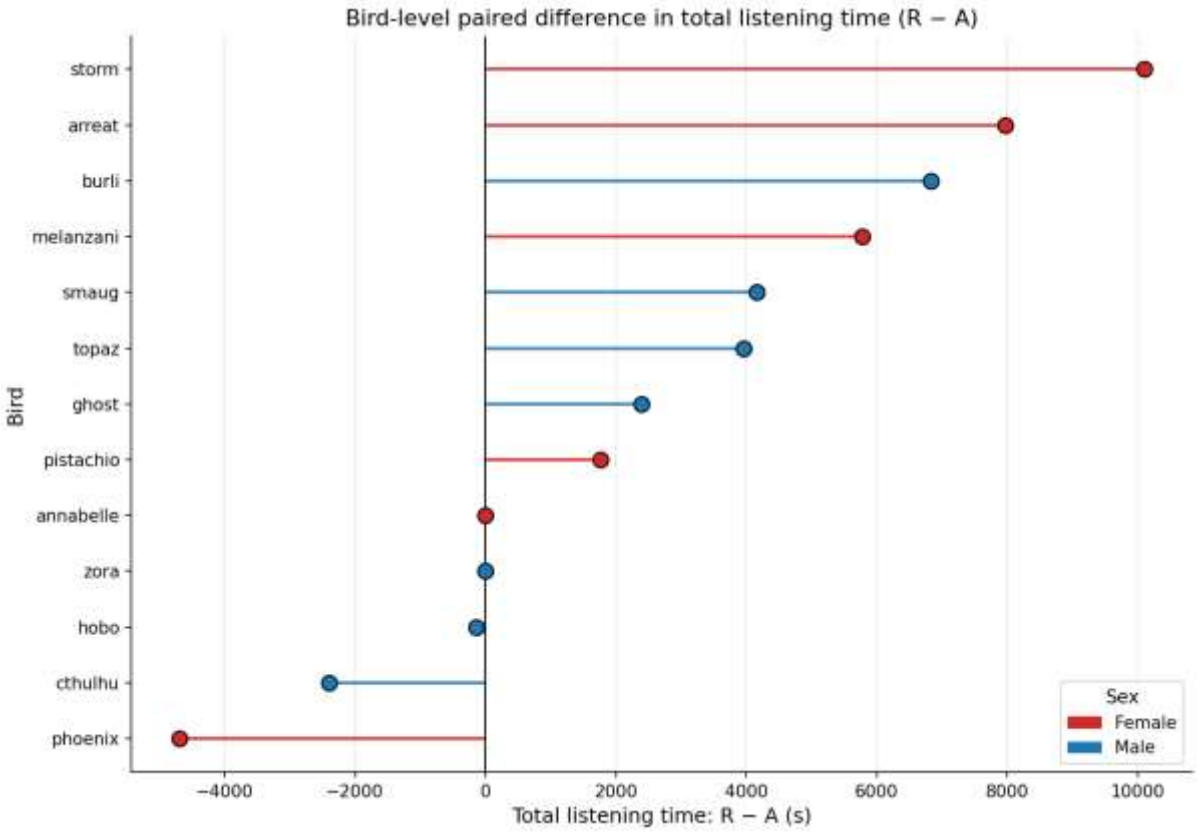


Figure 3.3: Bird-level paired difference in total listening time (rhythmic minus arrhythmic), summed across the sessions each bird completed. Each row represents one bird; the dot marks that bird's R-minus-A total in seconds, and the horizontal stem shows distance from zero. Positive values (right of the vertical line) indicate that the bird spent more total time on the rhythmic perch than on the arrhythmic perch. Dots and stems are coloured by sex (red = female, blue = male). Birds are ordered from largest negative difference (bottom) to largest positive difference (top). N = 13 birds (6 female, 7 male).

Table 3.7 reports the paired-difference distribution at the bird level. Of the 13 birds, 8 had longer total time on R than on A (4 female, 4 male), 1 bird was tied (annabelle), and 4 birds had longer total time on A than on R (1 female, 3 male). The mean R − A difference across all birds was +2750,1 s, with a median of +2389,0 s.

Table 3.7: Bird-level paired total-listening-time differences (rhythmic minus arrhythmic, summed across all three sessions), summarised by group.

Group	N birds	Mean R-A (s)	Median R-A (s)	Birds with R>A	Birds with R=A	Birds with R<A
Overall	13	2750,1	2389	8	1	4
Female	6	3491	3774,5	4	1	1
Male	7	2115	2389	4	0	3

Notes: Mean and median are computed across birds within each group. Bird counts indicate how many birds in each group had R total greater than, equal to, or less than A total. The paired tests reported in

Table 3.8 were conducted on log-transformed totals; the linear-scale differences shown here describe the same paired structure.

The within-bird comparison of log-transformed rhythmic and arrhythmic totals was tested with a paired-samples t-test (Table 3.8). Totals were log-transformed prior to testing because bird-level totals varied across orders of magnitude in this sample (from a few seconds for very low-engagement birds to over 14000 s for the highest-engagement birds), and the log transformation brings these differences onto a comparable additive scale. Mean log-rhythmic total exceeded mean log-arrhythmic total, t(12) = 2,20, p = ,048, Cohen's d_z = 0,61. A Wilcoxon signed-rank test was conducted as a non-parametric sensitivity check; this test yielded a marginal p-value (W = 15,0, p = ,064).

Table 3.8: Bird-level Rhythmic vs Arrhythmic tests

Test	Statistic	p	Effect size / note
Paired t-test on log totals	2,2009	0,0481	Cohen's dz = 0.6104
Wilcoxon signed-rank	15	0,064	marginal

Note. Tests conducted on log-transformed bird-level totals (log(total + 1)) for the rhythmic-versus-arrhythmic contrast. Cohen's d_z is the standardised mean of paired differences, computed as the mean within-bird difference divided by the standard deviation of those differences.

The bird-level rhythmic-minus-arrhythmic difference (computed on the log scale) was then entered into an ordinary least-squares regression with sex as the sole predictor (Table 3.9). Sex did not significantly predict the bird-level rhythmic preference (*b = -0,088, SE = 0,362, p = ,812*); the model explained essentially none of the variance in the difference scores (R^2 = *,005*)

Table 3.9: OLS model of bird-level rhythmic preference by sex

Term	Estimate	SE	t	p	95% CI
Intercept	0,4283	0,2652	1,6148	0,1347	[-0,1555, 1,0121]
Male (vs female)	-0,0883	0,3615	-0,2443	0,8115	[-0,8839, 0,7073]

Note. Dependent variable: bird-level rhythmic-minus-arrhythmic difference, computed on the log scale as log(R + 1) − log(A + 1). Reference category for sex = female. N = 13 birds. R^2 = ,005.

In summary, mean total rhythmic listening time exceeded mean total arrhythmic listening time at the bird level, with a significant paired t-test on log-transformed totals and a marginal non-parametric sensitivity check. The paired-differences table shows that the effect is broadly distributed across the sample (8 of 13 birds with R > A) rather than driven by a small number of outliers. No significant sex difference was observed in the magnitude of this rhythmic-minus-arrhythmic effect.

3.4 Exploratory analyses including the silent condition: listening time

The next analysis tested Prediction 2 (Section 1.6.2): whether the silent condition would help disambiguate attraction to rhythmic structure from avoidance of arrhythmic structure. The analysis is exploratory rather than confirmatory because it involves three stimulus types and stimulus-by-sex interaction terms, with a smaller effective per-cell sample than the two-stimulus comparisons in Sections 3.2 and 3.3. The analytic plan is described in Section 2.6.5.

Aggregated across all bird-session observations, mean listening times were 1608,2 s on arrhythmic perches, 2524,9 s on rhythmic perches, and 1573,9 s on silent perches (Table 3.10). Between-bird variability was substantial in all three conditions, with standard deviations of comparable magnitude (*A: SD = 2136,4 s; R: SD = 2502,6 s; S: SD = 1983,9 s*).

Table 3.10: Descriptive statistics for total listening time by stimulus

Stimulus	Mean time	Median time	SD	n
A	1608,205	761	2136,405	39
R	2524,897	1600	2502,632	39
S	1573,923	749	1983,921	39

Notes. Time in seconds. n = bird-session observations (13 birds × 3 sessions; annabelle's missing Session 3 is treated as 0 s).

Descriptive statistics separated by sex are reported in Table 3.11. Female birds had a higher mean listening time on rhythmic perches (*M = 3119,8 s*) than on arrhythmic perches (*M = 1956,2 s*), and a lower mean on silent perches (*M = 743,2 s*) than on either acoustic perch type. Male birds showed a different ordering: they had a higher mean listening time on silent perches (*M = 2286,0 s*) than on either acoustic perch type, with rhythmic (*M = 2015,0 s*) close to but higher than arrhythmic (*M = 1310,0 s*). The standard deviation on male silent listening time (*SD = 2361,3 s*) was substantially larger than on female silent listening time (*SD = 938,7 s*), reflecting greater between-male variability in silent-perch engagement. Distributions of total listening time by stimulus and sex are shown in Figure 3.4.

Table 3.11: Descriptive statistics for listening time by stimulus and sex

Sex	Stimulus	Mean time	Median time	SD	n
Female	A	1956,167	909	2452,018	18
	R	3119,833	2658	2712,927	18
	S	743,167	269,5	938,68	18
Male	A	1309,952	697	1832,792	21
	R	2014,952	1176	2247,763	21
	S	2286	1451	2361,311	21

Notes. Time in seconds. n = bird-session observations (6 female birds × 3 sessions = 18, with annabelle's S3 treated as 0; 7 male birds × 3 sessions = 21).

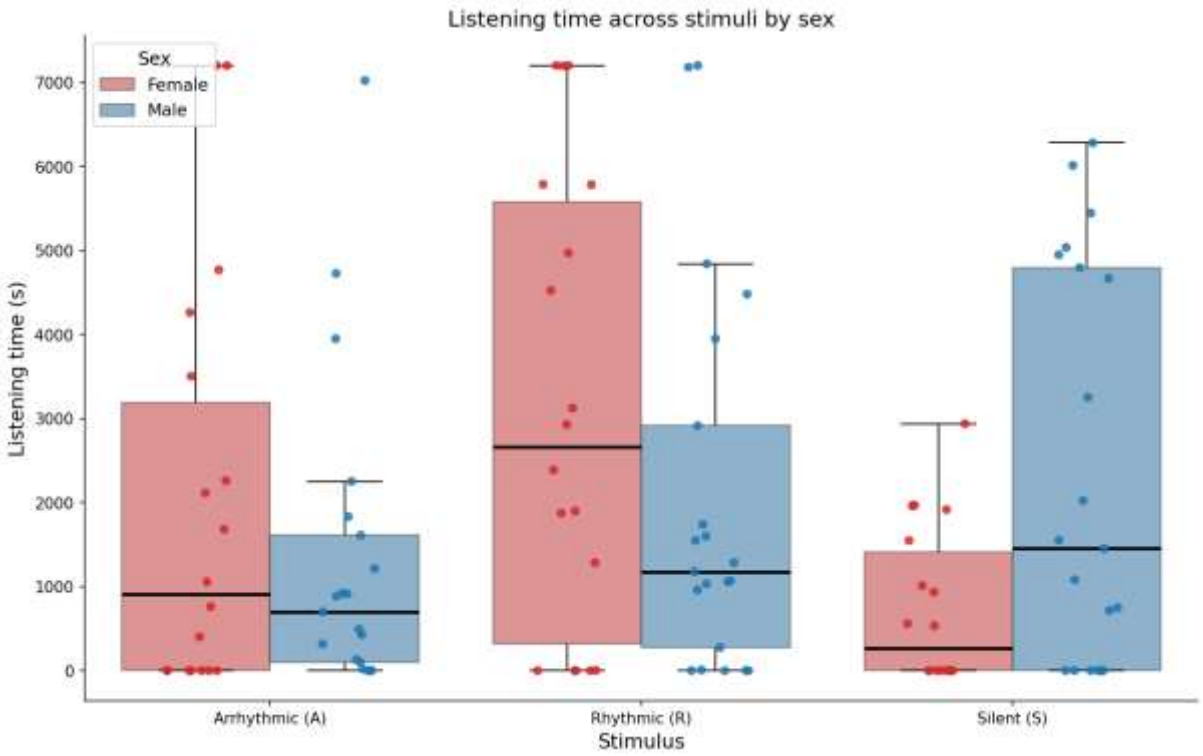


Figure 3.4: Distributions of total listening time on arrhythmic (A), rhythmic (R), and silent (S) perches, separated by sex. Boxes show the interquartile range with median (bold black line); individual dots show per bird-session values, jittered for visibility. The y-axis is capped at 7200 s, the maximum possible per-session listening time. Female n = 18 bird-session observations (6 birds; annabelle's missing Session 3 zero-padded); male n = 21 bird-session observations (7 birds).

The mixed-effects model (Table 3.12) tested the effects of stimulus type, session number, sex, and stimulus-by-sex interactions on log-transformed listening time. The reference categories were arrhythmic stimuli in Session 1, with female as the reference sex. The contrast between rhythmic and arrhythmic stimuli did not reach significance (*b = 1,249, SE = 0,899, p = ,165, 95% CI [-0,513, 3,011]*). The contrast between silent and arrhythmic stimuli was also not significant (*b = -1,168, SE = 0,899, p = ,194, 95% CI [-2,930, 0,594]*). The main effect of sex was non-significant (*b = 0,603, p = ,697*), as were the main effects of session (*Session 2 vs. 1: p = ,311; Session 3 vs. 1: p = ,436*). Neither stimulus-by-sex interaction reached significance: rhythmic-by-male was non-significant (*b = -0,762, p = ,534*), and silent-by-male was non-significant (*b = 1,013, p = ,408*). Although neither interaction was statistically supported, the silent-by-male coefficient was positive and the rhythmic-by-male coefficient was negative, descriptively consistent with the sex-differentiated ordering observed in the cell-level descriptives (female R > A > S; male S > R > A).

