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Titel | Title

Melopsittacus undulatus and the Chamber of Preference – Acceptance of Artificial Calls and the Importance of Segment Order

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Abstract

Recent research shows that budgerigar songs, like human language, can be broken down into meaningless segments that form meaningful patterns. Studies using human language analysis techniques found that these birds structure their songs around similar subunits, with consonant-like sounds at the beginning and vowel-like sounds at the end (Mann et al., 2021). Gutscher et al. (2019) demonstrated that budgerigar songs can be broken down into small segments that can be used to produce realistic “budgerigar” sounds by synthesis.

The aim of this study is to address the limited understanding of how budgerigar songs work and how they perceive the subunits of their vocalisations, by testing different vocalisation patterns and auditory perception across a series of three experiments. In this study, 15 budgerigars (5 males and 10 females) from two separate colonies were tested across three experiments to examine their acoustic preferences. In Experiment 1, birds chose between familiar (own group) and unfamiliar (other group) unmodified budgerigar songs. Overall budgerigars spent a similar amount of time on each option. Male birds did spend more time on the “silent” condition than on familiar songs but did not show a difference between silence and unfamiliar songs. Females preferred no option over another. Experiment 2 offered a choice between natural and artificially generated budgerigar sounds (based on Gutscher et al., 2019). Male birds listened significantly longer to silence over both stimuli types, but females spent more time with artificial than natural stimuli. In Experiment 3, birds chose between artificial songs with a likely (natural) and an unlikely (randomized) segment order. The birds did not prefer likely over random segment order. They listened significantly longer to silence than both stimulus sets.

The results did not fully align with expectations, though the methods remain suitable for testing acoustic preferences. Results of other studies suggest the issue may lie with the birds used – likely due to habituation to these kind of auditory preference experiments – highlighting the need for further research especially using new, non-habituated and naive individuals.The results show, that a preference for familiarity can be overshadowed by neophilia and that artificial sounds can excite curiosity. Preference test stimuli need to be sufficiently interesting for the birds to engage in experiments like this study.

1. Introduction

Animal communication is omnipresent in everyday life but is still one of the least understood parts of our surrounding nature. Communication has been defined as the transfer of information produced by a sender and perceived by a receiver, which results in a behavioural change of the receiver (Bradbury and Vehrencamp, 2011). Animal communication has become a more popular study topic in science over the last few decades, but we have barely scratched the surface of its complexity (Hebets and Papaj, 2005).

Although they have similar auditory capabilities to humans, most mammals have a few anatomical limitations that deny the complexity in which humans can form sounds (Dent et al., 1997), especially control of the larynx and vocal tract (Fitch, 2011). Newer studies analyzing radiographs of living vocalizing macaque monkeys (*Macaca fascicularis*) have shown that they have the anatomical requirements to produce vowels. They conclude that monkeys instead lack the neural circuitry enabling complex vocal control (Fitch et al., 2016). In comparison to apes and humans, birds have some anatomical differences in their auditory systems (Dent et al., 1997), yet can mimic a wide variety of human speech sounds. Birds produce sound with a syrinx, which is located where the trachea branches into two bronchi, while the mammal's larynx sits in the back of the throat. Both birds and mammals produce sound by exhaling air to set tissue (labia in birds and vocal folds in mammals) in vibration. The syrinx has two sound generators (labia) that each generate different frequency bands, resulting in the ability to produce two independent sounds simultaneously (Songbirds- Riede & Goller, 2010; Parrots- Oliveira et al., 2023; Budgerigar- Abdel-Maksoud et al., 2020). Despite different sound producing anatomy, humans and birds have some similarities regarding manipulation of produced sounds by adjusting the geometry of the oral and pharyngeal cavity, such as muscles of the mouth floor, the tongue and the strap muscle (Riede & Goller, 2010). Parrots even use their tongue and tracheal resonances to produce vowels (Dent et al., 1997).

Vocal learning and entrainment are key mechanisms for learning communication, including songs and even language. Especially vocal learning is a trait that is crucial for acquiring speech (Jarvis, 2019). Vocal learning describes learning and producing novel vocalizations after hearing the acoustic signals of others (Vernes et al., 2021). Entrainment is the capability to match behavioural events in time with external stimuli, usually sound (Hoeschele et al., 2015). It was shown that some birds, such as starlings and parrots, are able to modify their vocalizations throughout their lifetime and also learn to mimic human speech. That means that they can extract the important acoustic features of speech (Dent et al., 1997). Vocal learning is expressed in many songbirds (Dent et al., 1997) and entrainment is found in a few human distantly related species such as grey parrots (*Psittacus erithacus*,) and african elephants (*Loxodonta africana*; Schacher et al. 2009; Tyack 2008). Recent studies show that californian sea lions (*Zalophus californianus*) and chimpanzees (*Pan species*), neither known for vocal learning, can synchronize with a beat, suggesting entrainment might not require vocal learning abilities (Cook et al. 2013; Hattori et al. 2013). This changes the idea that vocal learning is necessary for rhythmic synchronisation and highlights the need for more research in non vocal learning species in addition to vocal learning species (Hoeschele et al. 2015).

Looking at distantly related species with these abilities and comparing the physiological and neuronal similarities could help us understand the mechanisms of acoustic communication (Dent et al., 1997; Hoeschele et al., 2015). These abilities and traits combined with the anatomical similarities in vocal production show that birds, especially parrots, might be an ideal model organism for psychoacoustic studies, especially those which are able to learn new sounds (Dent et al., 1997; Hoeschele et al., 2015).

There are many studies that investigate the similarities and differences of human and bird vocal production and communication. Budgerigars (*Melopsittacus undulatus*), a small Australian parrot species living in large flocks show similarities to humans in their auditory processing abilities. They are capable of phase matched tapping to auditory cues which resembles the human ability to synchronize movements with rhythmic sounds (Hasegawa et al., 2011). This suggests that these birds have an auditory sensitivity that allows them to perceive and respond to rhythmic patterns like humans. By comparison, rhesus monkeys (*Macaca mulatta*)

have shown limited ability to perform similar tasks when relying solely on auditory cues, instead showing a stronger preference for visual cues (Zarco et al., 2009). Humans and birds seem to have more similarities in vocal perception and processing than humans with other more closely related species. This auditory sensitivity aligns with findings in other avian species, like Java Sparrows (*Padda oryzivora*) which show a preference for certain types of music and exhibit the ability to distinguish between consonant and dissonant sound intervals (Watanabe and Nemoto, 1998). A similar preference for consonance and dissonance has been found in new born chicks (*Gallus gallus*). When given the option the chicks engage with consonant music (Chiandetti and Vallortigara, 2011). However, Wagner et al. (2020) did not find such evidence when performing the same experiment on budgerigars and humans. Only female humans showed a preference for consonant music. Similar problems occurred in the study of Plantinga and Trehub (2014), where human infants did not show a preference for consonant music but longer exposure to consonant or dissonant, both resulted in a familiarisation with the stimuli. These findings suggest that while vocal learning and rhythmic synchronization may align more closely between birds and humans than between humans and other primates, preferences for musical elements like consonance appear to be more variable and influenced by species-specific, developmental or contextual factors.

As mentioned earlier, another area of similarity between humans and some families of birds is their ability to engage in vocal learning, where individuals modify their own vocalisations based on environmental input and social cues. Budgerigars are well-known vocal learners and are able to imitate conspecifics, other bird species and even human speech (Brittan-Powell et al., 1997). They develop complex contact and food-begging calls that are influenced by their social environment (Brittan-Powell et al., 1997; Hile et al., 2000). Hile et al. (2000) showed that budgerigars develop a shared contact call, which is generally the result of the male imitating parts of the females pre-existing calls. Brittan-Powell et al. (1997) were able to show that budgerigars raised in isolation or limited exposure (hand-reared) to conspecifics show less complex vocalisations compared to birds raised in natural social environments. This effect would not be expected in species that are not vocal learners, suggesting that social interaction and exposure to conspecifics are critical for development of vocal complexity in budgerigars.

This ability to learn and modify calls by imitation and interaction with parents and other conspecifics in budgerigars is similar to the vocal learning seen in humans, where infants learn to produce speech sounds by imitating parents and other caregivers (Wilbrecht and Nottebohm, 2003). It was shown that budgerigars are able to perceive lexical stress, which is a key feature in many human languages such as English and German, and can learn to generalize stressing rules to new stimuli (Hoeschele and Fitch, 2016). This could suggest a sophisticated level of auditory processing that is also crucial for language and music perception in humans. Although language-like stimuli are less biologically relevant for non-human animals, it helps to study these same patterns across species in order to find important aspects of the perception of communication and language (Hoeschele and Fitch, 2016). Recent studies have provided evidence that language and music are much more closely related than previously believed (Patel, 2003). Both domains are processed in closely linked brain regions in humans, suggesting that they may share common evolutionary origins (Peretz et al., 2015).