Table 3.12: Exploratory mixed-effects model of listening time by stimulus, sex, and session (dependent variable: log time + 1)

Term	Estimate	SE	z	p	95% CI
Intercept	4,479	1,192	3,757	0,0002	[2,143, 6,816]
R (vs A)	1,249	0,899	1,389	0,1648	[-0,513, 3,011]
S (vs A)	-1,168	0,899	-1,299	0,194	[-2,93, 0,594]
Male (vs female)	0,603	1,551	0,389	0,6974	[-2,437, 3,644]
Session 2 (vs 1)	0,623	0,614	1,014	0,3105	[-0,581, 1,827]
Session 3 (vs 1)	0,479	0,614	0,78	0,4356	[-0,725, 1,683]
R × Male	-0,762	1,225	-0,622	0,5341	[-3,163, 1,64]
S × Male	1,013	1,225	0,827	0,4082	[-1,388, 3,415]

Note. Reference category = arrhythmic stimulus, Session 1, female. N = 117 observations from 13 birds. Bird identity included as random intercept (variance = 5,34); bird-by-session variance component estimated at 0,00. Model converged.

In summary, no contrast involving the silent condition reached statistical significance in the listening-time analysis, and no stimulus-by-sex interaction was statistically supported. The descriptive ordering of mean listening time across the three stimulus categories differed between female and male birds (Table 3.10 and Table 3.11): females showed R > A > S, while males showed S > R > A.

3.5 Visit-count analysis: rhythmic versus arrhythmic visits

The next confirmatory analysis tested visit counts as an independent measure of preference, complementing the listening-time analyses in Sections 3.2 and 3.3. The analytic plan is described in Section 2.6.6.

Table 3.13: Descriptive statistics for rhythmic and arrhythmic visit counts by session

Session	Stimulus	Visit counts			n
		Mean	**Median**	**Std**	
1	A	15,154	4	38,592	13
	R	13,462	5	24,643	13
2	A	20,846	9	25,625	13
	R	17,462	3	21,208	13
3	A	21,923	21	27,579	13
	R	20,231	13	22,694	13

Notes. *n = number of bird-session observations per cell. A preliminary Poisson model showed substantial overdispersion (ratio = 37.16), motivating the use of the negative binomial GEE reported in* Table 3.14.

Descriptive statistics for visit counts by session are reported in Table 3.13. Mean visit counts increased across sessions for both stimulus types (*A: 15,2 → 20,8 → 21,9; R: 13,5 → 17,5 → 20,2*). Aggregated across sessions, mean visit counts were comparable on arrhythmic perches (*M = 19,3, SD = 30,4*) and rhythmic perches (M = 17,1, SD = 22,5), with arrhythmic marginally higher. The session-level trajectories of mean visit counts are shown in Figure 3.5.

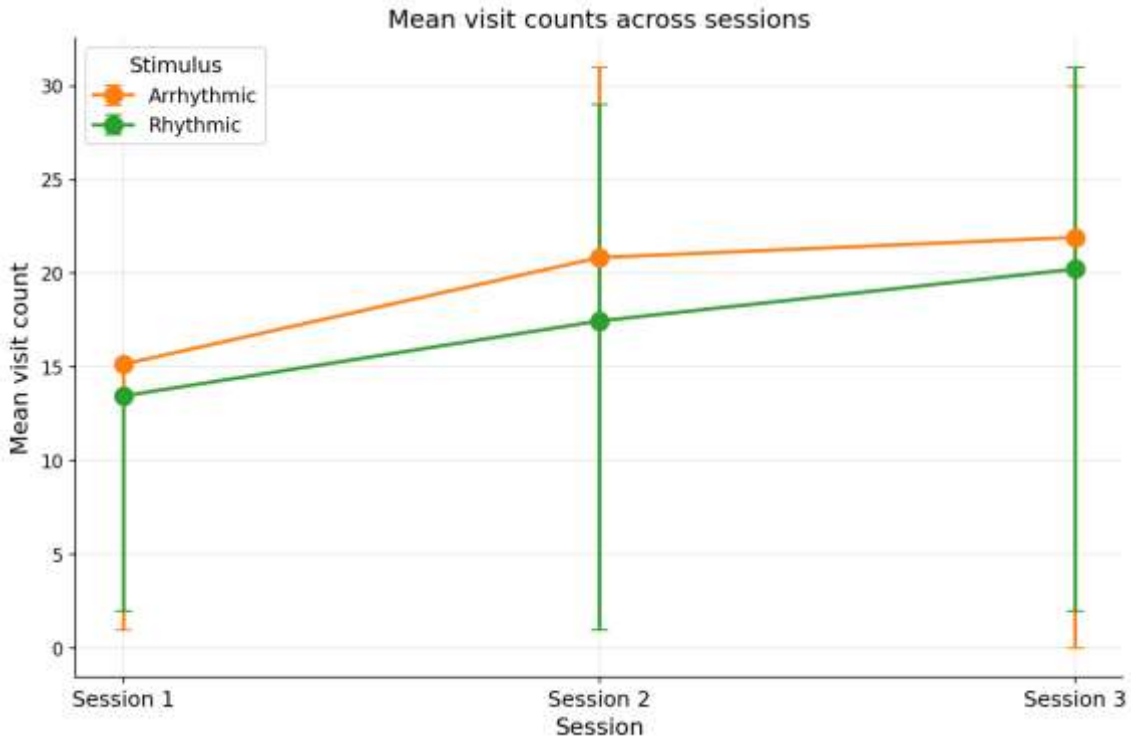


Figure 3.5: Mean visit counts for arrhythmic and rhythmic stimuli across the three sessions. Points represent the mean across all eleven birds; error bars show the 25th–75th percentile range, reflecting between-bird variability at each session. Lines connect session means within stimulus type to indicate the session-level trajectory

The negative binomial GEE model (Table 3.14) tested the effects of stimulus type, session number, sex, and the stimulus-by-session interaction on visit counts. The reference categories were arrhythmic stimuli in Session 1, with female as the reference sex. A preliminary Poisson model showed substantial overdispersion (overdispersion ratio = 37,16), confirming the need for the negative binomial approach. The contrast between rhythmic and arrhythmic visit counts was not significant in Session 1 (*b = -0,033, SE = 0,241, p = ,893, 95% CI [-0,504, 0,439]*). Neither session interaction reached significance (*R × Session 2: b = -0,146, p = ,576; R × Session 3: b = -0,014, p = ,953*). The main effects of session were also non-significant (*Session 2 vs. 1: b = 0,541, p = ,441; Session 3 vs. 1: b = 0,429, p = ,515)*. The main effect of sex did not reach conventional significance, with male birds showing a higher intercept than female birds (*b = 0,817, SE = 0,527, p = ,121, 95% CI [-0,217, 1,851]*).

Table 3.14: Negative binomial GEE model of rhythmic versus arrhythmic visit counts

Term	Estimate	SE	z	p	95% CI
Intercept	2,0892	0,5093	4,1023	< 0,001	[1,0911, 3,0874]
Session 2 (vs 1)	0,5405	0,7009	0,7711	0,4406	[-0,8333, 1,9143]
Session 3 (vs 1)	0,4285	0,6584	0,6508	0,5152	[-0,8619, 1,7189]
Male (vs female)	0,8169	0,5274	1,549	0,1214	[-0,2167, 1,8505]
R vs A (session 1)	-0,0325	0,2405	-0,135	0,8926	[-0,5039, 0,439]
R × Session 2	-0,1462	0,2617	-0,5587	0,5764	[-0,6592, 0,3668]
R × Session 3	-0,0137	0,2331	-0,0589	0,953	[-0,4706, 0,4431]

Notes. Reference category = arrhythmic stimulus, Session 1, female. N = 78 observations from 13 birds. Negative binomial GEE with exchangeable correlation structure clustered within bird.

In summary, the rhythmic-versus-arrhythmic contrast in visit counts was not significant at any session, and no significant change in this contrast across sessions was observed.

3.6 Exploratory analyses including the silent condition: visit counts

The next analysis tested visit counts with the silent condition included as a third stimulus category. As with the corresponding listening-time analysis in Section 3.4, this analysis is exploratory rather than confirmatory because it involves three stimulus types and stimulus-by-sex interaction terms, with a smaller effective per-cell sample than the two-stimulus comparisons in Section 3.5. The analytic plan is described in Section 2.6.7.

Aggregated across all bird-session observations, mean visit counts were 19.3 on arrhythmic perches, 17.1 on rhythmic perches, and 28.1 on silent perches (Table 3.15). The standard deviation on the silent condition (*SD = 64,3*) was approximately twice as large as on either acoustic condition (*A: SD = 30,4; R: SD = 22,5*), reflecting substantial between-bird variability in silent-perch visit frequency.

Table 3.15: Descriptive statistics for visit counts across A, R, and S

Stimulus	Mean visits	Median visits	SD	n
A	19,308	5	30,445	39
R	17,051	5	22,458	39
S	28,128	4	64,311	39

Notes. *n = bird-session observations. The high SD on the silent condition reflects between-bird variability, documented in* Table 3.16 and Figure 3.6.

Descriptive statistics separated by sex are reported in Table 3.16. Female birds had similar mean visit counts on arrhythmic (*M = 11,2*) and rhythmic perches (*M = 11,2*), with a marginally higher mean on silent perches (*M = 11,7*). Male birds had higher mean visit counts on silent perches (*M = 42,2*) than on either acoustic perch type, with arrhythmic visit counts (*M = 26,2*) marginally higher than rhythmic visit counts (*M = 22,0)*. The standard deviation on male silent visit counts (*SD = 84,5*) was substantially larger than on female silent visit counts (*SD = 18,0*). Distributions of visit counts by stimulus and sex are shown in Figure 3.6.

Table 3.16: Descriptive statistics for visit counts across A, R, and S by sex

Sex	Stimulus	Mean visits	Median visits	SD	n
Female	A	11,222	4,5	17,427	18
	R	11,222	3	15,895	18
	S	11,722	2	17,976	18
Male	A	26,238	11	37,332	21
	R	22,048	13	26,206	21
	S	42,19	15	84,461	21

Notes. *n* = bird-session observations.

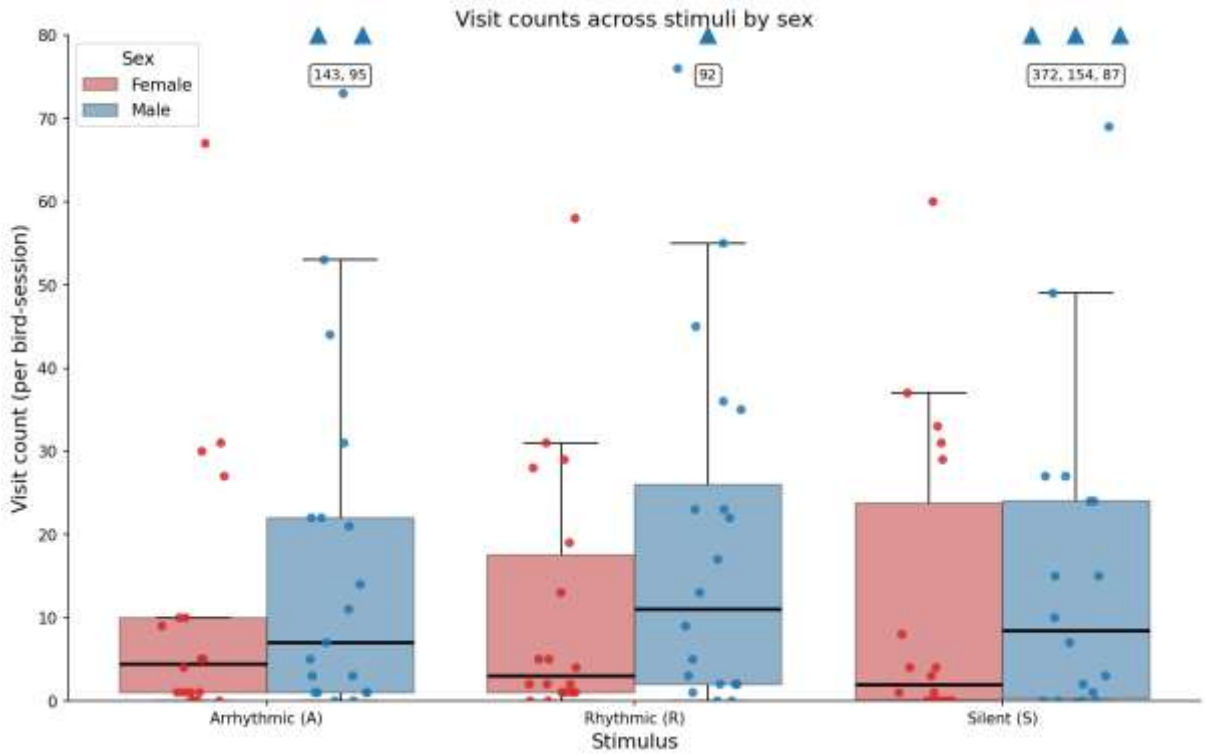


Figure 3.6: Distributions of visit counts on arrhythmic (A), rhythmic (R), and silent (S) perches, separated by sex. Boxes show the interquartile range with median (bold black line); individual dots show per bird-session visit counts, jittered for visibility. The y-axis is capped at 80; values exceeding the cap are shown as triangles at the top of the relevant column with their counts labelled. Female n = 18 bird-session observations (6 birds; annabelle's missing Session 3 zero-padded); male n = 21 bird-session observations (7 birds).