Given their ability to engage in vocal learning, entrainment and their plasticity in communication, combined with their low maintenance requirements and relatively long lifespan, budgerigars are a valuable model organism to study auditory cognition and communication. Additionally, budgerigars are capable of complex social interactions and adaptive learning in vocal communication. They provide an excellent opportunity to explore the evolutionary origins of communication in birds and their parallels in humans.

With the advanced capabilities of computers come great new ways to investigate acoustic communication in further detail. Hasegawa et al. (2011) used computer simulations to discriminate coincidences in vocal and visual tapping entrainment to metronomes in budgerigars. Sasahara and Ikegami (2007) created a computer model of a simulated bird group based on studies with Bengalese finches (*Lonchura striata domestica*) to investigate the evolution and dynamic of bird songs. In their experiment, male song syntax became more complex when females timed their vocalizations to match the gaps of the males. They found that predatory pressure has a negative effect on the song complexity. The ability of females to recognize novelty, however, had a positive effect on the complexity of the songs. These results show, similar to studies performed by Brittan-Powell et al. (1997) and Hile et al. (2000) with budgerigars, the high plasticity in bird songs and in addition,

that female perception and preference controls complexity and diversity in male songs and group songs. This suggests that syntax is a very important part of communication in birds and that computer generated sounds can help identify important units. Laboratory experiments with artificial stimuli have been helpful in revealing perceptual skills and perceptual-motor coordination in non-human species. Computer generated sounds allow a more precise and wider manipulation of sounds to investigate which parts and properties of songs are important for animal communication (Hoeschele et al., 2015).

Recent research has begun to challenge the long-standing presumption that combinatorial vocalisation, the ability to create novel units by combining small meaningless elements, is unique to humans. Animal vocalisations were thought to be composed of a finite set of fixed calls (Hockett and Hockett, 1960). Human language is structured around syllables, which are formed by combining phonemes (smallest unit) and serve as fundamental building blocks of words and sentences (Jackendoff, 2003). However, building on Jackendoff's Hypothesis, Mann and Hoeschele (2020) propose that animal vocalisations may also be structured around phoneme-like subunits, arguing that research needs to go deeper if we really want to know whether other animals have human-like capabilities.

Mann et al. (2021) demonstrated that syllables in budgerigar songs are composed of consonant-like and vowel-like segments, which are organized non-randomly. Consonant-like segments tend to appear at the beginning of a vocalisation and vowel-like segments are more likely at the end. Vowel-like segments are typically quieter and longer in duration than consonant-like segments. Those patterns mirror those found in human language and suggest that the structure and organisation of these calls share fundamental principles with human language. Building on that idea, Gutscher et al. (2019) applied Hidden Markov Models (HMMs) and the HMM-based Speech Synthesis System (HTS), a tool that is commonly used in human speech synthesis, to break down budgerigar songs into simpler components. They created new "budgerigar" songs (resynthesized Songs) based on the segments. In a rating study human listeners perceived those created songs as natural. If budgerigars themselves perceive these resynthesized versions as natural too remains to be tested, which is part of this very study. This outcome would imply that budgerigars do not strictly require the specific physical characteristics of natural sounds for vocal recognition. Such findings would open new avenues for

investigating the cognitive and neural basis of auditory processing in vocal learners and may add new nuances to current models of vocal learning. By separating acoustic structures from biological origin, the limits of the recognition system can be tested and would validate the use of artificial stimuli in research. Future research could leverage this flexibility to systematically manipulate and test the limits of perceptual invariance, with the aim to fully understand how vocal learning systems evolve and operate. Additionally, understanding how birds recognize artificial songs could help create and train models of machine learning systems in bioacoustics and animal behaviour analysis.

This study is designed in three separated experiments to test three key predictions regarding budgerigar song perception and structure with relevance for understanding the evolution of language. For the first experiment we predict that budgerigars will show a preference for familiar songs over unfamiliar ones. This preference is based on prior research suggesting that animals, including birds, favour familiar stimuli, providing further evidence that budgerigars can distinguish between different auditory stimuli and if the birds show a preference for sounds they have been exposed to. It could provide information on the bird's personality as it can choose between familiar comforting sounds and curiosity for new unfamiliar sounds. This experiment also serves a practical purpose by allowing the birds to acclimate to the experimental setup, ensuring they are comfortable with the procedure and the testing apparatus before being exposed to artificially processed stimuli. Second, we hypothesize that budgerigars will not show a different response to artificial songs compared to their responses to natural songs, considering the growing body of research indicating that some birds can process computer-generated, artificial sounds similarly to natural conspecific vocalizations (Dooling et al., 1989; Schneider and Woolley, 2011; Radziwon et al., 2011; Mezrai et al., 2022). Should the budgerigars show differential responses to artificial sounds, this would indicate that they clearly perceive a distinction between them, warranting further research into suitability of such stimuli. If no difference is observed, it may suggest that the sounds are either sufficiently naturalistic or equally appealing to the birds. Finally, we predict that segment order in budgerigar songs is meaningful to the birds, similar to the order of consonant-like and vowel-like segments in human language and therefore budgerigars would prefer likely segment order over random segment order. This would support the idea that animal vocalisations, including budgerigar songs, share

fundamental organisation principles with human language, such as use of basic units that are arranged in specific order to convey meaning.

In sum, this study is designed to investigate whether budgerigars exhibit preference for familiar songs, respond similarly to artificial songs compared to natural ones, and whether they recognize an underlying organisation in these crafted vocalisations. These findings will contribute to the ongoing debate about evolutionary roots of language, suggesting that the mechanisms underlying vocal complexity and structure in animals share common features with those found in human language.

2. Materials and Methods

2.1. Participants

15 adult budgerigars between 1 and 6 years old were used. They were from two colonies that were held in separated, acoustically isolated rooms – 5 females from each colony, 2 males from colony 1 and 3 males from colony 2. The birds were kept at the animal care facility in the Department of Cognitive Biology (University of Vienna, Althanstraße 14, 1090 Wien) in aviaries (Room 1: 2 Aviaries with 2x1x2 m; Room 2: 1 Aviary with 2x1.5x2 m) containing 4-10 individuals. The study was performed from July 2020 to September 2021. Unfortunately, 3 birds died between the three experiments (1 after Experiment 1 and 2 after Experiment 2; For the total number of birds in each experiment see 2.4. Experimental Procedure). The aviaries were maintained on a 12-hour day-night cycle and food (Avifood's "Harrison's Bird Food, Adult Lifetime Superfine - Maintenance Formula for Small Birds" and since Q3 2021: "Versele-Laga NutriBird B14") and fresh water was provided every day.

2.2. Experimental Setup

As seen in Figure 1., the experimental setup is the same used by Wagner et al. (2020), a modified version of the setup used in Gentner and Hulse (2000). It consists of a hexagonal aviary with three perches in front of three speakers (FE108 full-range speaker, Fostex, Tokyo, Japan; frequency range 200–16 000 Hz). As shown in Figure 1, each perch is equipped with an infrared sensor (IR Break Beam Sensor - 3mm LEDs, Adafruit Industries, New York, NY, USA), that logs the time each bird spends sitting on the perch and the number of visits to the perch. The signal was recognised by an Arduino Uno REV 3 chip (BCMI, Turin, Italy) and caused the playback of stimuli over the three adjacent speakers of the chamber from MacBook Pro (Apple Inc., Cupertino, CA, USA). A delay of 300 ms in playback activation was used to prevent triggering while the bird is flying through the infrared beams. This functionality was programmed in "Python".