The negative binomial GEE model (Table 3.17) ested the effects of stimulus type, session number, sex, and stimulus-by-sex interactions on visit counts. The reference categories were arrhythmic stimuli in Session 1, with female as the reference sex. The contrast between rhythmic and arrhythmic visit counts was not significant (*b = 0,028, SE = 0,068, p = ,682, 95% CI [-0,105, 0,160]*). The contrast between silent and arrhythmic visit counts was also not significant (*b = 0,077, SE = 0,186, p = ,680, 95% CI [-0,288, 0,442]*). The main effect of sex did not reach conventional significance (*b = 0,909, SE = 0,547, p = ,096*). The main effects of session were non-significant (*Session 2 vs. 1: b = 0,446, p = ,461; Session 3 vs. 1: b = 0,571, p = ,330*). The silent-by-male interaction was non-significant (*b = 0,324, SE = 0,380, p = ,393*). The rhythmic-by-male interaction was negative and marginally significant (*b = -0,213, SE = 0,112, z = -1,897, p = ,058, 95% CI [-0,432, 0,007]*), indicating that male birds showed a less positive R-versus-A visit contrast than female birds.

Table 3.17: Exploratory negative binomial GEE model of visit counts across A, R, and S

Term	Estimate	SE	z	p	95% CI
Intercept	2,0247	0,4569	4,4313	< 0,001	[1,1292, 2,9202]
R (vs A)	0,0277	0,0677	0,4099	0,6819	[-0,1049, 0,1604]
S (vs A)	0,0769	0,1864	0,4126	0,6799	[-0,2884, 0,4421]
Male (vs female)	0,9094	0,5465	1,6638	0,0961	[-0,1618, 1,9806]
Session 2 (vs 1)	0,4464	0,6051	0,7376	0,4607	[-0,7396, 1,6323]
Session 3 (vs 1)	0,5708	0,5864	0,9733	0,3304	[-0,5786, 1,7201]
R × Male	-0,2126	0,112	-1,8973	0,0578	[-0,4321, 0,007]
S × Male	0,3244	0,3796	0,8547	0,3927	[-0,4195, 1,0684]

Notes. Reference category = arrhythmic stimulus, Session 1, female. N = 117 observations from 13 birds. Negative binomial GEE with exchangeable correlation structure clustered within bird.

In summary, no contrast involving the silent condition reached statistical significance in the visit-count analysis. The rhythmic-by-male interaction was marginal (*p = ,058*): male birds showed a less positive R-versus-A visit contrast than female birds. This was the largest sex-related effect observed across all analyses reported in the chapter and is in the same direction as the sex pattern reported by Hoeschele and Bowling (2016).

3.7 Visit-duration analysis: rhythmic vs. arrhythmic visits

The next confirmatory analysis tested visit duration as an independent measure of preference. Whereas total listening time and visit count characterise overall occupancy and approach behaviour respectively, visit duration captures how long birds remained at a perch once they had visited it. The analytic plan is described in Section 2.6.8. As established in that section, visit-duration distributions were heavily right-skewed, with a small number of very long visits driving means substantially above the corresponding medians. The analysis therefore used bird-level median visit durations as the summary measure and a non-parametric within-bird bootstrap to test the rhythmic-versus-arrhythmic contrast. Visits with duration ≤ 0 are excluded from this analysis (per Section 2.6.8). Three birds (annabelle, melanzani, and zora) are also excluded due to insufficient data for stable bird-level median estimates: annabelle was tested in only two of the three sessions, and melanzani and zora each produced very few total visits across the experiment. These exclusions are noted in the relevant tables and figure.

Descriptive statistics for visit duration by session and stimulus are reported in Table 3.18. Across individual visits, median visit durations were generally short across sessions (*Session 1: A Mdn = 3 s, R Mdn = 8 s; Session 2: A Mdn = 9 s, R Mdn = 8 s; Session 3: A Mdn = 8 s, R Mdn = 8 s*), with very large within-cell standard deviations reflecting the right-skew of the underlying distributions.

Table 3.18: Descriptive statistics for arrhythmic and rhythmic visit durations by session

Session	Stimulus	Visit Duration			n
		Mean	**Median**	**Std**	
1	A	130,22	3	721,41	162
	R	194,17	8	788,32	147
2	A	98,26	9	547,82	251
	R	109,81	8	555,37	214
3	A	35,09	8	281,92	278
	R	131,65	8	670,25	254

Notes. Visit duration in seconds. n = number of individual visits contributing to each (session, stimulus) cell after exclusion of visits with duration ≤ 0 and exclusion of annabelle, melanzani, and zora. Silent visits are not included in this table; they are reported in Section 3.8 (exploratory analysis including the silent condition). See Section 2.6.8 for analytic detail.

The paired-difference structure of the bootstrap input is summarised in (Table 3.19). Of the 10 birds entering the analysis, 6 had longer median visit duration on R than on A (3 female, 3 male), 1 bird was tied (hobo), and 3 birds had longer median A than median R (1 female, 2 male). The overall mean paired difference was +177,6 s; the median paired difference across birds was +1,5 s, reflecting that most birds had R and A medians within a few seconds of each other.

Table 3.19: Bird-level paired visit-duration differences (median R minus median A for each bird, computed across all visits pooled from the three sessions), summarised by group

Group	N birds	Mean R-A (s)	Median R-A (s)	Birds with R>A	Birds with R=A	Birds with R<A
Overall	10	177,6	1,5	6	1	3
Female	4	430,88	6,5	3	0	1
Male	6	8,75	0,5	3	1	2

Notes: Bird-level median visit durations computed across all visits pooled from the three sessions. Bird counts indicate how many birds in each group had median R visits longer than, equal to, or shorter than their median A visits. The bootstrap in Table 3.20 resamples these paired bird-level differences. annabelle, melanzani, and zora are excluded.

The bootstrap analysis (Table 3.20) tested the rhythmic-versus-arrhythmic contrast in bird-level median visit duration overall, by sex, and by session. The overall contrast was positive and supported: the mean bootstrap difference between rhythmic and arrhythmic median visit duration was 176,3 s, with a 95% confidence interval of [0,6, 523,0] and P(R – A > 0) = ,989. The sex-stratified analysis showed that this contrast was supported in female birds (*mean difference = 427,8 s, 95% CI [-0,5, 1285,6], P(diff > 0) = ,953*) but not in male birds, where the contrast was small in magnitude with a confidence interval close to zero (mean difference = 8,8 s, 95% CI [-0,5, 25,2], P(diff > 0) = ,925). The session-stratified analyses produced wider confidence intervals than the overall contrast, reflecting smaller within-session samples. Session 1 (*mean difference = -35,1 s, P(diff > 0) = ,387*) and Session 2 (*mean difference = -600,8 s, P(diff > 0) = ,315*) did not show evidence of a positive contrast. Session 3 showed a positive trend that was not clearly supported (*mean difference = 397,4 s, 95% CI [-6,2, 1190,8], P(diff > 0) = ,750*). Bird-level paired median visit durations for rhythmic and arrhythmic perches are shown in Figure 3.7.

Table 3.20: Robust bootstrap analysis of rhythmic versus arrhythmic visit duration

Group	Contrast	Birds (n)	Mean difference	CI low	CI high	P(diff > 0)
Overall	R - A	10	176,254	0,6	523,004	0,9885
Sex: F	R - A	4	427,806	-0,5	1285,625	0,9534
Sex: M	R - A	6	8,779	-0,5	25,167	0,9249
Session 1	R - A	8	-35,145	-339,947	275,812	0,3868
Session 2	R - A	9	-600,779	-2398,83	585,5	0,3151
Session 3	R - A	9	397,365	-6,167	1190,778	0,7498

Notes. Robust within-bird bootstrap (10000 iterations). The contrast is the bird-level difference in median visit duration (rhythmic minus arrhythmic). 95% confidence intervals from the bootstrap distribution. P(diff > 0) is the proportion of bootstrap samples in which the difference was positive. Birds = number of birds contributing to each contrast; this varies across rows because not every bird

produced visits to both rhythmic and arrhythmic perches in every session. annabelle, melanzani, and zora are excluded throughout. See Section 2.6.8 for analytic detail.

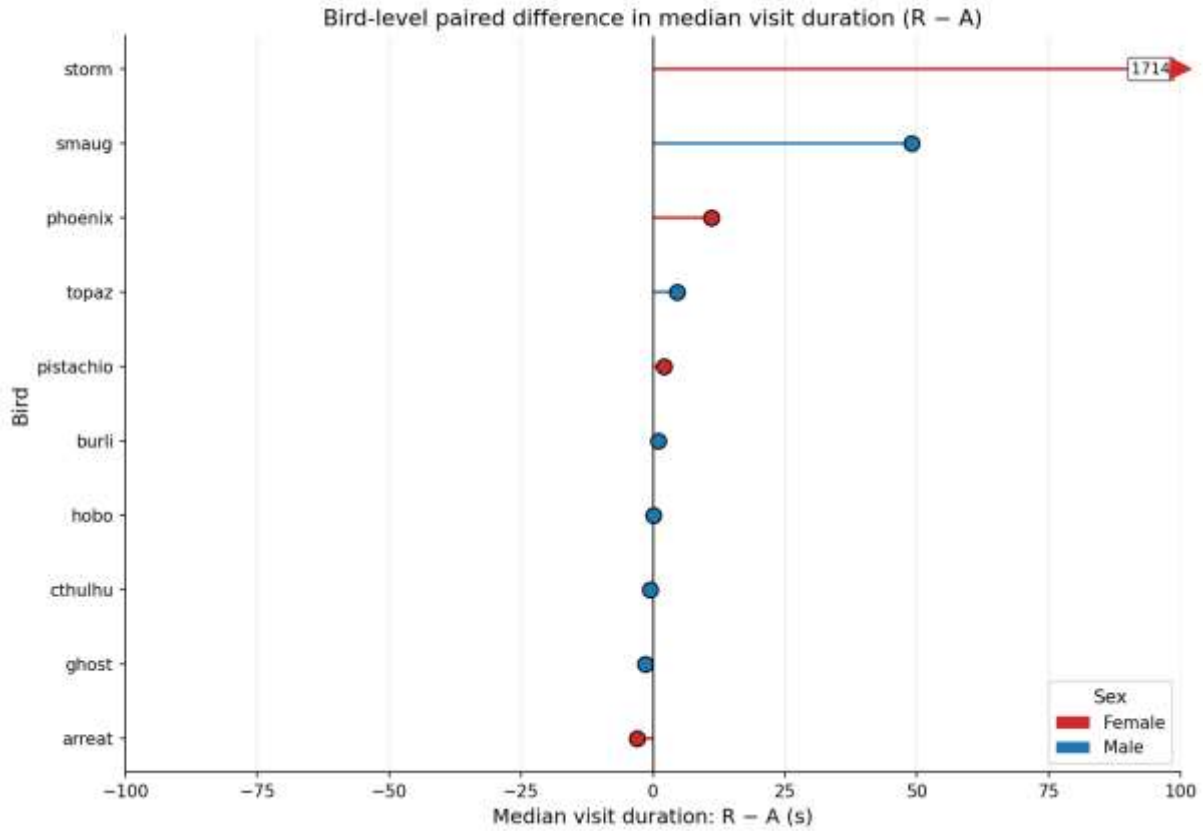


Figure 3.7: Bird-level paired difference in median visit duration (rhythmic minus arrhythmic) for each bird, computed across all visits pooled from the three sessions. Each row represents one bird; the dot marks that bird's median(R) minus median(A) in seconds, and the horizontal stem shows distance from zero. Positive values indicate longer typical visits on the rhythmic perch. Dots and stems are coloured by sex (red = female, blue = male). Birds are ordered from largest negative difference (bottom) to largest positive difference (top). Values exceeding ±100 s are shown as triangle markers at the axis boundary with their actual values labelled (storm: +1714 s). N = 10 birds (4 female, 6 male); annabelle, melanzani, and zora excluded.

In summary, overall there was a prefrence towards rhythmic versus arrhythmic in visit-duration which was statitically supported, although Table 3.19 shows that the overall mean is influenced disproportionately by one bird (storm) with a paired difference of +1714 s; the median paired difference across the sample was only +1,5 s. Sex-stratified analyses showed that the contrast was supported in female birds but not in male birds. Session-stratified analyses produced wider confidence intervals reflecting smaller within-session samples; only Session 3 showed a positive trend.

3.8 Exploratory analysis: Visit-duration with the inclusion of silent condition

The next analysis tested visit duration with the silent condition included as a third stimulus category. As with the corresponding listening-time and visit-count exploratory analyses (Sections 3.4 and 3.6), this analysis is exploratory rather than confirmatory because of the three-stimulus structure. The same robust within-bird bootstrap framework used in Section 3.7 was applied. The analytic plan is described in Section 2.6.9.

Table 3.21: Descriptive statistics for arrhythmic, rhythmic, and silent visit durations by sex

Sex	Stimulus	Mean	Median	Std	n
Female	A	155,59	9	745,59	180
	R	232,1	9	866,89	186
	S	63,47	24	171,37	196
Male	A	53,83	7	398,52	511
	R	98,63	7	549,82	429
	S	74,08	13	282,59	648

Notes. Visit duration in seconds. n = number of individual visits contributing to each (sex, stimulus) cell after exclusion of visits with duration ≤ 0, and exclusion of annabelle, melanzani, and zora. See Section 2.6.9 for analytic detail.

Descriptive statistics for visit duration by sex and stimulus, including the silent condition, are reported in Table 3.21. Female birds had the longest mean visit duration on rhythmic perches (*M = 232,1 s, n = 186 visits*), followed by arrhythmic perches (*M = 155,6 s, n = 180*), and the shortest on silent perches (*M = 63,5 s, n = 196*). However, female median visit durations told a different story: highest on silent perches (*Mdn = 24 s*), then close to equal on arrhythmic (*Mdn = 9 s*) and rhythmic (*Mdn = 9 s*) perches; the difference between mean and median on the rhythmic perch reflects the right-skew documented in Section 3.7. Male birds had the longest mean visit duration on rhythmic perches (*M = 98.6 s*) and shorter means on arrhythmic (*M = 53.8 s*) and silent (*M = 74.1 s*) perches, with the male silent median (*13 s*) substantially exceeding both male acoustic medians (*both 7 s*). Bird-level median visit durations across the three stimulus categories, separated by sex, are shown in Figure 3.8.