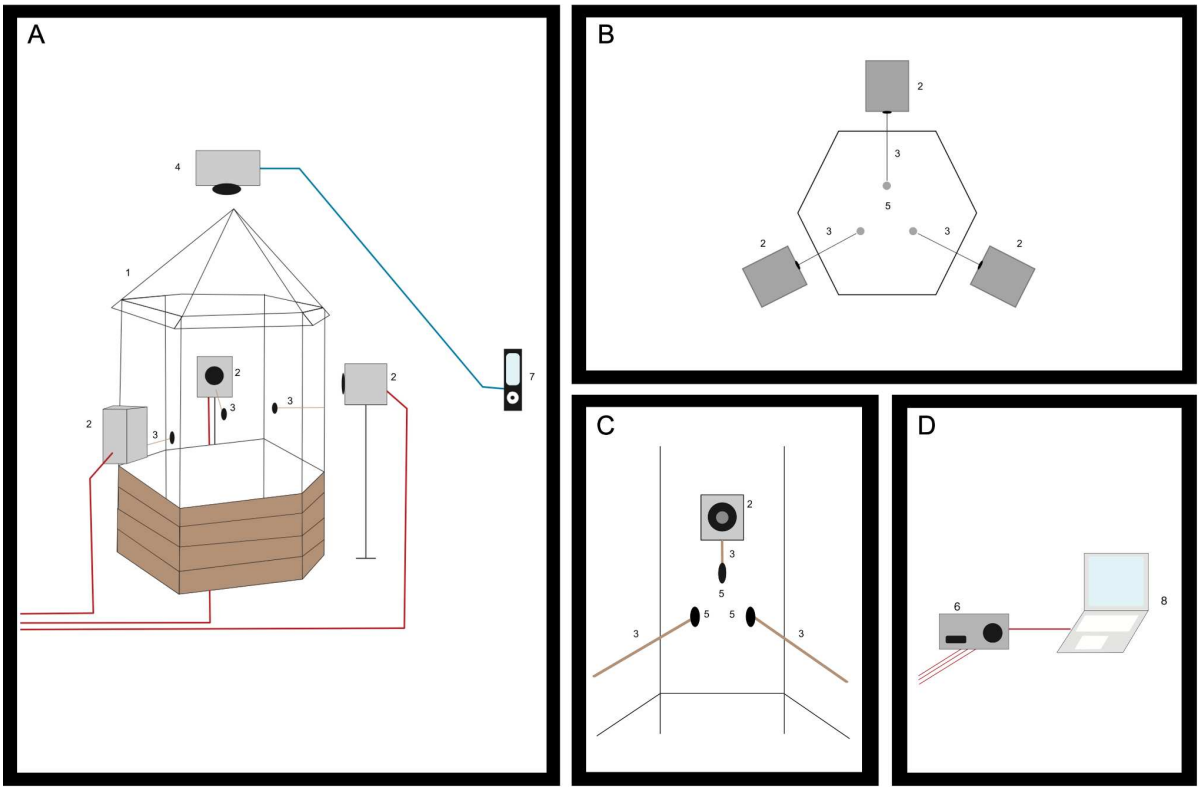

Figure 1: Schematic figure of the experimental setup. A- The hexagonal testing apparatus (1) surrounded by the three speakers (2) and the dedicated perches (3) inside the aviary. A fourth speaker (4) played ambient background sounds from an MP3-Player (7- HIFI Walker MP3 Player). B- Aerial perspective of the hexagonal experimental apparatus. Three speakers (2) are positioned around the testing aviary. Each has a perch (4) equipped with an infrared emitter and sensor (5). C- Inner side perspective of the three perches (4) with Infrared detectors (5) in front of a speaker (2). D- The speakers (2) are connected with an amplifier (6) that adjusts the volume of stimuli played from a laptop (8).

A speaker (M-Audio AV 40, Cumberland, RI, USA) on top of the experimental setup played background budgerigar chatter sounds (budgerigar warble sounds). This ambient background sound was recorded before the start of the experiments from each of the two colony rooms. These were played to ensure the birds did not feel isolated during the experiments. Each bird heard the background sound recorded from its own colony. The speaker was placed either above (Experiment 1) or below (Experiment 2 and 3) the chamber.

A random sample of the different sets of playback sound was measured with a sound pressure meter (Voltcraft SL-400, Conrad Electronic, Hirschau, Germany). The amplitude of the stimuli was set to approximately 65-70 dB, as measured from

the middle of each perch. The background sound was set to 50 dB, measured in the center of the chamber at perch height.

2.3. Stimuli

In order to record the stimuli, we habituated the budgerigar colonies to human presence and recording equipment. The birds were in their usual social environment during the recordings. The songs were recorded with a Sennheiser directional shotgun microphone (Sennheiser, Vienna, Austria). A GoPro Hero 4 (GoPro, San Mateo, Ca, USA) was mounted on the microphone to identify the individuals vocalising (similar to Mann et al. 2021). Before the experiments, eight male budgerigars were recorded, four from each colony. In the following, they will be referred to as “singers”. The number of birds was chosen to avoid the possibility of a “better singer” bias. With only one bird for each colony there would be a possibility that one of the singers would have been more skilled than the other which could lead to false results. The song-files were recorded as 48kHz wav files with 16 bits. Before the experiments the sampling rate of the audio files was reduced to 44.1 kHz, because the higher sampling rates caused problems with the program used for testing.

In each experiment, two sets of stimuli and an additional no-sound (silence) option were randomly assigned to the three different perches in the testing apparatus. In Experiment 1, unmodified budgie recordings were used as stimuli. The birds were presented with familiar sounds from their own colony, called the “familiar” condition, and unfamiliar sound from the second, foreign, colony, denominated as the “unfamiliar” condition. Each Stimuli set consists of 54 sounds between 0:06 and 3:30 minutes.

For Experiment 2 of the experiment, artificial stimuli were generated based on all the natural budgerigar songs recorded (both colonies combined) used in Experiment 1. Artificial songs were generated using the HMM/DNN-based Speech Synthesis System (HTS), following the algorithm built by Gutscher et al. (2019). In short, the natural songs were deconstructed into small elemental units, referred to as segments (Mann and Hoeschele, 2020), which were found to be essential components for budgerigar communication. The segments were then used to

resynthesize new, artificial "bird" songs. Resynthesis was performed by transforming the original songs into Mel-Cepstral Feature Frequency (MCFF) representations, which retained important frequency aspects of the sounds. These modified characteristics were then synthesized using a vocoder, successfully reproducing the songs with the spectral characteristics required for communication. The stimuli were then normalized and cleaned using Praat, a phonetic analysis software package developed by Paul Boersma and David Weenink, to normalize the stimulus amplitude and reduce noise. A bandpass filter (300-20,000 Hz) with 50 Hz smoothing was utilized to present clean, stable stimuli. These novel sounds were subsequently compared with the natural songs used in Experiment 1 to identify their perceptual relevance and effectiveness in the laboratory. Each stimuli set therefore consists of 108 Sounds between 0:06 and 3:30 minutes.

In Experiment 3, all stimuli were artificial and created based on Mel-Cepstral Feature Frequency (MCFF) representations. The files were generated through a combination of natural song segmentation, clustering, and both probable and fully randomized resynthesis processes. Initially, the natural songs were segmented, and these segments were clustered into categories. To create the artificial songs, the segment order from the original natural songs was preserved, and the corresponding segments were resynthesized based on the cluster labels. In the case of the probable songs, n-gram language models, trained on a corpus of phone-like unit sequences, were used to sample the most probable element sequences (taking into account sequence length and begin/end symbols), which were then concatenated to form the song. For the artificial songs with random segment order, elements were randomly chosen with replacement from a pool of possible segment categories.The stimuli sets consist each of 200 sounds between 0:01 and 2:09 minutes.

2.4. Experimental Procedure

For each experiment, a budgerigar was placed into the testing apparatus. The bird was provided ad libitum with food and water at the bottom of the apparatus. Then it was left alone for two hours and allowed to move freely inside the testing apparatus. During the experiment, the bird was presented with two different sets of stimuli categories. A third silence option was given to provide the budgerigar the opportunity not to listen to any of the given stimuli (control stimulus).

Each animal was tested in three experiments. For Experiment 1, the birds could choose between “familiar” and “unfamiliar” calls. In Experiment 2, the budgerigar could choose between natural budgerigar songs and artificial resynthesized songs. In Experiment 3, the test animals were given fully synthesized songs as both stimuli. One with natural segment order and one with randomized order.

The birds had to complete at least 3 sessions per experiment and needed to spend at least 20 minutes on each stimulus perch for their data to be included. If this criterion was not achieved the bird was tested in a fourth or fifth (maximum) session. This criterion ensured that the birds were aware of the different options. Some birds did not reach this threshold and were disqualified from further testing (Experiment 2: 1 bird, Experiment 3: 2 birds; Total number of birds in Experiment 1: 15 birds, Experiment 2: 13 birds, Experiment 3: 10 birds). However, the data from the experiments they participated in was still used in the analysis as long as the birds did listen to all the stimuli options. The speakers from which each sound is played was pseudorandomized for every bird in every session to prevent a preference for particular perches. Each stimulus set location was rotated between the sessions to ensure that no stimulus set consistently came from the same speaker or direction.