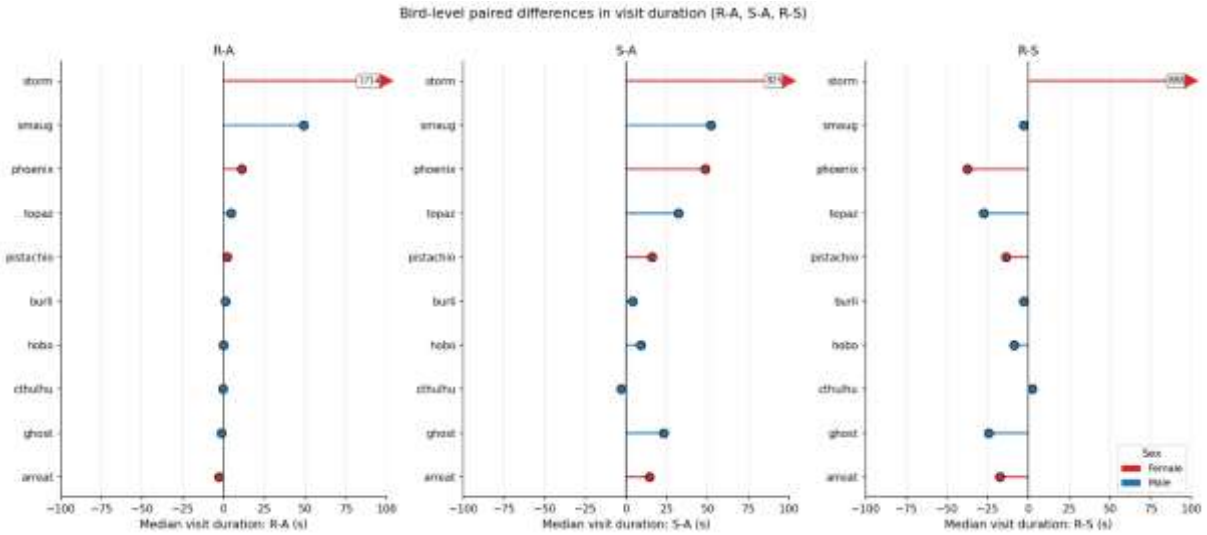


Figure 3.8: Bird-level paired differences in median visit duration across three pairwise contrasts (R − A, S − A, R − S), computed for each bird across all visits pooled from the three sessions. Each panel shows one contrast; positive values indicate longer typical visits on the first stimulus type. Birds appear in the same order across all three panels (sorted by R − A) so that individual birds can be tracked across contrasts. Dots and stems are coloured by sex (red = female, blue = male). Values exceeding ±100 s are shown as triangle markers at the axis boundary with their actual values labelled. N = 10 birds (4 female, 6 male); annabelle, melanzani, and zora excluded.

The overall bootstrap contrasts are reported in Table 3.22. The R – A contrast remained positive and supported in this exploratory analysis (*mean difference = 176,3 s, 95% CI [0,6, 523,0], P(diff > 0) = ,989),* confirming that inclusion of the silent condition did not alter the confirmatory finding from Section 3.7. The S – A contrast was strongly supported (*mean difference = 101,5 s, 95% CI [13,6, 267,3], P(diff > 0)* =

1,000), indicating that across the sample, birds had longer median visit durations on silent perches than on arrhythmic perches. The R – S contrast was not clearly supported (*mean difference = 74,8 s, 95% CI [-20,6, 259,3], P(diff > 0) = ,640*), although the point estimate was positive.

Table 3.22:Exploratory bootstrap contrasts among arrhythmic, rhythmic, and silent visit duration: overall

Group	Contrast	Birds (n)	Mean difference	CI low	CI high	P(diff > 0)
Overall	R - A	10	176,254	0,6	523,004	0,9885
Overall	S - A	10	101,452	13,55	267,3	1
Overall	R - S	10	74,802	-20,6	259,25	0,64

Notes. Robust within-bird bootstrap (10000 iterations). Birds = number of birds contributing to each contrast. annabelle, melanzani, and zora excluded.

Sex-stratified bootstrap contrasts are reported in Table 3.23. In female birds, the R – A contrast was supported (*mean difference = 427,8 s, 95% CI [-0,5, 1285,6], P(diff > 0) = ,953*). The S – A contrast was also strongly supported (*mean difference = 224,5 s, 95% CI [15,3, 622,8], P(diff > 0) = 1,000*), and the R – S contrast was not supported (*mean difference = 203,3 s, 95% CI [-31,6, 662,0], P(diff > 0) = ,680*), although the point estimate was positive. In male birds, the R – A contrast was small in magnitude and not clearly supported (*mean difference = 8,8 s, 95% CI [-0,5, 25,2], P(diff > 0) = ,925*). The S – A contrast was supported in the positive direction (*mean difference = 19,5 s, 95% CI [5,7, 34,8], P(diff > 0) = 1,000*), indicating longer median visit durations on silent perches than on arrhythmic perches in male birds. The R – S contrast was supported in the negative direction (*mean difference = -10,7 s, 95% CI [-19,8, -2,2], P(S – R > 0) = ,998*), equivalent to a supported S > R contrast in male birds.

Table 3.23: Exploratory bootstrap contrasts among arrhythmic, rhythmic, and silent visit duration: by sex

Group	Contrast	Birds (n)	Mean difference	CI low	CI high	P(diff > 0)
Female	R - A	5	341,722	-0,8	1029,7	0,9454
	S - A	4	224,485	15,25	622,75	1
	R - S	4	203,32	-31,625	662	0,6798
Male	R - A	6	8,779	-0,5	25,167	0,9249
	S - A	6	19,487	5,667	34,833	0,9998
	R - S	6	-10,709	-19,833	-2,167	0,0015

Notes. Robust within-bird bootstrap, sex-stratified. *Birds* = number of birds contributing to each contrast; this varies because not every bird produced visits in every condition.

Session-stratified bootstrap contrasts are reported in Table 3.24. The R – A contrast was not clearly supported in any individual session (Session 1*: mean difference = -35,1 s, P(diff > 0) = ,387;* Session 2: *mean difference = -600,8 s, P(diff > 0) = ,315;* Session 3: *mean difference = 397,4 s, P(diff > 0) = ,750*). The S – A contrast was not supported in Session 1 (*mean difference = 11,2 s, P(diff > 0) = ,615*) but was strongly supported in both Session 2 (*mean difference = 128,4 s, 95% CI [12,8, 344,8], P(diff > 0) = 1,000*) and Session 3 (*mean difference = 25,3 s, 95% CI [15,6, 33,2], P(diff > 0) = 1000*). The R – S contrast was not clearly supported in Session 1 (*mean difference = 858,8 s, P(diff > 0) = ,666*) and showed a positive trend that was not clearly supported in Session 2 (*mean difference = 92,0 s, P(diff > 0) = ,658*). In Session 3, the R – S contrast was supported in the negative direction (*mean difference = -27,1 s, 95% CI [-39,1, -15,9], P(S – R > 0) ≈ 1,000*), equivalent to a supported S > R contrast in Session 3.

Table 3.24: Exploratory bootstrap contrasts among arrhythmic, rhythmic, and silent visit duration: by session

Group	Contrast	Birds (n)	Mean difference	CI low	CI high	P(diff > 0)
Session 1	R - A	9	-32,071	-304,722	247	0,3869
	S - A	6	11,185	-83,5	94	0,6148
	R - S	7	858,801	-467,571	3071,643	0,6662
Session 2	R - A	10	-551,88	-2159,1	527,501	0,3056
	S - A	8	128,395	12,812	344,75	1
	R - S	8	91,989	-30,503	322,939	0,6576
Session 3	R - A	9	397,365	-6,167	1190,778	0,7498
	S - A	8	25,315	15,562	33,188	1
	R - S	8	-27,149	-39,125	-15,873	0,0001

Notes. Robust within-bird bootstrap, session-stratified. Birds = number of birds contributing to each contrast. P(diff > 0) values rounded; the Session 3 R – S value is < ,001. annabelle, melanzani, and zora excluded.

In summary, the inclusion of the silent condition did not overturn the overall R > A contrast established in Section 3.7 and revealed a new supported contrast: S > A overall, at the sample level. Sex-stratified analyses revealed contrasting patterns: female birds showed a supported R > A contrast and a supported S > A contrast, with no clearly supported R-vs-S ordering, while male birds showed a small and not clearly supported R-vs-A contrast, a supported S > A contrast, and a supported S > R contrast. The supported S > A finding was visible in Sessions 2 and 3 but not Session 1; the supported S > R finding within males emerged in Session 3

3.9 Summary

The analyses reported in this chapter yielded the following findings. The preliminary analysis showed no evidence of stable physical perch-location bias, supporting the validity of the place-preference design (Section 3.1). In the listening-time analyses, the session-level mixed-effects model revealed a session-dependent rhythmic-versus-arrhythmic preference, with the contrast not supported in Session 1 or Session 2 and statistically significant in Session 3 (*R × Session 3: b = 3,150, p = ,025*; Section 3.2). The bird-level aggregate analysis showed mean rhythmic listening time exceeding mean arrhythmic listening time, with a significant paired t-test on log-transformed totals (*t(12) = 2,20, p = ,048, Cohen's d_z = 0.61*) and a marginal Wilcoxon signed-rank test (*p = ,064*); the paired-differences distribution showed 8 of 13 birds with longer total time on R than A (4 of 6 females, 4 of 7 males), and no sex effect emerged in this analysis (Section 3.3). The exploratory listening-time analysis with the silent condition included did not yield statistically supported contrasts involving silence, although descriptive ordering of mean listening time across the three stimulus categories differed between sexes: female birds showed R > A > S, while male birds showed S > R > A (Section 3.4).

In the visit-count analyses, the negative binomial GEE model showed no significant rhythmic-versus-arrhythmic difference in visit counts at any session, and no significant change in this contrast across sessions (Section 3.5). The exploratory three-stimulus model yielded one effect that approached but did not reach statistical significance: a rhythmic-by-sex interaction (*b = -0,213, p = ,058*), with male birds

showing a less positive R-versus-A visit contrast than female birds. This was the largest sex-related effect observed across all analyses reported in the chapter (Section 3.6).

In the visit-duration analyses, the robust within-bird bootstrap showed an overall rhythmic-versus-arrhythmic contrast that was positive and supported (*mean difference = 176,3 s, 95% CI [0,6, 523,0], P(diff > 0) = ,989),* although the bird-level paired-differences distribution showed that this overall mean was influenced disproportionately by a single bird (storm) with a paired difference of +1714 s; the median paired difference across the sample was only +1,5 s. Sex-stratified analyses showed that this contrast was supported in female birds but not in male birds. Session-stratified analyses produced wider confidence intervals reflecting smaller within-session samples; only Session 3 showed a positive trend (Section 3.7). The exploratory three-stimulus visit-duration analysis confirmed that the overall rhythmic-versus-arrhythmic contrast was preserved when silent visits were included in the dataset, and additionally revealed a supported overall silent-versus-arrhythmic contrast (*mean difference = 101,5 s, P(diff > 0) = 1,000*) that had not emerged from the listening-time or visit-count analyses. Sex-stratified analyses showed contrasting visit-duration patterns: female birds showed both a supported R > A contrast and a supported S > A contrast, while male birds showed a small and not clearly supported R-vs-A contrast alongside supported S > A and S > R contrasts. Session-stratified analyses showed support for the silent-versus-arrhythmic contrast in Sessions 2 and 3, and for the silent-versus-rhythmic contrast in Session 3 (Section 3.8)

4 Discussion

This chapter takes up the findings reported in Chapter 3 and considers what they mean for the question of rhythmic preference in budgerigars. The Results chapter reported the analyses descriptively and inferentially without engaging in interpretation; the present chapter treats the same findings as evidence to be situated within the comparative literature on rhythm perception, vocal learning, and musicality, and within the methodological context of the place-preference paradigm itself. Section 4.1 summarises the headline findings as a recap, and the substantive discussion follows in the subsequent sections.

4.1 Summary of findings

The present study extended earlier place-preference work on budgerigar rhythm preference (Hoeschele & Bowling, 2016) in three ways: by using stimuli derived from natural budgerigar vocalisations rather than artificial percussion, by introducing a silent comparison condition to disambiguate attraction from avoidance, and by analysing visit duration and visit counts alongside listening time. Thirteen budgerigars (6 females, 7 males) were tested across three two-hour sessions in a three-perch apparatus, with a perch-location bias check confirming that no physical perch was preferred independently of stimulus assignment. All 13 birds contributed to the listening-time and visit-count analyses (annabelle's missing Session 3 was zero-padded for session-level analyses); the visit-duration bootstrap analyses (Sections 3.7 and 3.8) excluded three birds (annabelle, melanzani, zora) whose visit counts were too low to support stable bird-level median estimates, leaving 10 birds for those analyses. Five findings structure the discussion that follows.

First, in listening time, a rhythmic-versus-arrhythmic preference emerged across sessions rather than at first exposure. Listening times were nearly identical in Session 1 and diverged substantially by Session 3 (*R × Session 3 interaction p = ,025*), driven by both an increase in rhythmic engagement (*≈ 42%*) and a larger decrease in arrhythmic engagement (*≈ 66%*). The bird-level aggregate analysis showed mean rhythmic listening time exceeding arrhythmic across the combined sessions, with moderate evidence sensitive to test choice (*paired t-test on log totals p = ,048, Cohen's d_z = 0,61; Wilcoxon p = ,064*). The paired-differences distribution showed 8 of 13 birds with longer total time on R than A (4 of 6 females, 4 of 7 males), indicating that the effect is broadly distributed across the sample rather than driven by a small number of outliers.

Second, this listening-time preference was not expressed through more frequent approach. The visit-count GEE model showed no rhythmic-versus-arrhythmic effect at any session, with descriptive visit counts marginally favouring arrhythmic perches. The exploratory three-stimulus visit-count model produced the largest sex-related effect observed across all analyses, a rhythmic-by-sex interaction that approached but did not reach statistical significance (*b = -0,213, p = ,058*), in the same direction as the pattern reported by Hoeschele and Bowling (2016).

Third, visit duration revealed sex-differentiated rhythmic preferences with statistical support at the sample level. The robust within-bird bootstrap supported a positive

overall rhythmic-versus-arrhythmic contrast (*mean difference = 176,3 s, P(R – A > 0) = ,989*), supported in female birds (*P = ,953*) but not in male birds, where the contrast was small and the confidence interval close to zero (*P = ,925*). However, the bird-level paired-differences distribution showed that this overall result was influenced disproportionately by a single bird (storm, paired difference = +1714 s); the median paired difference across the 10 birds in this analysis was only +1,5 s. Considered jointly with the visit-count finding, the two measures suggest that female and male rhythmic preferences may be expressed through different behavioural channels: a sustained-engagement profile in some females (longer individual visits on rhythmic perches), and a frequency-based profile in some males (more visits, shorter per visit). This sex-differentiated channel reading is descriptively coherent across measures while statistically scattered, and is taken up in Section 4.3.

Fourth, the silent condition revealed engagement patterns that a two-choice design could not detect. In listening time, female birds showed an R > A > S ordering and male birds showed an S > R > A ordering, although the listening-time mixed-effects model did not statistically support either sex-by-stimulus contrast. Visit-duration analyses provided more directly interpretable evidence: at the overall sample level, median visit durations on silent perches were exceeding median visit durations on arrhythmic perches (S – A*: mean difference = 101,5 s, P(diff > 0) = 1,000*), supported by both sexes (female S > A: *P = 1,000; male S > A: P = ,9998*) and visible in Sessions 2 and 3. In male birds specifically, median visit durations on silent perches also exceeded those on rhythmic perches (R – S: *P(S – R > 0) = ,998*), with the same contrast emerging at the sample level in Session 3 (*P(S – R > 0) ≈ 1,000*). The supported S > A contrast is a new finding that did not appear in earlier place-preference work and has direct bearing on the attraction-versus-avoidance question (Section 4.4).

Fifth, the cross-session pattern across all three measures shows a developmental trajectory consistent with apparatus habituation: Session 1 was characterised by few but long visits across all stimulus types (consistent with cautious initial behaviour in a novel apparatus), with later sessions showing higher visit frequencies and shorter individual durations. This shift from few-long visits toward many-short visits unfolded differently for the two sexes. Females settled on the rhythmic perch from Session 1 with sustained occupancy, briefly explored alternatives in Session 2, and returned to a rhythmic-only sustained engagement pattern in Session 3 with disengagement from the alternatives. Males showed initial comparable engagement across rhythmic and arrhythmic perches and sustained occupancy on the silent perch in Session 1, transitioning across sessions toward frequent-but-brief visits across all three perches, with rhythmic perches accumulating substantial total time through approach frequency by Session 3. Sex-related findings are scattered across analyses but descriptively directional: females expressed a rhythmic preference primarily through visit duration; males expressed it primarily through visit frequency.

The findings partially replicate the sex-specific pattern reported by Hoeschele and Bowling (2016), but in measures their two-choice, time-based design did not analyse: visit counts (where the rhythmic-by-sex interaction was the largest sex effect, though marginal at *p = ,058*) and visit duration (where the female-supported R-vs-A contrast reproduces the female-prefers-rhythmic direction, although carried partly by one bird in the present sample). The present design extensions enabled the disambiguation of

multiple plausible interpretations of these patterns, including possible roles for rhythmic structure per se, for unfamiliar male vocal material as a sex-differentiated social signal, and for cross-session habituation to a novel apparatus. These interpretations are taken up in the sections that follow.

4.2 The developmental trajectory across sessions

Across the three sessions, the behaviour of birds in the apparatus can be thought of as the result of the joint operation of at least three underlying processes: habituation to a novel testing environment, preference for one stimulus type over another, and exploration of the available options. These three processes likely operate on different timescales, and each may itself be sex-differentiated. Habituation is expected to dominate the early phase of testing, when the apparatus and stimuli are unfamiliar; it produces cautious patterns of occupancy in which birds make few but long visits and confine themselves to relatively narrow regions of the apparatus. Preference is expected to manifest as differential allocation of behaviour across the three stimulus types, observable when habituation has progressed sufficiently for stimulus-specific differences to emerge. Preference itself can take different forms across time: spontaneous preference, recognisable from early behaviour as differential salience, and developed preference, emerging only after exposure to the available options. Exploration is expected to manifest as broad engagement with multiple stimulus types, particularly when one option's relative value is still being evaluated; it should produce patterns of frequent visits with relatively short individual durations. The same total time at a given perch can be produced by different combinations of these processes, which is why the joint analysis of listening time, visit count, and visit duration is informative beyond what any single measure can provide. Importantly, the relative contribution of each process can differ between sexes as well as across sessions: the rate of habituation, the strength and direction of preference, and the propensity for exploration may each be sex-differentiated, and the same observable pattern in a given session can therefore reflect different mixtures of these assumed three processes for male and female birds. The discussion that follows treats the cross-session trajectory as the product of these three processes operating in parallel, with their relative contributions varying across sessions and differing between sexes. This framework is interpretive rather than mechanistic: it provides an organising structure for the observed patterns but does not constitute independent evidence for the existence of separable processes.

In Session 1, both sexes showed a behavioural profile consistent with being dominated by habituation. Mean visit counts were low across all three perches and individual visits were comparatively long (visit-level median durations ranging from a few seconds to several tens of seconds depending on the bird, with bird-specific mean visit durations as high as several minutes in some conditions). This combination, few but long visits, corresponds to a sustained-occupancy profile rather than an exploratory-sampling one, and is consistent with cautious initial behaviour in a novel apparatus documented for budgerigars elsewhere (Medina-Garcia, Jawor, & Wright, 2017). Listening times in Session 1 reflected this cautious profile: rhythmic and arrhythmic listening times were comparable (*means of 2196 s and 2177 s respectively*), and the formal contrast yielded no evidence of differentiation (b = *-0,725*, p = *,466*). The Session 1 result could then be read as comparable engagement with both stimulus types under conditions where

habituation effects dominate over stimulus-specific differentiation rather than indifference to the rhythmic-arrhythmic contrast.

Across subsequent sessions, the profile shifted. Median visit counts increased modestly at the sample level (*from 4-5 in Session 1 to 13-21 in Session 3*) while median visit durations remained stable (around 8-9 s across all sessions). However, the mean visit durations went from very long (*130-190 s in session 1 to 35-130 s in session 3*), showing that for some birds the drop in visit duration was quite sharp. This shift from few-long visits toward more-frequent shorter visits is the descriptive signature of habituation: as the apparatus becomes familiar, birds move between perches more freely, and individual visits become correspondingly briefer. The magnitude of this shift differed substantially between sexes, with male visit counts increasing markedly across sessions while female visit counts changed little; a sex-differentiated habituation pattern taken up further in Section 4.3.

What emerged within this broader habituation shift was the rhythmic-versus-arrhythmic differential in listening time. By Session 2, mean listening times had begun to diverge in favour of rhythmic stimuli, although not yet at conventional significance (*b = 1,541, p = ,274*). By Session 3, the divergence was substantial (3126 s vs. 750 s) and statistically supported (R × Session 3 interaction *b = 3,150, p = ,025*). The trajectory was driven by both an approximately 42% increase in rhythmic listening time and an approximately 66% decrease in arrhythmic listening time. Both changes operate together: birds developed engagement with rhythmic stimuli while losing engagement with arrhythmic stimuli. Within the three-process framework, this differential emergence can be understood as preference asserting itself once habituation has reduced the cautious initial response.

The rhythmic preference observed in listening time was not, however, mirrored in approach behaviour. The visit-count GEE model showed no rhythmic-versus-arrhythmic effect at any session (Session 1: *b = -0,033, p = ,893;* Session 2 and 3 interactions *p = ,576 and ,953*), and median visit counts within each session were broadly comparable across the two stimulus types. Birds were not visiting rhythmic perches more often; they were staying longer per visit when they did. The visit-duration analysis provides the formal test of this engagement claim. The robust within-bird bootstrap on bird-level median visit durations supported a positive overall rhythmic-versus-arrhythmic contrast (*mean bootstrap difference = 176,3 s, P(R – A > 0) = ,989*), indicating that across the sample, individual birds had longer median rhythmic visits than median arrhythmic visits. However, the bird-level paired-differences distribution shows that the overall result is influenced disproportionately by one bird (storm); the median paired difference across the sample was only +1,5 s. The within-session bootstrap confidence intervals were too wide to support R > A in any single session.

This pattern corresponds to the preference signature of the three-process framework: at the bird level, rhythmic stimuli received fewer-but-longer typical visits relative to arrhythmic stimuli, the signature of sustained engagement, when it occurred, even though within any single session the visit-level medians for the two stimulus types were comparable. If the relevant process were attraction or salience in a transient sense, with rhythmic stimuli being more attention-grabbing in the moment, we would expect rhythmic perches to draw more visits, not just longer typical visits per bird. We did not observe this in any session in any analysis. What distinguishes the two stimulus types

at the bird level is what happens once a bird has arrived: across the sample, some birds maintained longer median visit durations on rhythmic perches than on arrhythmic perches, with the contrast most evident particularly in one bird.

The asymmetric trajectory in listening time has a natural interpretation in terms of predictability. Rhythmic tracks were constructed by repeating a 1.5 s bar 40 times, so within-track structure was identical across repetitions; arrhythmic tracks jittered each event by ±200 ms independently, so successive repetitions did not preserve the same temporal pattern. Rhythmic stimuli therefore became increasingly predictable as a track unfolded; arrhythmic stimuli remained unpredictable throughout. Beat perception is fundamentally predictive in nature (Patel & Iversen, 2014): listeners actively anticipate upcoming onsets rather than merely reacting to them, and this predictive engagement is part of what distinguishes beat-related processing from simpler timing detection. The within-track predictability of the rhythmic stimuli is therefore not a methodological artefact to partition out from rhythmicity but a property functionally inseparable from it. Predictable structure supports successful prediction of upcoming events and thereby sustains engagement across exposure; unpredictable structure cannot, because no stable expectations can form. The cross-session decline in arrhythmic engagement reflects the gradual loss of behavioural value as unpredictability becomes apparent across repeated exposure, while the cross-session increase in rhythmic engagement reflects the predictable structure becoming more available as exposure accumulates.

The temporal shape of the present effect bears on how earlier results are interpreted. Hoeschele and Bowling (2016) used a single 5-minute session per bird and found no overall group-level rhythmic preference in budgerigars. The present results suggest that a 5-minute window may capture only the initial phase of behaviour in this paradigm, when habituation/exploration dominates and stimulus-specific differentiation has not yet emerged at the group level. In the present Session 1, occupancy of rhythmic and arrhythmic perches was comparable in listening time; the differential that defines a preference appeared only later. The two studies are therefore not necessarily in conflict; they may sample the same underlying phenomenon at different temporal phases. Sex-related findings, which scatter across measures and sessions in the present data and require a more complex reading, are taken up in Section 4.3.

4.3 Sex-differentiated channels of rhythmic preference

The sex-related findings in the present study require careful examination, both because Hoeschele and Bowling (2016) reported sex as a central organising dimension of budgerigar rhythm preference and because the present data show partial replication that takes a specific form: the rhythmic preference is sex-differentiated not in whether it exists, but in how it is expressed. Female and male birds in this study both showed Session 3 rhythmic preferences in listening time, but the underlying behavioural channels differed. The present section develops this reading by combining the visit-count, visit-duration, and bird-level descriptive evidence into a coherent sex-stratified picture, while being explicit about where the statistical support is strong, where it is marginal, and where it rests on descriptive coherence alone.

Across the formal analyses, no sex-related effect reached conventional statistical significance, but one came close: the rhythmic-by-sex interaction in the exploratory three-stimulus visit-count model (*b = -0,213, p = ,058*). The negative coefficient indicates that the rhythmic-versus-arrhythmic visit contrast was less positive (or in the opposite direction) for males than for females. This is the same direction reported by Hoeschele and Bowling (2016): females tend toward rhythmic stimuli, males away from them, and represents a partial directional replication of their pattern. This replication, however, is expressed in a different behavioural channel than the time-based one their study reported. In the time-based listening-time analyses of the present study, the formal stimulus-by-sex interactions did not reach significance, and the bird-level aggregate analysis showed no sex difference in overall rhythmic preference (*b = -0,088, p = ,812*). The visit-count R × sex interaction is the largest sex effect observed in the study, but its marginal p-value means it should be interpreted as suggestive rather than confirmatory.

The visit-duration analysis adds a second sex-stratified line of evidence. The robust within-bird bootstrap supported a positive overall rhythmic-versus-arrhythmic contrast, and the sex-stratified contrasts indicated that this overall result was carried by female birds. The female bootstrap supported R > A (*mean difference = 427,8 s, P(R – A > 0) = ,953*), while the male bootstrap showed a contrast small in magnitude with a confidence interval close to zero (*mean difference = 8,8 s, P = ,925*). At the descriptive level, two of the four female birds in the visit-duration sample (storm and phoenix) showed positive paired R – A differences, with storm's paired difference (+1714 s) dominating the female mean. The female-supported bootstrap result therefore rests on a small sample (4 birds, after exclusion of annabelle, melanzani, and zora) and is heavily influenced by one bird. The honest reading is that female bird-level median visit durations on rhythmic perches tend to be longer than on arrhythmic perches in this sample, with one bird carrying most of the magnitude; male bird-level median visit durations are essentially indistinguishable between the two stimulus types. The female pattern hints at a sustained-engagement behavioral profile in the three-process framework: the rhythmic preference is expressed through how long females remain on rhythmic perches once they arrive.