2.5. Data Analysis

The data analysis and figures were done with R (4.4.3 for Windows) and RStudio (2024.12.1+563). The data was analyzed using a linear mixed model (LMM) with the lme4 package (version 1.1-36), followed by ANOVA tests (lme4, car - 3.1-3) to identify statistically significant effects (condition, sex, session, position) and interactions (sex-condition). If there was a main effect of sex found, an LMM with only female and only male data was analysed separately. All models included mean time birds spend on each perch-visit as a dependent variable and subjects as a random effect. A secondary analysis using a model with total time (aggregated time) as a dependent variable was conducted, too. If there was a significant main effect or interaction found, post-hoc (emmeans - 1.10.7) analyses were conducted to explore these effects in greater detail. A significance threshold of $\alpha = 0.05$ was used. The graphics were designed in R Studio with ggplot (3.5.1).

3. Results

3.1. Experiment 1

In this experiment, the birds were presented with familiar songs, unfamiliar songs and silence. The main analysis investigated how much time was spent on each perch per visit over the course of the sessions each bird had to absolve.

Overall the birds spent similar amounts of time on each of the three options (Anova $\chi_2(2) = 0.583$, $p = 0.747$; Relative time spent on stimuli sets in all sessions: familiar - 28.59%, unfamiliar - 32.14%, Silence - 39.28%; Figure 2). However, the linear mixed model yielded a significant interaction for condition and sex ($\chi_2(2) = 8.163$, $p = 0.017$). For males (LMM only males) there was a main effect found in condition ($\chi_2(2) = 12.835$, $p = 0.002$; Meantime of perch-visits: familiar - 167.29s, unfamiliar - 144.45s, silence - 92.19s; Relative time spent on stimuli sets in all

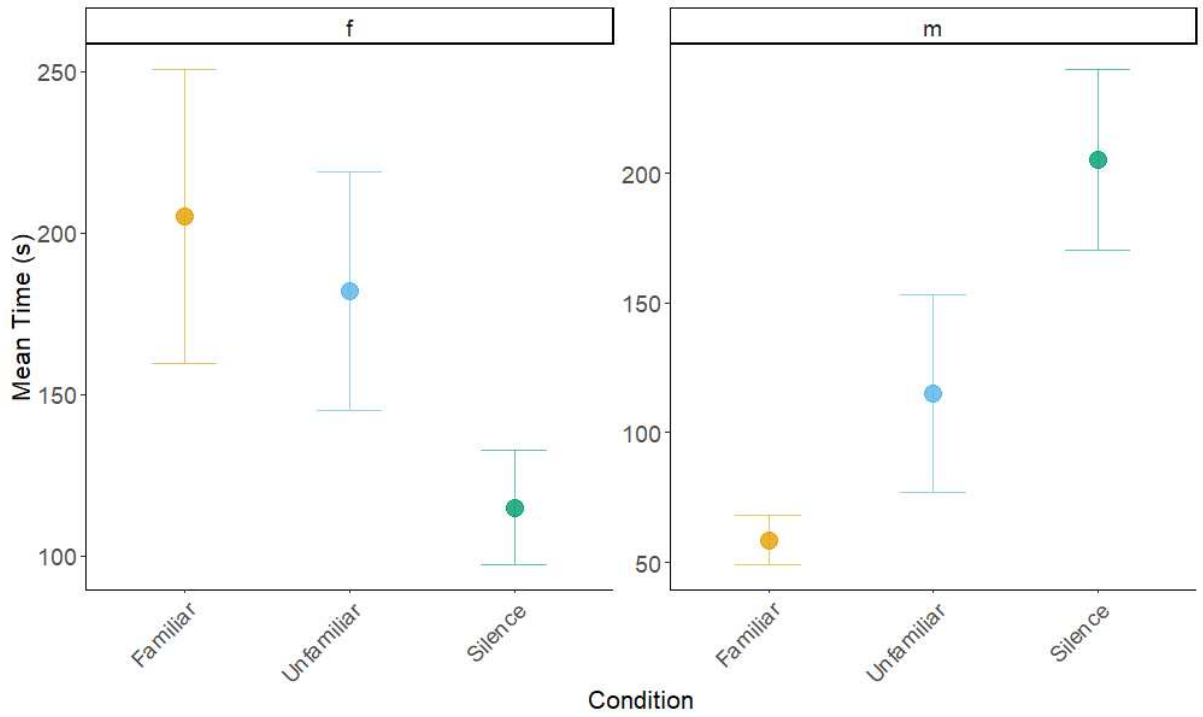

Figure 2.: Mean time birds spent listening to familiar, unfamiliar and silence stimuli per perch-visit in Experiment 1, including standard error. n=15 (5 male and 10 female).

sessions: familiar - 13.65%, unfamiliar - 24.6%, Silence - 61.75%). A post-hoc analysis with pairwise comparisons indicated that for males the silence condition was preferred more than familiar condition ($p = 0.001$) but there was no difference between silence and unfamiliar ($p = 0.102$) or familiar and unfamiliar ($p = 0.383$) as seen in Figure 4. In females (LMM only females) there was no significant difference for condition ($\chi_2(2) = 0.588$, $p = 0.745$; Meantime of perch-visits: familiar - 57.54s, unfamiliar - 112.37s, silence - 198.44s; Relative time spent on stimuli sets in all sessions: familiar - 36.22%, unfamiliar - 35.99%, Silence - 27.79%; Figure 3). For additional experiment data see appendix (7.1).

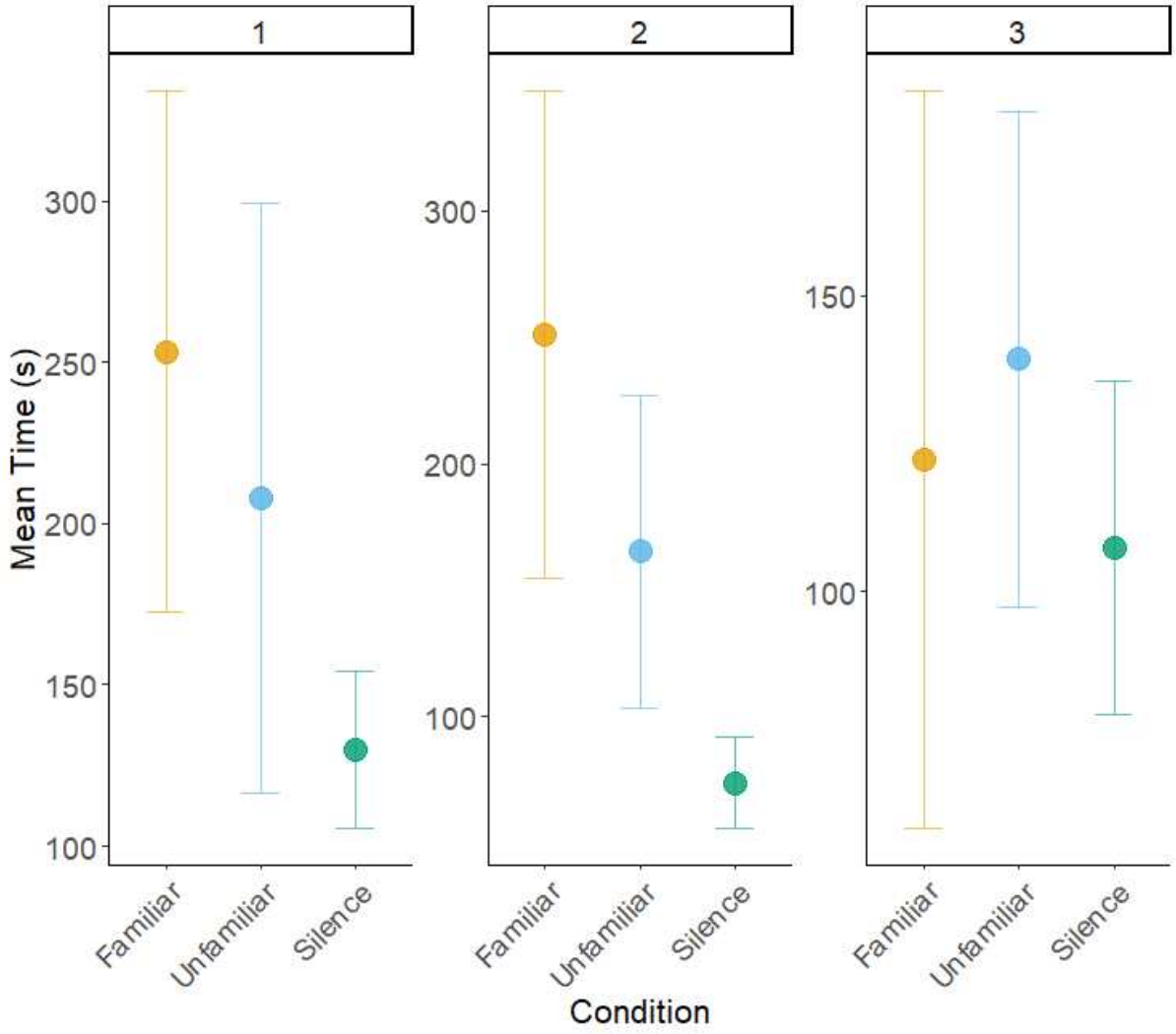

Figure 3.: Mean time female birds spent listening to familiar, unfamiliar and silence stimuli in separated sessions per perch-visit in Experiment 1, including standard error. n=10

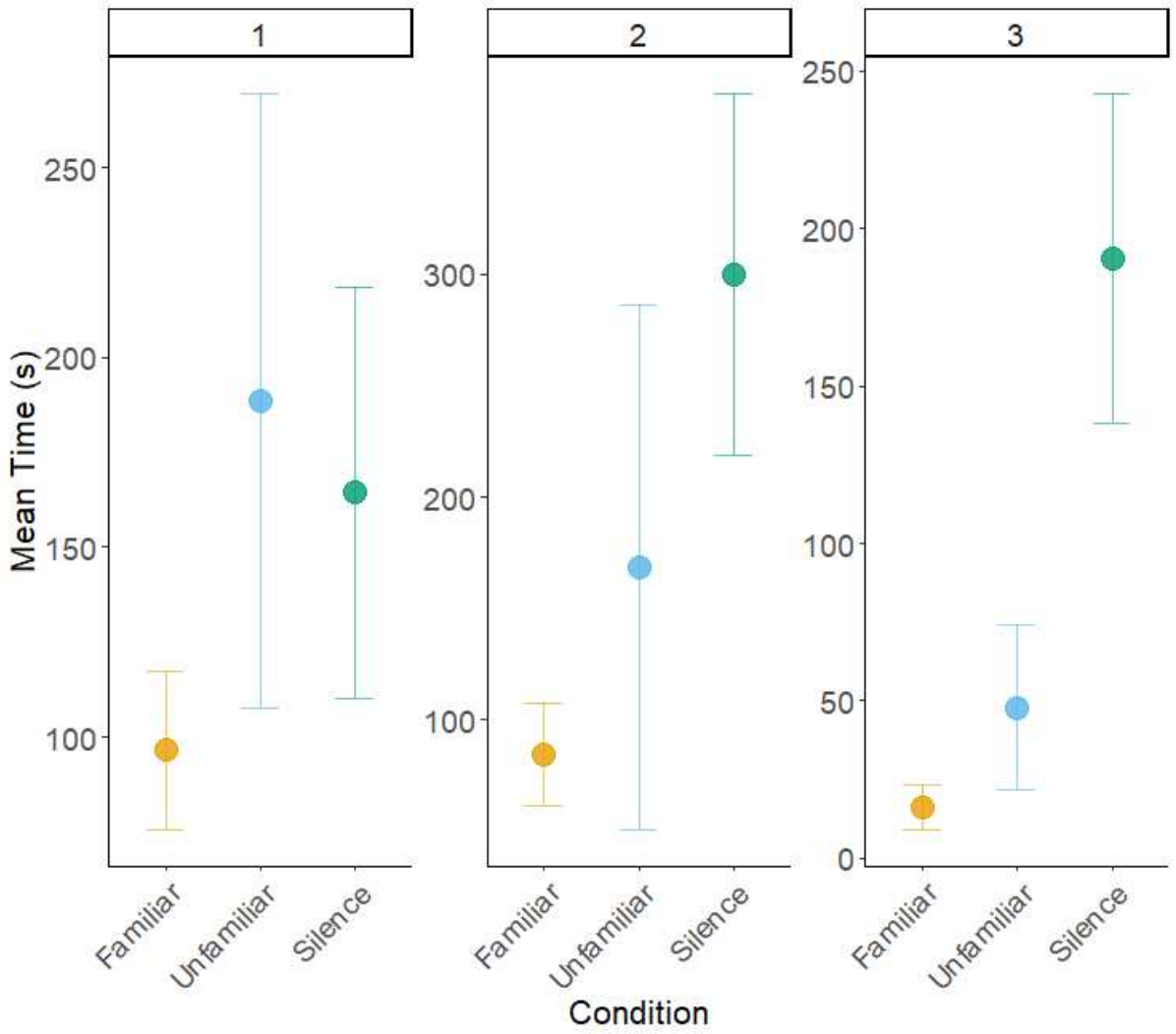

Figure 4.: Mean time male birds spent listening to familiar, unfamiliar and silence stimuli in separated sessions per perch-visit in Experiment 1, including standard error. n=5

When looking at aggregated times, the model revealed an interaction between sex and condition ($\chi^2(2) = 12.4737$, $p = 0.002$; see Figure 13 in Appendix). A post-hoc analysis with pairwise comparisons showed that male budgerigars preferred silence over familiar ($p = 0.002$) and over unfamiliar ($p = 0.010$). Females did not show a difference in hearing time.

3.2. Experiment 2

In Experiment 2, the birds could choose between original budgerigar songs (all budgerigar song recordings of both groups), artificially generated songs (resynthesized from all natural song recordings) and silence. Unfortunately one bird died and one bird was disqualified for not meeting the criterion in Experiment 1. Thus, 13 birds (8 female and 5 male) were tested. The main analysis investigated how much time was spent on each perch per visit over the course of the sessions each bird had to absolve.

The linear mixed model (both sexes) showed a significant effect of condition ($\chi^2(2) = 8.355$, $p = 0.015$) and an interaction between condition and sex ($\chi^2(2) = 11.219$, $p = 0.003$) when analysing the time spent listening to the stimuli sets per landing (Relative time spent on stimuli sets in all sessions: Natural - 23.16%, Artificial - 27.6%, Silence - 49.23%). The follow up contrasts show that the birds overall spent more time with silence than natural sounds ($p < 0.001$) and artificial sounds ($p = 0.032$). They also spent more time listening to artificial sounds compared to natural

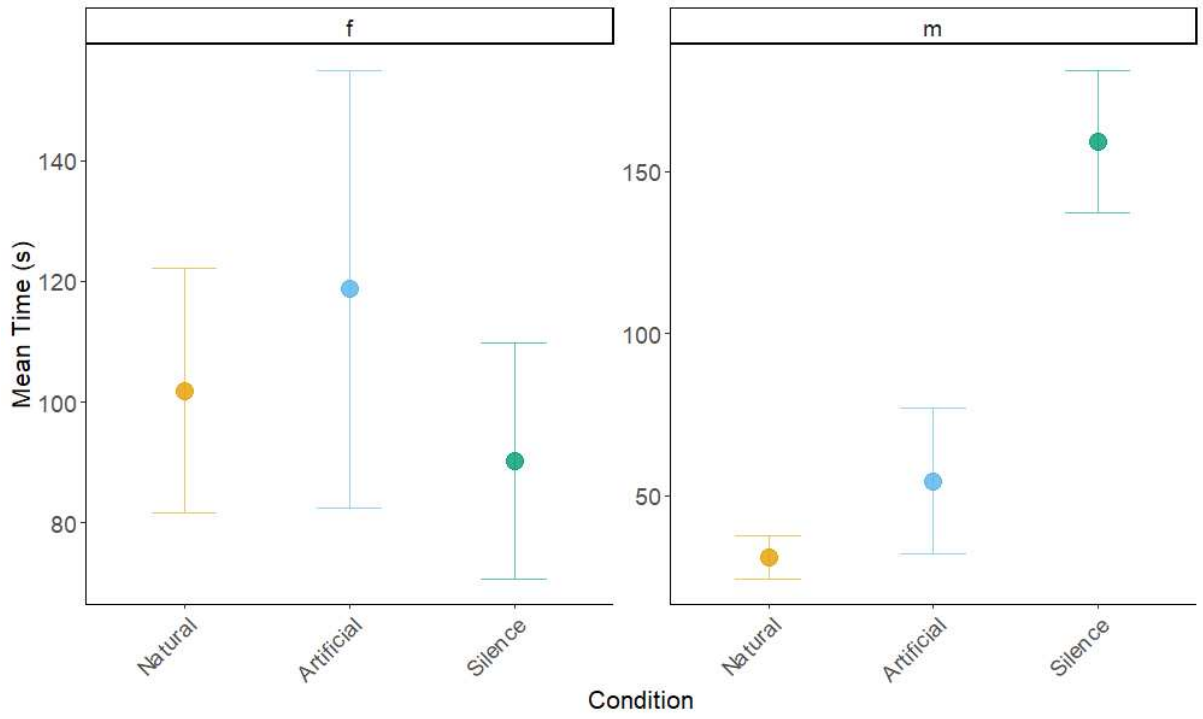

Figure 5.: Mean time birds spent listening to natural, artificial and silence stimuli per perch-visit in Experiment 2, including standard error. n=13 (5 male and 8 female).