The male pattern in approach behaviour is different but, on the descriptive evidence, not absent. Male visit counts in Session 3 were higher than in Session 1, and the visit-count R × sex interaction shows that the relationship between sex and stimulus type operates through approach frequency in males in the same direction reported by Hoeschele and Bowling (2016). Combined with the bird-level totals, where the male R-versus-A descriptive ordering favours R (*means of 6045 s versus 3930 s*) at the aggregate level, the male pattern is consistent with a Session 3 rhythmic preference expressed through approach behaviour rather than through committed individual visits. Within the three-process framework, this corresponds to the exploratory-engagement profile: many short visits accumulating to substantial total time, with the rhythmic preference visible (descriptively) in how total approach behaviour is distributed across stimulus types rather than in how long any single visit lasts. The visit-count GEE model captures this descriptively, with the marginal R × Male interaction (*p = ,058*) the formal indication that males distribute their approach behaviour differently across stimulus types than females do.

The two sexes therefore appear to express rhythmic preference through different channels, although the statistical support for this distinction is mixed. Females (some of them) accumulated time on rhythmic perches through longer individual visits, with bird-level median visit durations on R exceeding those on A in the female-stratified bootstrap. Males accumulated time on rhythmic perches through more-frequent shorter visits, with the rhythmic-by-sex visit-count interaction approaching significance. The same total-time outcome, substantial rhythmic engagement by Session 3, was reached through different routes for the two sexes.

Two further considerations qualify the sex-differences picture. First, the developmental trajectory itself is sex-differentiated. The female rhythmic preference was present in some form from Session 1: female bird-level mean rhythmic listening time in Session 1 was 3391 s, compared to 2132 s for arrhythmic, and female median visit durations on R in Session 1 (34 s in the visit-duration analytic sample) exceeded those on A (*23.5 s*). The male rhythmic preference developed across sessions, with Session 1 showing comparable male engagement across rhythmic and arrhythmic perches at the listening-time level (*means of 1172 s and 2216 s, descriptively favouring arrhythmic*) and a substantial male engagement with the silent perch (treated in Section 4.4). The female preference was therefore early and (where present) duration-based; the male preference was later and frequency-based.

Second, the partial replication of Hoeschele and Bowling (2016) needs to be qualified by what their design and the present design jointly cannot resolve. The two studies differ in stimulus type (artificial percussion versus natural budgerigar vocalisations) and in session structure (a single 5-minute session versus three two-hour sessions). Their study used artificial stimuli and sampled only the initial phase of behaviour; the present study used vocal stimuli and sampled extended phases. The fact that the sex pattern they reported in time spent appears in the present data as a marginal visit-count R × sex interaction and a female-supported visit-duration contrast, rather than in time spent at the group level, is consistent with two interpretations that the present design cannot distinguish. Either the sex-differentiated rhythmic preference is a stable phenomenon that expresses itself differently across procedural contexts, with the channel of expression depending on session length and stimulus type; or the sex pattern reflects a sex-differentiated response to unfamiliar male conspecific vocalisation, which the present study introduced by using budgerigar vocalisations for stimulus generation but theirs did not, and the partial replication is partly coincidental. The stranger-male confound is taken up further in Sections 4.4 and 4.5.

The present findings do not, taken together, license a strong claim about budgerigar sex differences in rhythm preference as a single fixed effect. They support a more cautious reading: sex influences how budgerigars engage with rhythmic and arrhythmic acoustic playback in this paradigm in a way that is descriptively coherent across measures (more visit-duration in females, more visit-frequency in males), but the formal statistical support for any individual sex contrast is marginal or rests on a small sub-sample. The sex pattern observed here is descriptively coherent across measures while statistically scattered across them, and that coherence-versus-scatter mismatch is one of the diagnostic features of an under-powered design rather than evidence that no sex effect exists. Larger samples with sex-stratified power planning would be needed to characterise these patterns more precisely; the present study is

consistent with the existence of a sex-differentiated preference but cannot characterise its full structure or rule out that the descriptive pattern is a sample-specific artefact.

4.4 The silent condition: attraction, avoidance, and sex-differentiated use

The third stimulus condition was introduced specifically to address an interpretive limitation in earlier place-preference work. As discussed in Section 1.6, comparing two competing acoustic options yields only relative information: a bird that spends more time near rhythmic than arrhythmic stimuli may be attracted to rhythm, may be avoiding arrhythmia, or may be choosing between two stimulus types neither of which holds particular value. The silent condition was intended to disambiguate these readings by providing an absolute reference point.

A clarification about the silent condition is important before interpreting the data. The third perch was silent in the sense that no experimental stimulus was played from its associated speaker, but ambient noise from the budgerigars' home aviary was played continuously throughout each session through a ceiling-mounted speaker above the apparatus. This ambient playback was present during all sessions and across all perches, providing a consistent acoustic backdrop of familiar conspecific vocalizations. The "silent" condition is therefore better described as an ambient-only condition: a perch at which birds were exposed to the familiar background of their own aviary but did not receive any experimental stimulus playback. This distinction matters: a preference for the silent perch is not a preference for the absence of sound but a preference for familiar ambient flock sound over experimental playback of constructed stimuli.

The descriptive listening-time pattern across the three perches shows a sex-related divergence that the formal model could not statistically support. Females allocated time across the three perches in an R > A > S pattern, while males showed an S > R > A pattern. The exploratory listening-time mixed-effects model did not yield support for any contrast involving the silent condition (R vs. A: *p = ,165;* S vs. A: *p = ,194;* sex-by-stimulus interactions: *p = ,534 and ,408*), reflecting the small sample and the high between-bird variability in this measure. The listening-time descriptive split is therefore real in the data but underpowered in the formal analysis.

The visit-duration analysis provides more direct statistical evidence on the silent-condition pattern, and it reveals a result that did not emerge from the listening-time or visit-count analyses. The exploratory bootstrap with all three stimulus categories supported an overall S > A contrast (*mean difference = 101,5 s, 95% CI [13,6, 267,3], P(S − A > 0) = 1,000*): across the sample, birds had longer median visit durations on silent perches than on arrhythmic perches. This contrast was supported within both sexes (female S > A: *mean difference = 224,5 s, P(diff > 0) = 1,000;* male S > A: *mean difference = 19,5 s, P(diff > 0) = ,9998*), and across sessions 2 and 3. The supported S > A finding is the most directly interpretable evidence from this study bearing on the attraction-versus-avoidance question. It is consistent with a reading in which birds avoid arrhythmic stimuli relative to both rhythmic stimuli and silent condition (ambient sound). The rhythmic-over-arrhythmic effect observed in listening time and in the female visit-duration bootstrap may therefore reflect, at least in part, an aversive response to arrhythmic playback rather than a positive draw toward rhythmic playback alone.

The within-male picture is more specific. In male birds, the supported S > A contrast was accompanied by a supported S > R contrast (R – S: *mean difference = -10,7 s, P(S – R > 0) = ,998*), with the S > R contrast also supported at the overall sample level in Session 3 (*P(S – R > 0) ≈ 1,000*). The female pattern in visit duration showed a supported R > A contrast and a supported S > A contrast, with no clearly supported R-versus-S ordering. The two sexes therefore showed different orderings on visit duration: females showed R and S both longer than A (R ≈ S > A, with no clear order between R and S), while males showed S longer than both A and R (S > R ≈ A). The session-stratified analyses showed that the S > A contrast was supported in Sessions 2 and 3, and the S > R contrast in Session 3.

The male silent-perch trajectory has a particular shape that the three-process framework helps interpret. In Session 1, male median listening time on the silent perch (*715 s*) was substantial relative to male R (*274 s*) but lower than male A (*913 s*), with mean values that descriptively put S between R and A. By Session 2, male mean listening time on the silent perch (*1962 s*) had grown to roughly the same magnitude as male R (*2460 s*), with both substantially above male A (*1261 s*). By Session 3, male mean listening time on the silent perch (*2883 s*) was the highest of the three male means, exceeding R (*2413 s*) and well above A (*453 s*). The function of the silent perch for male birds therefore shifted across sessions: from initial occupancy comparable to the acoustic perches, then growing relative engagement in Session 2, to dominant relative engagement in Session 3. The within-male visit-duration bootstrap supports the silent-perch preference at the bird-level median across all sessions; the session-stratified pattern shows that this preference developed rather than appearing immediately.

Females used the silent perch differently. Across all three sessions, female silent-perch occupancy was low at both the visit-count and total-time levels, with mean listening times on S well below mean times on R and well below mean times on A in Sessions 1 and 3 (*Session 1 F-S mean = 262 s; Session 3 F-S mean = 898 s*). Yet at the visit-duration level, females whose silent visits did occur tended to make those visits longer than their arrhythmic visits — the female S > A contrast (*P = 1,000*) is supported by the bootstrap even though females spent comparatively little total time on the silent perch. The combination of low female silent-perch total time with longer typical female silent-perch visits indicates that when females did sample the silent perch, they tended to stay; they simply did so infrequently. This is a different sex pattern than the listening-time descriptive split alone conveys and should be noted in sex-differentiated patterns of behavior.

Two interpretations of the male silent-perch pattern remain available. The first is that the male preference for the silent perch reflects a form of acoustic disengagement: males in this study did not find either sound type intrinsically attractive and preferred the ambient-only condition. Under this reading, the modest male rhythmic-over-arrhythmic preference visible in Session 3 listening time is a relative preference within a broader pattern of acoustic disengagement. The second interpretation, available specifically because of the use of ecologically relevant stimulus material, is that the male preference for the silent perch reflects a sex-differentiated response to the unfamiliar male vocal source from which the stimuli were derived. Stranger conspecific vocalizations are not neutral acoustic material in budgerigars; male and female

budgerigars differ in their behavioural and neural responsiveness to mate calls versus unfamiliar male calls (Eda-Fujiwara, et al., 2011; Eda-Fujiwara, et al., 2016), and budgerigars are highly social, audience-sensitive, and known to modify vocal behaviour based on the presence and identity of conspecifics. Under this reading, prolonged playback of an unfamiliar male's vocal material may have been experienced by male budgerigar listeners as socially unsettling rather than attractive, and the silent perch was the only perch at which a male bird could occupy a space without being subjected to such playback. The two interpretations are not mutually exclusive, and the present design cannot distinguish them. The first explanation by itself does not seem very likely, however: engagement with each acoustic stimulus exceeded 10% in each session, and at least one acoustic perch received nearly as much time as the silent perch, suggesting genuine interest in all three options alongside the silent-perch preference.

What the silent condition does establish, with the supported overall S > A finding in particular, is that the design extension introduced by including a non-stimulus reference perch reveals patterns that a strict two-choice design could not detect. The supported S > A contrast specifically reframes the rhythmic-over-arrhythmic effect from a story of attraction to one in which avoidance plays a role: arrhythmic playback is on average more aversive than the ambient-only condition, and rhythmic playback is on average more engaging than arrhythmic but not, at the overall sample level, more engaging than the ambient condition. The earlier study used artificial percussion, which removes the stranger-male confound but also removes any link to the social significance of conspecific male vocal material; the present study uses naturalistic male material, which adds ecological validity but introduces a confound the earlier design did not have. Resolving these alternatives will require designs that systematically vary stimulus familiarity and signaler sex, with substantially larger samples for sex-stratified analyses.

A final observation about the silent-condition data concerns individual-level heterogeneity. Inter-individual variability was substantial across all stimulus types and not specifically inflated for the silent condition: the standard deviation on male silent-perch listening time was comparable to the standard deviations on male arrhythmic and rhythmic listening times. Individual differences in budgerigar neophobia, exploration, and response to laboratory stimuli are well-documented (Medina-Garcia, Jawor, & Wright, 2017), and the inter-individual variability observed here is consistent with that broader picture. Group-level means on the silent perch should therefore not be read as uniform preferences shared by all birds within a sex; they reflect averages that include considerable between-bird variation.

4.5 Stimulus choice and ecological validity

The stimulus material used in the present study was constructed from natural budgerigar vocalizations, in deliberate contrast to the artificial percussion-based stimuli used by Hoeschele and Bowling (2016). This choice was motivated by ecological validity: a feature can be more confidently described as behaviourally meaningful to a species when the relevant test uses sounds that resemble the species' own acoustic world. The choice produced one substantive interpretive gain — the developing rhythmic preference observed here was found in a context closer to budgerigar natural

acoustic experience — but it also introduced sources of variance that artificial stimuli would not have carried.

The most consequential issue, treated in Section 4.4, is the use of vocalizations from an unfamiliar adult male budgerigar. Conspecific vocal material in budgerigars carries social information about identity, sex, and familiarity, and male and female budgerigars are known to differ in their behavioural and neural responsiveness to such material (Eda-Fujiwara, et al., 2011; Eda-Fujiwara, et al., 2016). A consequence is that any sex difference observed in the present data may reflect not only sex differences in rhythm preference but also sex-differentiated responses to unfamiliar male conspecific vocalization. The two are confounded in the present design and cannot be cleanly separated. The supported overall S > A contrast reported in Section 3.8 sharpens rather than resolves this confound: it indicates that the experimental stimuli (collectively) generated less sustained engagement than the ambient-only condition for at least some categories of birds, but the supported R > A contrast in females shows that the rhythmic-arrhythmic distinction is not collapsed by this overall pattern. Both effects are descriptively coherent with a stranger-male reading and with a rhythm-preference reading, and the present design cannot adjudicate between them.

A second issue concerns tempo. All stimuli in the present study were generated at 160 beats per minute. The rhythmic preference observed here is therefore strictly a preference at this tempo and cannot be assumed to generalise across tempi. This matters because beat-related auditory-motor abilities in vocal learners are often described as "tempo-flexible," meaning that the underlying perceptual capacity should support entrainment or preference across a wide range of beat rates rather than being narrowly tuned to a single tempo (Patel, 2014; 2021). Hasegawa et al. (2011) demonstrated tempo-flexible synchronization in budgerigars, but with a bias toward faster tempi close to the time scale of natural budgerigar vocalizations. The present design does not address whether the rhythmic preference observed here would persist at slower or faster tempi.

A third issue concerns the source of the vocal material. All five vocalization samples were extracted from a single adult male budgerigar. This decision provided acoustic consistency: every rhythmic and arrhythmic track was constructed from the same five samples in different temporal arrangements; but it conflates the "stranger male" category with the specific acoustic properties of one bird. Replicating the design with vocalizations from multiple stranger males, or comparing stranger material with mate-derived or female-derived material, would establish whether the present findings reflect a generalisable preference structure or are partly bound to the source bird used here.

Together, these stimulus considerations mean that the rhythmic preference described here should be understood as a preference observed under specific acoustic conditions, not as a general fact about budgerigar rhythm perception. Birds developed an occupancy-based preference for rhythmic over arrhythmic structure when the stimuli were constructed from a single unfamiliar male's vocalizations at a single tempo. Whether the same preference would emerge with familiar conspecific material, with female-derived material, with non-vocal acoustic content matched for ecological relevance, or at other tempi, is not addressed by this study. The interpretive richness gained through ecological validity therefore comes at the cost of generalisability, and

the appropriate next step is not to abandon ecological validity but to vary the dimensions on which the present design held material constant.

4.6 Theoretical implications

The present findings bear on three theoretical questions: the role of vocal learning in rhythm-related behaviour, the position of rhythm within the broader concept of musicality, and whether rhythmic structure has motivational significance for non-human animals. Each is taken up briefly, with the caveat that the present design does not directly test any of them.

Vocal learning and rhythm. The vocal learning hypothesis proposes that the neural circuitry supporting complex vocal learning provides a preadaptation for beat perception and synchronization, and that this preadaptation is most clearly expressed in species capable of advanced vocal mimicry ((Patel, 2006; 2014; 2021). The present finding that budgerigars develop a sustained-engagement preference for rhythmic over arrhythmic acoustic structure under naturalistic conditions is consistent with this framework, in the broad sense that an advanced vocal learner showed differential engagement with temporal structure. The findings, however, do not test the strongest version of the hypothesis, which concerns precise, predictive, and tempo-flexible beat perception and synchronization. Four caveats are warranted: the present study tested preference rather than synchronisation, the single-tempo design does not test tempo flexibility, the developing rather than immediate emergence of the preference suggests that any claim about rhythmic preference in budgerigars should be qualified by reference to exposure history, and the supported S > A contrast at the sample level indicates that part of the rhythmic-versus-arrhythmic effect may reflect avoidance of arrhythmic structure rather than positive engagement with rhythmic structure alone. The present data are best read as adding a behavioural-preference dimension to the existing case for budgerigars as a comparative model of rhythm-related processing in a vocal-learning species, rather than as a direct test of the underlying neural-evolutionary claims.

Musicality and behavioural salience. The framing of musicality used here treats it as a set of component abilities: sensitivity to rhythm, pitch, temporal grouping, and other dimensions, rather than as a unified trait (Honing, Ten Cate, Peretz, & Trehub, 2015; Hoeschele, Merchant, Kikuchi, Hattori, & ten Cate, 2015). On this view, the relevant question is not whether other species "have music" but whether they share particular component abilities that contribute to music perception and production in humans. The present findings contribute to this question on one specific component: budgerigars show differential engagement with temporal structure, and that engagement is sustained rather than merely orienting. A rhythmic stimulus that birds approach but do not stay near is consistent with mere perceptual salience; a rhythmic stimulus that birds stay near, at the bird-level median across the sample, is more naturally read as one that has acquired behavioural value. The present findings tighten the case for rhythm sensitivity as a real component ability in this species, in the sense that it functions not only as a perceptual capacity but as a dimension of acoustic structure that can influence spontaneous spatial behaviour. The supported S > A contrast adds a complementary point: not all forms of temporal organisation are behaviourally equivalent, and arrhythmic structure specifically appears to generate

less sustained engagement than ambient sound: a dissociation that a single-stimulus-type design could not have revealed.

The motivational dimension. The third theoretical question concerns whether rhythmic structure has anything resembling a motivational dimension for budgerigars. The present design cannot establish reward in a strict sense, because no operant contingency, no consummatory behaviour, and no measure of physiological state was included. What the design can support is a more cautious claim: that rhythmic structure has enough behavioural salience to bias spontaneous spatial occupancy in a low-demand, free-choice setting. The bird-level median pattern, longer typical visits on rhythmic perches than on arrhythmic ones, is consistent with the kind of motivational pull that has been documented in human studies of groove (Janata, Tomic, & Haberman, 2012). The present data do not establish that budgerigars experience anything analogous to groove, but they support the more general claim that rhythmic structure functions as a behaviourally meaningful dimension of acoustic experience for this species. This is a meaningful contribution to the broader question of whether the perceptual abilities relevant to musicality have any behavioural pull beyond detection.

4.7 Limitations

Several features of the design warrant explicit acknowledgement.

The most consequential limitation is sample size. Thirteen birds (seven males, six females) provide limited statistical power for any analysis, and especially for sex-stratified analyses or analyses involving the silent condition. The pattern of sex-related findings observed here, marginal in one exploratory model, descriptively coherent across measures, and partially replicating an earlier study, is the pattern that small-sample comparative work tends to produce. Stronger inferences would require larger samples, possibly through coordinated multi-laboratory designs.

A related limitation is that some of the visit-duration findings reported here rest on a small subset of the sample. The bootstrap analyses excluded annabelle (missing Session 3 and very few recorded visits), melanzani, and zora (each with very few recorded visits), leaving 10 birds for the visit-duration analyses and only 4 for the female-stratified contrasts. The overall R > A bootstrap result is supported but influenced disproportionately by one bird (storm); the female-stratified R > A contrast rests on a 4-bird sub-sample with one bird contributing most of the magnitude. These are honest features of the data and have been reported transparently in Chapter 3, but they place a limit on how confidently the visit-duration findings can be generalised.

A second limitation concerns the stimulus design, addressed in detail in Section 4.5. The use of unfamiliar male vocal material confounds rhythm preference with possible sex-differentiated responses to unfamiliar male conspecific vocalization. The use of a single tempo (160 bpm) limits the generalizability of the rhythmic preference to other tempi. The use of a single source bird limits generalisation beyond the specific acoustic properties of that bird. The asymmetric within-track structure of the stimuli, rhythmic tracks repeating one bar 40 times, arrhythmic tracks jittered independently per repetition, means that within-track repetition and within-bar rhythmicity were conflated in ways future designs could disentangle.

A third limitation concerns the temporal trajectory of the preference. The differential rhythmic-versus-arrhythmic occupancy was not present in Session 1 and developed only by Session 3. This is theoretically interesting and was treated as a substantive finding, but it also means that the rhythmic preference described here is not a spontaneous or first-encounter preference, especially in male birds. Whether the underlying process is rhythm-specific learning, asymmetric habituation to arrhythmic content, predictive engagement with regular structure, or general adaptation to the apparatus cannot be fully resolved by the present design.

A fourth limitation concerns the analytic structure. Although the confirmatory-versus-exploratory distinction was applied throughout, the final analytic plan was developed during analysis rather than fully pre-specified, and the most striking sex-related finding (the marginal visit-count rhythmic-by-sex interaction, the supported S > A visit-duration contrast) emerged from an exploratory model. P-values from exploratory analyses were not corrected for multiple comparisons.

A final limitation concerns the absence of physiological or neural measures. The interpretations advanced in the theoretical-implications section, particularly those concerning motivational dimension and behavioural salience, are inferential conclusions drawn from spatial occupancy data. Direct measures of arousal, attention, or reward would substantially strengthen claims of the kind that place-preference data alone can only support cautiously.

4.8 Future directions

Several directions for future research follow from the limitations and open questions identified above.

The most immediate is replication with larger and sex-stratified samples. The pattern of sex-related findings would benefit substantially from a study designed with sex stratification as a planned analysis from the outset, with sample size determined by formal power analysis for the sex-by-stimulus interaction. Coordinated multi-laboratory studies of the kind increasingly proposed for animal cognition research (Farrar, Boeckle, & Clayton, 2020) would help address the sample-size constraint that is endemic to comparative work in this area.

A related priority is systematic manipulation of stimulus source. Comparing rhythmic preferences across stimuli derived from a bird's mate, from a familiar non-mate, from an unfamiliar male, from female conspecifics, and from acoustically matched non-vocal material would establish whether the rhythmic preference observed here generalises across stimulus types or is specifically bound to the social meaning of unfamiliar male vocalization. Such a design would also clarify whether the descriptive sex split observed in the silent condition reflects sex differences in rhythm preference, in response to male vocal material, or in some combination of the two.

Tempo manipulation is a third direction. Testing rhythmic preference across multiple tempi, including tempi inside and outside the natural range of budgerigar vocal behaviour, would establish whether the preference observed here is tempo-flexible or tempo-specific. This is particularly relevant for connecting place-preference findings to the broader literature on beat perception and synchronization (Patel, 2021).

The temporal trajectory of the preference is a fourth direction worth pursuing. The present finding that rhythmic preference emerges across sessions raises questions about what the relevant timescale of rhythmic engagement actually is. Within-session analyses at finer temporal resolution would establish whether the differential begins to emerge within minutes or only across days. Direct comparison of short-session and long-session designs in the same birds would test whether earlier studies' use of brief sessions captured a different phase of the same phenomenon.

Beyond these design-level improvements, two broader directions deserve mention. First, combining place-preference paradigms with measures of physiological arousal, neural activation, or trained synchronization would allow stronger claims about the motivational dimension of rhythmic structure than place-preference behaviour alone supports. Second, cross-species comparisons using comparable place-preference designs would help establish whether the developing-engagement profile observed here is specific to vocal-learning species, broadly distributed across taxa with different cognitive and ecological profiles, or a feature of the place-preference paradigm itself. The combination of within-species manipulation and across-species comparison is the most promising route to disentangling what the present findings reveal about rhythm-related behaviour in budgerigars from what they reveal about the paradigm itself.

4.9 Conclusion

The present study used a place-preference paradigm with ecologically relevant stimuli to ask whether budgerigars show preference for rhythmic over arrhythmic acoustic structure, whether such preference reflects attraction or avoidance, and how preference is best characterised across multiple behavioural measures. Three findings stand out.

First, a rhythmic preference did emerge, but it developed across sessions rather than appearing at first exposure. The asymmetric trajectory in listening time, substantial increase in rhythmic engagement, larger decrease in arrhythmic engagement, is consistent with a process in which preference asserts itself once habituation has reduced the cautious initial response. Read through the three-process framework introduced in Section 4.2, the cross-session shift reflects habituation operating broadly while preference operates stimulus-specifically.

Second, the rhythmic preference seems to be expressed through different behavioural channels in male and female birds. Female birds carried the preference through sustained engagement: their bird-level median visit durations on rhythmic perches were reliably longer than on arrhythmic perches, and this contrast was supported in the visit-duration bootstrap. Male birds carried the preference through approach frequency: their visit-count R × sex interaction was the most supported sex effect across analyses, and their substantial Session 3 total time on rhythmic perches accumulated through many short visits rather than committed long visits. Both sexes showed a Session 3 rhythmic preference; they reached it through different routes.

Third, the silent condition revealed a result that no two-choice design could detect: an overall supported preference for silent perches over arrhythmic perches in visit duration ($P(S - A > 0) = 1{,}000$), supported within both sexes and in Sessions 2 and 3. This is the strongest direct evidence in the study bearing on the attraction-versus-

avoidance question. It is consistent with a reading in which arrhythmic stimuli are aversive relative to both rhythmic stimuli and ambient sound. The rhythmic-over-arrhythmic effect observed in listening time and in the female visit-duration bootstrap therefore likely reflects a combination of positive attraction to the rhythmic stimuli as well an aversion to the arrhythmic one. Within male birds specifically, the silent-perch preference also extended to longer visits than on rhythmic perches (S > R supported), suggesting that for males, ambient sound was preferred over experimental stimuli of either temporal type. The male silent-perch pattern is consistent with two interpretations the present design cannot distinguish: a sex-differentiated form of acoustic disengagement, or a sex-differentiated response to unfamiliar male conspecific vocalisation. Both are biologically plausible and both can be tested in future designs.

Together, these findings strengthen the case that rhythmic structure has behavioural salience for budgerigars in a free-choice setting, qualify the conditions under which such salience is expressed, and complicate earlier interpretations of sex-related rhythm preference in this species. They do not licence strong claims about rhythm as reward, sex as a stable predictor of rhythm preference, or rhythm preference as immediately spontaneous. They do support a more cautious framing in which rhythmic structure functions as one component of acoustic experience that influences spontaneous spatial behaviour in a vocal-learning species when given time to develop and when carried by acoustic material with social meaning. The methodological extensions introduced here, ecologically relevant stimuli, the silent condition, the joint analysis of three behavioural measures, and the longer testing windows, produced a richer picture of budgerigar rhythm-related behaviour than the original two-choice design was able to provide. These dissociations from the richer picture can be useful directions for future work.

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6 Appendix

6.1 Ethical Statement (Approval Number 2015-005)

universität wien

Experiments with approval Number: 2015-005

Title of Project: Budgerigar (*Melopsittacus undulatus*) Acoustic Perception

Principal Investigator: Dr. Marisa Hoeschele (post-doc of Prof. W. Tecumseh Fitch)

Species: Budgerigar (*Melopsittacus undulatus*)

Quantity (m/f): 16 (8m/8f)

Origin: pet store

Animal Keeping: The birds are housed in two groups of eight birds in visually separated aviaries. Each aviary is 1x2x1 meter in size, and contains branches, perches of different sizes, swings, 2 baths. Other enrichment, and wood chips covering the floor. Each aviary contains two food and one water bowl where they are given fresh food (AviFood Harrison's Bird Food Adult lifetime super fine maintenance formula for small birds; FL, USA) and water daily. Because it is difficult to detect illness in birds early enough, and a heat lamp can greatly increase a sick bird's well being, a heat lamp is also available 24/7 by a perch in each aviary that the birds can sit by if they choose. The daylight period within the room is maintained on a stable 12:12h light:dark cycle.