ones ($p = 0.022$). The model (only male data) indicated an effect of condition in male birds ($\chi_2(2) = 38.837$, $p < 0.001$). As seen in Figure 5 and 7., male birds listened significantly longer to silence than to both acoustic stimuli (natural vs. Silence: $p < 0.001$; Silence vs. artificial: $p < 0.001$), but did not listen to natural or artificial songs longer (Natural vs. Artificial: $p = 0.423$; Mean-time of perch-visits: natural - 9.79s, artificial - 51.25s, silence - 150.26s; Relative time spent on stimuli sets in all sessions: Natural - 14.17%, Artificial - 17,97%, Silence - 67.86%). In Female birds (Figure 6) the LMM (only female data) indicated a difference in condition ($\chi_2(2) = 6.671$, $p = 0.036$) and the follow up contrasts reveal that they listened significantly longer to artificial compared to natural stimuli ($p = 0.041$). There was no difference between natural and silence ($p = 0.092$) or artificial and silence ($p = 0.876$; Mean-time of perch-visits: natural - 70.58s, artificial - 71.83s, silence - 54.21s; Relative time spent on stimuli sets in all sessions in all sessions: Natural - 29.9%, Artificial - 34.82%, Silence - 35.28%). For additional experiment data see appendix (7.1).

When looking at aggregated times, the model (both sexes, total time) indicated a strong interaction between condition and sex ($\chi_2(2) = 14.785$, $p < 0.001$; Figure 14 in Appendix). In male budgerigars the model showed an effect in condition (Males only: $\chi_2(2) = 70.737$, $p < 0.001$). Follow up contrasts showed that silence is preferred over natural ($p < 0.001$) and artificial ($p < 0.001$). Females did not show a preference for either of the stimuli sets (Females only: $\chi_2(2) = 0.428$, $p = 0.807$).

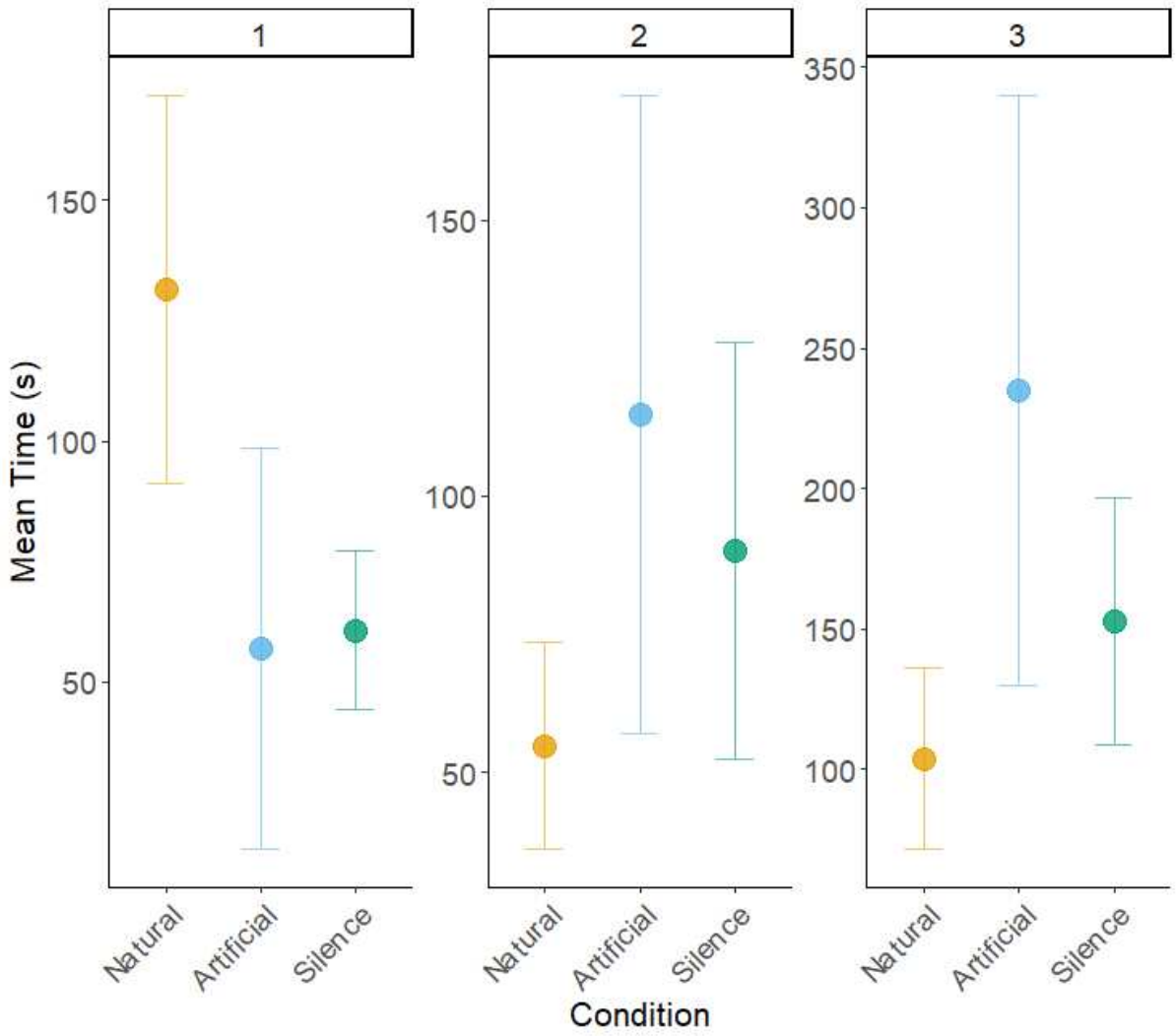

Figure 6.: Mean time female birds spent listening to natural, artificial and silence stimuli in separated sessions per perch-visit in Experiment 2, including standard error. n=8

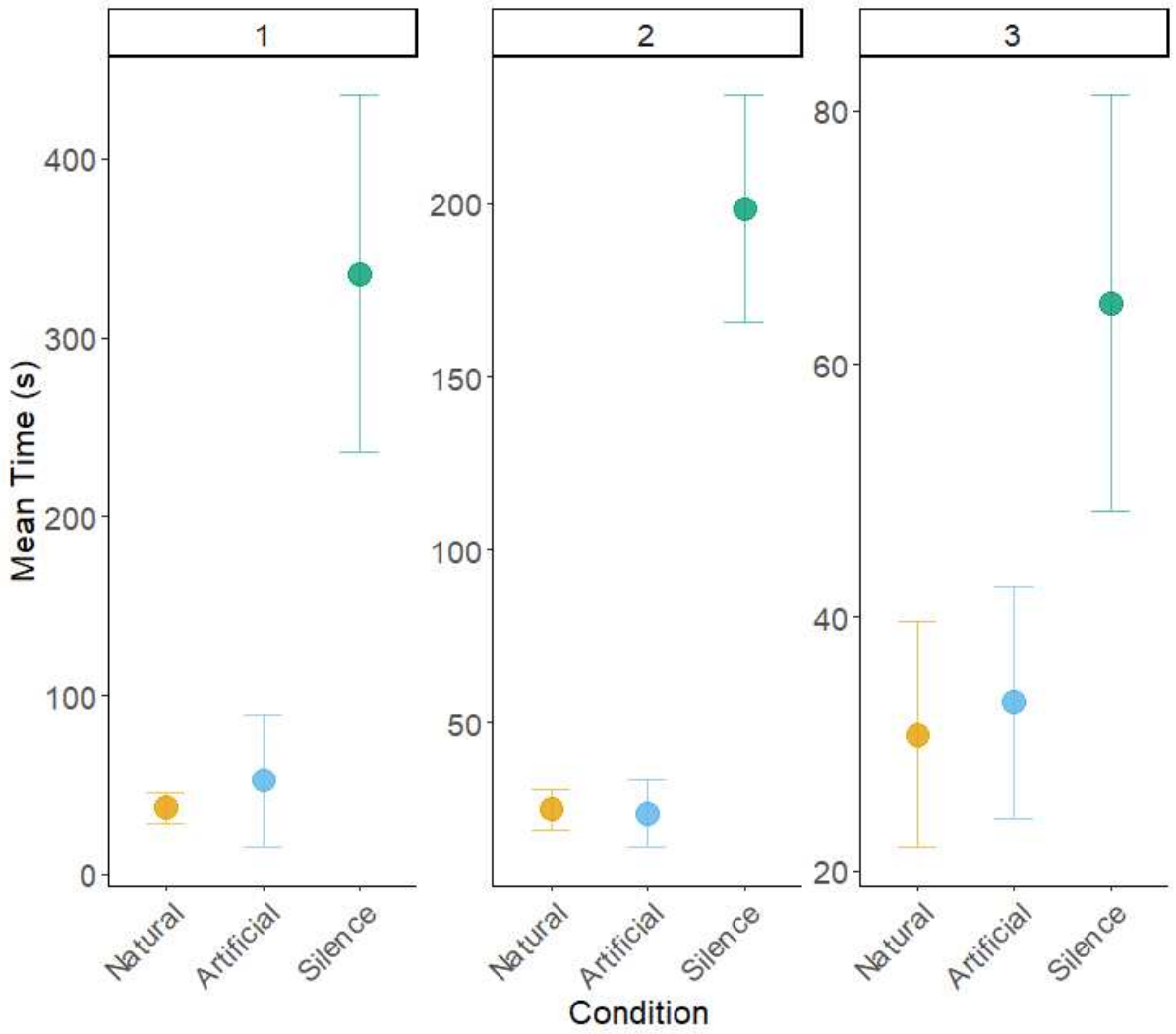

Figure 7.: Mean time male birds spent listening to natural, artificial and silence stimuli in separated sessions per perch-visit in Experiment 2, including standard error. n=5

3.3. Experiment 3

In Experiment 3, the birds could choose between artificial sounds with a likely segment order, random segment order, and silence. As mentioned in the Stimuli section (3.3) a large number of the available male birds had been assigned to the "singers". Unfortunately, at the time the experiment took place there were not enough male birds left (2 birds were no longer included because of death and 1 bird because of not reaching the criterion) in the colonies to compare the sexes. 10 birds were analysed- 2 males and 8 females. The main analysis investigated how much time

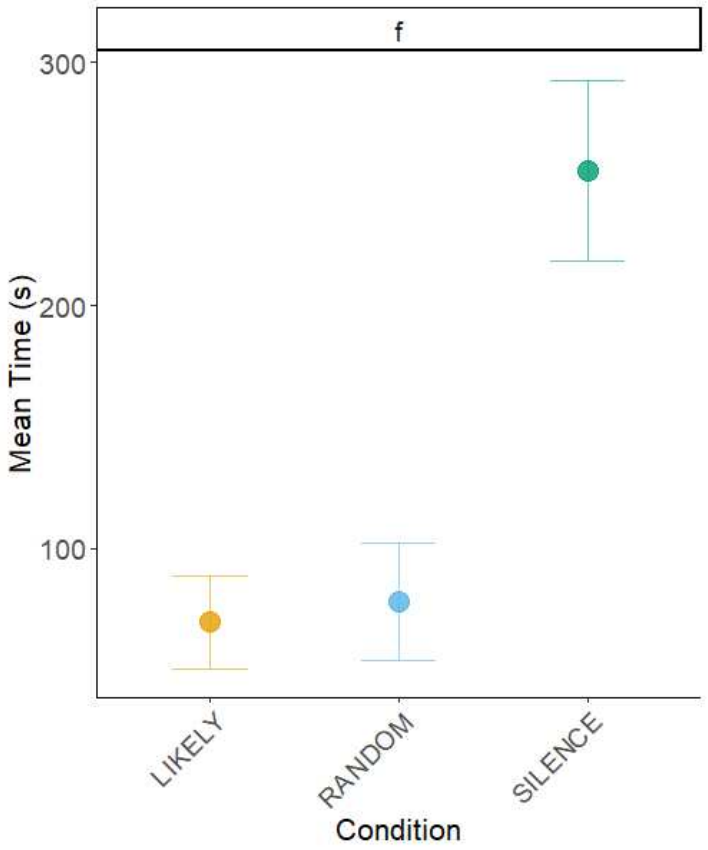

Figure 8.: Mean time female birds spent listening to artificial songs with likely or random segment order and silence stimuli per perch-visit in Experiment 3, including standard error. n=8.

was spent on each perch per visit over the course of the sessions each bird had to absolve.

The linear mixed model (both sexes) indicated a main effect of condition ($\chi_2(2) = 65.899$, $p < 0.001$). Further contrast analysis showed that the birds preferred silence significantly over likely ($p < 0.001$) and random stimuli ($p < 0.001$) but did not

show any preference between likely and random (p = 0.902; Relative time spent on stimuli sets in all sessions: Likely - 18.09%, Random - 19.39%, Silence - 62.52%). When just looking at the female birds (only female data) the results do not change ($\chi_2(2) = 48.811$, $p < 0.001$), shown in Figure 8 and 9 (Likely vs. random: p = 0.903; likely vs silence: p < 0.001; random vs. silence: p < 0.001; Mean-time of perch-visits: likely - 42.99s, random - 58.92s, silence - 226.31s; Relative time spent on stimuli sets in all sessions: Likely - 21.55%, Random - 18.94%, Silence - 59.51%). For additional experiment data see appendix (7.1).

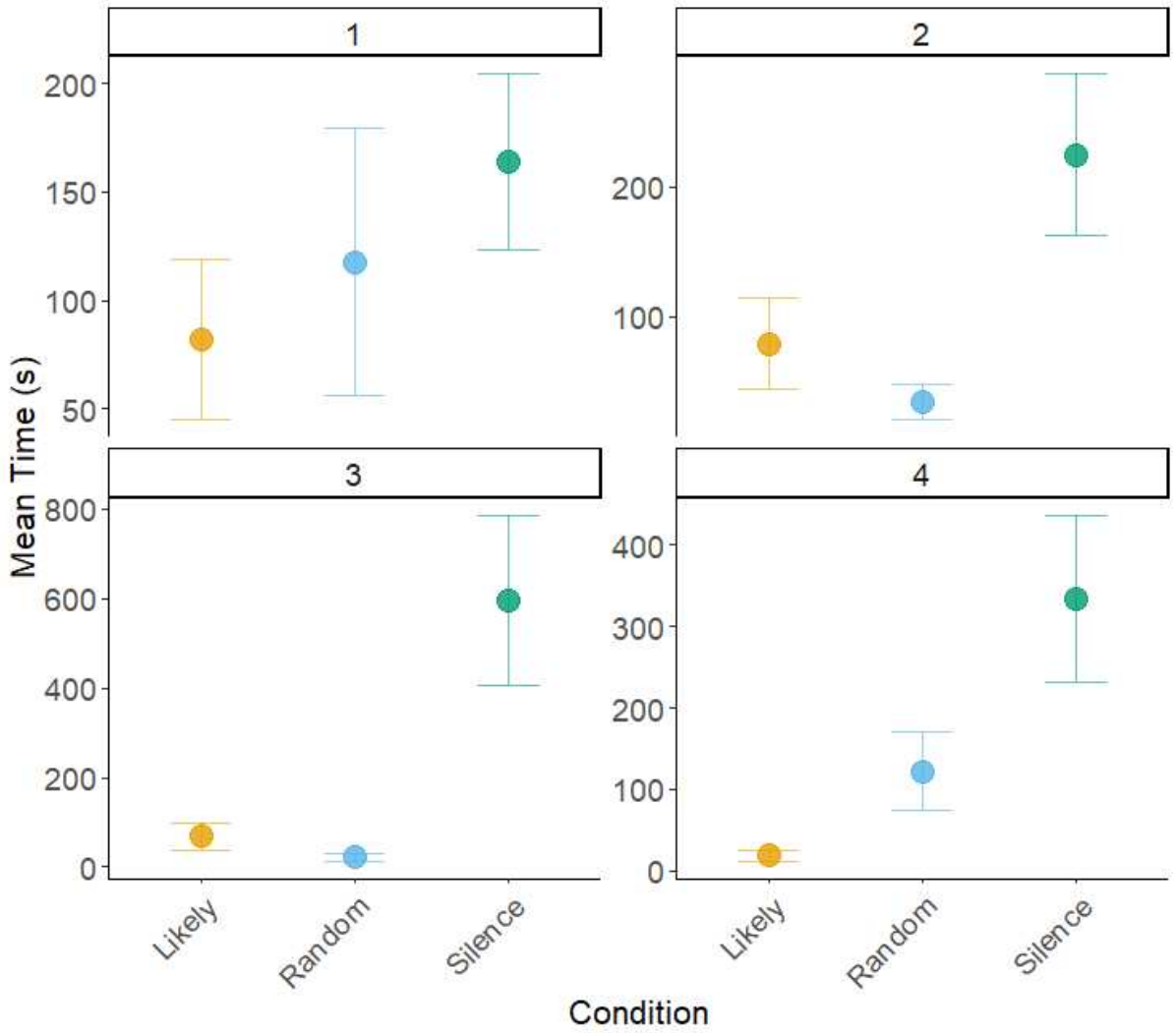

Figure 9.: Mean time female birds spent listening to likely, random and silence stimuli per perch-visit in separated sessions in Experiment 3, including standard error. n=8.