Animal Welfare: We have adhered to the Animal Behav our animal research guidelines and conduct research and house the birds in accordance to the Austrian law and local government guidelines.

Description of the Experiment: see enclosed

Description of the Intervention/ Manipulation: see enclosed

Responsible Veterinarian: Mag. Med. vet. Volker Harra

Scientific Member of the Animal Welfare Board: Eva Millesi

X Approval ☐ Modification ☐ Rejection

Remarks:

Date: 27/03/2015 Signature:

Advisory Veterinarian of the Animal Welfare Board: optional

☐ Approval ☐ Modifications ☐ Rejection

Remarks:

Date: Signature:

Summary (Extended Abstract)

Rhythm is one of the most widespread aspects of human music and is increasingly understood as a perceptual and behavioural capacity shared, in component form, across a range of non-human species. Vocal-learning species, and parrots in particular, have emerged as strong non-human models in the comparative study of rhythm-related processing. Among parrots, budgerigars (*Melopsittacus undulatus*) are particularly informative because they combine advanced vocal-learning capacity with a tractable laboratory profile. Earlier place-preference work in this species reported sex-specific preferences for rhythmic over arrhythmic stimuli, with female birds spending more time near rhythmic stimuli than male birds did (Hoeschele & Bowling, 2016). That study used a single five-minute session per bird and artificial percussion-based stimuli. Both of those design choices left open interpretive questions: whether the sex-specific preference would generalise to more ecologically relevant stimulus material, whether it would emerge or change across longer exposure, and whether the rhythmic-over-arrhythmic effect reflects positive attraction to rhythmic structure, avoidance of arrhythmic structure, or both.

The present study extended this earlier work in three deliberate ways. First, the acoustic stimuli were constructed from natural budgerigar vocalisations rather than from artificial percussion, bringing the experimental material closer to the species' own acoustic world. Second, a silent comparison condition was added to the standard two-stimulus design, on the reasoning that comparing rhythmic and arrhythmic playback against each other yields only relative information, whereas a non-stimulus reference condition allows attraction and avoidance to be at least partially distinguished. Third, the analyses examined three behavioural measures jointly: listening time, visit count, and visit duration, rather than the time-spent measure used in earlier work alone.

Thirteen budgerigars (six females, seven males), aged between two and five years, participated in the experiment across three two-hour sessions in a three-perch place-preference apparatus. Two perches were associated with rhythmic (R) and arrhythmic (A) playback constructed from the vocalisations of a single unfamiliar adult male budgerigar; the third perch remained silent (S). Continuous playback of an ambient recording of the home aviary was maintained throughout the experimental sessions. The assignment of stimuli to physical perches was counterbalanced both within each bird and across the three sessions, so that no stable spatial preference could confound stimulus-based preference. Listening time was analysed with linear mixed-effects models on log-transformed totals; visit counts were analysed with negative binomial generalized estimating equations (GEE) to accommodate overdispersion in the count data; visit durations, which were strongly right-skewed with extreme values, were analysed using a robust within-bird non-parametric bootstrap on bird-level median durations. Rhythmic-versus-arrhythmic contrasts were treated as confirmatory, and analyses incorporating the silent condition were treated as exploratory throughout.

A preliminary analysis confirmed that no physical perch was preferred independently of the stimulus assigned to it. The listening-time analyses revealed a session-dependent rhythmic preference rather than a spontaneous one. In Session 1, mean listening times on the rhythmic and arrhythmic perches were nearly identical, with no significant contrast between them. By Session 3, however, the means had diverged substantially: rhythmic listening time was approximately four times higher than arrhythmic listening time, with the rhythmic-by-Session 3 interaction reaching statistical significance. Both an increase in rhythmic engagement and a larger decrease

in arrhythmic engagement contributed to this divergence. The bird-level aggregate analysis (summing across sessions) showed that mean rhythmic listening time exceeded mean arrhythmic listening time across the sample, with the paired t-test on log-transformed totals reaching conventional significance and the non-parametric Wilcoxon check producing a marginal p-value. Eight of the thirteen birds had longer total time on the rhythmic perch than on the arrhythmic perch, indicating that the effect was broadly distributed across the sample. The visit-count analyses, in contrast, showed no rhythmic-versus-arrhythmic contrast at any session: birds did not visit rhythmic perches more often at any session, birds visited rhythmic and arrhythmic perches with comparable frequency despite the listening-time divergence.

The visit-duration analyses produced three main results. The bootstrap analysis showed statistical support for the overall rhythmic-versus-arrhythmic contrast, but bird-level inspection showed that this overall result was influenced disproportionately by one female bird with a substantially larger paired difference than any other individual in the sample. Sex-stratified analyses indicated that the R > A contrast was supported in female birds but not in male birds, where the contrast was near zero. The exploratory three-stimulus analysis revealed an additional finding that the two-stimulus design could not have detected: a statistically supported overall silent-versus-arrhythmic contrast, present in both sexes and emerging across Sessions 2 and 3. Within male birds, the silent perch was also preferred over the rhythmic perch in median visit duration. The exploratory visit-count model produced a marginal but directionally consistent rhythmic-by-sex interaction, with males showing a less positive R-versus-A pattern than females, in the same direction as the sex pattern reported in earlier work.

Taken together, these findings indicate that budgerigars develop a rhythmic-versus-arrhythmic preference across sessions when given ecologically relevant vocal stimuli, with the form of this preference appearing sex-differentiated though not fully statistically resolved in the present sample. The supported silent-over-arrhythmic contrast reframes the rhythmic-over-arrhythmic effect as one in which aversion to arrhythmic structure and attraction to rhythmic structure are likely operating simultaneously. This dual-process reading is consistent with both the listening-time trajectory (rhythmic engagement increasing while arrhythmic engagement decreased more sharply) and with the visit-duration pattern (the silent perch attracting longer typical visits than arrhythmic, in both sexes). The results partially replicate the sex-specific pattern reported by Hoeschele and Bowling (2016), but in measures that earlier work in this paradigm did not analyse, and the silent condition reveals engagement patterns inaccessible to two-choice designs. The findings should be qualified by sample size, by the use of vocalisations from a single unfamiliar male source, and by the developmental rather than spontaneous emergence of the rhythmic-versus-arrhythmic differential. Future work should test whether the present pattern generalises across stimulus sources, tempi, and session lengths, and whether the silent-over-arrhythmic finding extends to true silence (without ambient flock sound) or specifically tracks the contrast between experimental stimuli and familiar ambient acoustic context.

Zusammenfassung

Rhythmus ist eines der am weitesten verbreiteten Merkmale menschlicher Musik und wird zunehmend als perzeptuelle und verhaltensbezogene Fähigkeit verstanden, die in Komponentenform mit nicht-menschlichen Arten geteilt wird. Stimmlernende Arten, insbesondere Papageien, haben sich als starke Modelle in der vergleichenden Erforschung rhythmusbezogener Verarbeitung etabliert. Unter den Papageien sind Wellensittiche (*Melopsittacus undulatus*) besonders aufschlussreich, da sie fortgeschrittene Stimmlernfähigkeit mit einem laborfreundlichen Verhaltensprofil verbinden. Frühere Studien an dieser Art berichteten geschlechtsspezifische Präferenzen für rhythmische gegenüber arrhythmischen Stimuli, wobei weibliche Vögel mehr Zeit in der Nähe rhythmischer Stimuli verbrachten als männliche (Hoeschele & Bowling, 2016). Diese Studie verwendete eine einzelne fünfminütige Sitzung und künstliche perkussionsbasierte Stimuli. Beide Designentscheidungen ließen offen, ob sich die Präferenz auf ökologisch relevanteres Material verallgemeinern lässt, ob sie sich über längere Exposition entwickelt, und ob der Effekt Anziehung zu rhythmischer Struktur, Vermeidung arrhythmischer Struktur oder beides widerspiegelt.

Die vorliegende Studie erweiterte diese Arbeit auf drei Weisen. Erstens wurden die Stimuli aus natürlichen Wellensittich-Vokalisationen anstelle künstlicher Perkussion konstruiert. Zweitens wurde eine stille Vergleichsbedingung hinzugefügt, da ein Vergleich rhythmischer und arrhythmischer Wiedergabe untereinander nur relative Information liefert, während eine Referenzbedingung ohne Stimulus erlaubt, Anziehung und Vermeidung teilweise zu unterscheiden. Drittens untersuchten die Analysen drei Verhaltensmaße gemeinsam: Hörzeit, Besuchsanzahl und Besuchsdauer.

Dreizehn Wellensittiche (sechs Weibchen, sieben Männchen) im Alter zwischen zwei und fünf Jahren nahmen an drei zweistündigen Sitzungen in einer Apparatur mit drei Sitzstangen teil. Zwei Sitzstangen waren mit rhythmischer (R) und arrhythmischer (A) Wiedergabe verknüpft, konstruiert aus den Vokalisationen eines unbekannten erwachsenen Männchens; die dritte blieb stumm (S). Eine kontinuierliche Umgebungsaufnahme aus der Heimvoliere wurde während aller Sitzungen wiedergegeben. Die Zuordnung der Stimuli zu den Sitzstangen wurde innerhalb jedes Vogels und über Sitzungen hinweg ausbalanciert. Die Hörzeit wurde mit linearen Mixed-Effects-Modellen auf log-transformierten Summen analysiert; die Besuchsanzahl mit negativen binomialen Generalized Estimating Equations (GEE) zur Berücksichtigung der Überdispersion; die Besuchsdauern, stark rechtsschief mit Extremwerten, mittels eines robusten vogelinternen nicht-parametrischen Bootstrap-Verfahrens über vogelbezogene Mediane. Rhythmisch-versus-arrhythmische Kontraste galten als konfirmatorisch, Analysen mit der stillen Bedingung als explorativ.

Eine vorbereitende Analyse bestätigte, dass keine Sitzstange unabhängig vom Stimulus bevorzugt wurde. Die Hörzeitanalysen ergaben eine sitzungsabhängige rhythmische Präferenz und keine spontane. In Sitzung 1 waren die mittleren Hörzeiten nahezu identisch, ohne signifikanten Kontrast. In Sitzung 3 hatten sich die Mittelwerte erheblich auseinanderentwickelt: die rhythmische Hörzeit war ungefähr viermal höher

als die arrhythmische, wobei die Rhythmisch-mal-Sitzung-3-Interaktion Signifikanz erreichte. Sowohl ein Anstieg rhythmischen Engagements als auch ein stärkerer Rückgang arrhythmischen Engagements trugen zu dieser Divergenz bei. Die vogelbezogene Aggregatanalyse zeigte, dass die mittlere rhythmische Hörzeit die arrhythmische über die Stichprobe hinweg überstieg; der gepaarte t-Test auf log-transformierten Summen erreichte konventionelle Signifikanz, der Wilcoxon-Test einen marginalen p-Wert. Acht der dreizehn Vögel hatten längere Gesamtzeiten auf der rhythmischen als auf der arrhythmischen Sitzstange, was eine breite Verteilung des Effekts anzeigt. Die Besuchsanzahlanalysen zeigten dagegen keinen rhythmisch-versus-arrhythmischen Kontrast: die Vögel besuchten beide Sitzstangentypen trotz der Hörzeitdivergenz mit vergleichbarer Frequenz.

Die Besuchsdaueranalysen erbrachten drei Ergebnisse. Die Bootstrap-Analyse zeigte statistische Unterstützung für den rhythmisch-versus-arrhythmischen Gesamtkontrast, doch dieser wurde überproportional von einem weiblichen Vogel mit einer wesentlich größeren gepaarten Differenz beeinflusst. Geschlechtsstratifizierte Analysen wiesen darauf hin, dass der R > A-Kontrast bei Weibchen gestützt war, jedoch nicht bei Männchen, wo er nahe null lag. Die explorative Drei-Stimulus-Analyse ergab einen zusätzlichen Befund, den das Zwei-Stimulus-Design nicht hätte aufdecken können: einen statistisch gestützten still-versus-arrhythmischen Gesamtkontrast, in beiden Geschlechtern vorhanden und über Sitzungen 2 und 3 hinweg auftretend. Bei Männchen wurde die stille Sitzstange zudem gegenüber der rhythmischen in der medianen Besuchsdauer bevorzugt. Das explorative Besuchsanzahlmodell ergab eine marginale, aber direktional konsistente Rhythmus-mal-Geschlecht-Interaktion in derselben Richtung wie das in früherer Arbeit berichtete Muster.

Zusammengenommen entwickeln Wellensittiche eine rhythmisch-versus-arrhythmische Präferenz über Sitzungen hinweg bei ökologisch relevanten vokalen Stimuli, wobei die Form geschlechtsdifferenziert erscheint, jedoch in der vorliegenden Stichprobe nicht vollständig statistisch aufgelöst ist. Der gestützte still-über-arrhythmisch-Kontrast verändert die Interpretation des rhythmisch-über-arrhythmisch-Effekts dahingehend, dass Aversion gegenüber arrhythmischer Struktur und Anziehung zu rhythmischer Struktur wahrscheinlich gleichzeitig wirksam sind. Diese Dual-Prozess-Lesart ist sowohl mit dem Hörzeitverlauf als auch mit dem Besuchsdauermuster vereinbar. Die Ergebnisse replizieren teilweise das geschlechtsspezifische Muster von Hoeschele und Bowling (2016) in Maßen, die frühere Arbeiten nicht analysiert haben, und die stille Bedingung offenbart Muster, die ein Zwei-Wahl-Design nicht erfassen könnte. Die Befunde sind durch die Stichprobengröße, die einzelne unbekannte männliche Stimulusquelle und das entwicklungsbedingte statt spontane Auftreten der Differenzierung zu qualifizieren. Zukünftige Arbeiten sollten prüfen, ob sich das Muster über Stimulusquellen, Tempi und Sitzungsdauern verallgemeinern lässt und ob sich der still-über-arrhythmisch-Befund auf echte Stille ausdehnt oder spezifisch den Kontrast zwischen experimentellen Stimuli und vertrautem Umgebungskontext erfasst.