When looking at the aggregated times, the model (both sexes, total time) indicated an effect of condition ($\chi2(2) = 70.294$, $p < 0.001$; Figure 15 in Appendix). A

post-hoc analysis with pairwise comparisons showed that the birds heard silence more than likely ($p < 0.001$) and random ($p < 0.001$). There was no difference between likely and random ($p = 0.983$).

4. Discussion

This study consisted of three separate experiments (Experiments) and was designed to investigate whether budgerigars exhibit preference for familiar songs, respond differently to artificial songs compared to natural ones, and whether they recognize an underlying organisation in these crafted vocalisations. These findings contribute to the ongoing debate about evolutionary roots of language, suggesting that even if they have consonant-like and vowel-like segments in their sounds, a feature also found in human language, they may not use them in the same way as humans.

In the first experiment, we tested the birds' interest in novelty by presenting familiar vs. unfamiliar - novel - songs. Interestingly, male budgerigars actively avoided familiar songs and preferred silence, while females showed no significant preference. This suggests that budgerigars are open to engage with novel vocalisations. Following these results, the birds were presented with natural vs. artificial songs in the second experiment. Female budgerigars preferred artificial stimuli, indicating that the crafted songs were sufficiently engaging to support further tests of structural preference. However, in the final experiment, which tested artificial stimuli with a grammatically likely order against a random order, no significant preferences for either of those were found. This absence of preference suggests that either the birds habituated over the course of the experiments or they do not use segment order in a meaningful way. This would imply that, unlike human language where segment order conveys meaning, budgerigar songs serve more to display vocal prowess than structural information.

4.1. Experiment 1

In the first experiment, we wanted to find out how budgerigars treat new unfamiliar sounds. We predicted that the budgerigars would prefer familiar songs over unfamiliar ones. This expectation is based on prior research suggesting that animals, including birds, tend to favour familiar stimuli (Hile and Striedter, 2000). This experiment also served a practical purpose, allowing the birds to acclimate to the

experimental setup before being exposed to artificially processed stimuli. In this experiment, male birds did spend more time on silence than familiar sounds, but not compared to unfamiliar stimuli. Statistically speaking, male birds avoided familiar sounds. Female budgerigars did not show a preference for the given stimuli.

The results did not fully align with the predictions. The budgerigars did not spend more time listening to any of the given stimuli, which suggests no clear preference for familiar over unfamiliar songs. However, as seen in Figure 2, when looking at the sexes apart there is a difference. Males did spend significantly more time on silence than familiar songs but not unfamiliar songs. Because they statistically avoided familiar sounds but not unfamiliar sounds, one can argue that they have a light preference for unfamiliar sounds. Brittan-Powell et al. (1997) and Hile et al. (2000) showed that budgerigars develop shared calls as a result of mostly male birds imitating parts of females' pre-existing calls. These results could show a general interest in male birds to find and acquire new and interesting sound parts to add to their own song repertoire. Another point that could explain why males avoid familiar songs is that males usually sing to females as part of their courtship behaviour (Tu and Dooling, 2012). Both stimulus sets are mostly raw recordings of male birds from the two colonies. Male bird songs, especially from their own group, could be seen as competition in attracting female birds which could lead to male birds avoiding familiar songs in this type of preference experiment. The same argument would apply to unfamiliar songs, but curiosity to learn new song repertoire could counteract actual avoidance.

Female birds did not spend significantly more time on one of the given stimuli. However, during the experiments there was always a quiet familiar background sound playing from outside the experiment chamber which could be considered at least somewhat familiar when the birds chose the silence condition. Although not meaningful, this could hint on a light preference for familiar songs in both females and males. Budgerigars are very social birds that live in flocks and develop a shared song with group and family members (Farabaugh et al, 1994). Familiar songs would probably offer a feeling of peace and security. The fact that the background noise contained the songs of various group members and not only a song by one specific (male) individual, might reflect natural conditions (living in big flocks) better and therefore be more attractive to the tested birds. Similar problems occurred in Wagner et al. (2020) where budgerigars tend to prefer silence over consonant or dissonant

stimuli. They argue that in the silence condition the colony playback in the background would be most audible and, as highly social birds, it would not be surprising that budgerigars prefer this condition. One way to avoid such problems would be an additional habituation or familiarization phase where budgerigar could get used to the experimental setup. Future studies need to explore the differences of male and female birds with additional habituation mechanisms built in to get a better understanding of the effects of familiarity vs. curiosity. Additionally, adult and juvenile birds could show great differences in their preference.

4.2. Experiment 2

Now that we know that budgerigars are interested in novel vocalisations, because they did not prefer familiar songs, we can present them with new artificial sounds to test if those sounds are interesting enough for the birds. In the second experiment we predicted that budgerigars would respond to artificial songs similarly to how they respond to natural songs considering some bird species were able to process different artificial stimuli similar to natural stimuli (e.g. Dooling et al., 1989; Radziwon et al., 2011; Schneider and Woolley, 2011; Mezrai et al., 2022). In Gutscher et al. (2019) Human listeners found resynthesized budgie songs more appealing than natural or synthesized songs. In this experiment, where the artificial songs were created in the same way as the resynthesized songs in Gutscher et al. (2019), the (female) budgerigars listened to artificial songs significantly longer than to natural ones. Interestingly, this suggests that budgerigars, like humans, may find resynthesized versions of their species' vocalisations more engaging than the original, natural versions. This parallel in preference between species is worth highlighting explicitly. One possible explanation is that resynthesized songs may function as idealised vocalisations - they preserve species-typical acoustic patterns but remove extraneous variability, resulting in a cleaner perceptually salient signal. Alternatively, the resynthesized songs may be perceived as unusual, causing increased curiosity and attention in the birds. Further research would be needed to make sure whether this preference is driven by perceptual clarity or novelty or even a combination of both.

When looking at separated sexes, there is a clear difference. Male birds listened significantly longer to silence compared to both stimuli but did not respond differentially to natural and artificial stimuli. These findings may appear counterintuitive, yet they could suggest that the artificial stimuli are well-crafted, leading the budgerigars to treat them similarly to natural songs. This would mean that we have the same situation as in Experiment 1, when the male birds preferred silence over the given stimuli sets. The background noise featuring songs from various group members may better reflect natural flock conditions, making it more attractive to the birds, while natural - male - songs could be perceived as competition for courtship, potentially leading to avoidance in preference experiments.

However, female birds did listen to artificial songs significantly longer than natural songs, but did not respond differentially to either stimulus set compared to silence. Despite the expectation that natural songs would be more attractive to female birds, there are some points that could explain these findings. Female budgerigars may possess a more pronounced sensitivity to vocal nuances, particularly since females are the mate-choosing sex. Artificial songs might have vocal elements that are more appealing to females who are sensitive to subtle differences in song quality. However, on a neurological basis, it has been shown that at least one telencephalic vocal control region is larger in male than in female budgerigars (Nespor et al., 1996, Hile et al. 2000). This would suggest that male birds hear the difference better than females do and that the artificial stimuli may have sounded a little odd, maybe resembling even some kind of uncanny-valley effect, while females found it more appealing (similar to Wagner et al, 2020). As mentioned above, human listeners found artificial sound more appealing, but budgerigars have more pronounced hearing capabilities than humans (Dooling et al. 2002), which means female budgies should be able to hear the differences - even if they hear less details - just like male budgerigars. Another possibility is that female birds might be more attracted to novel stimuli, especially if the artificial songs offer new or unusual auditory experiences. New stimuli can sometimes be associated with new and potentially beneficial information or eligible mates with greater genetic diversity. Hile et al. (2000) showed that male budgerigars imitate and learn the songs of females in order to attract them. Because male budgerigars that imitate songs with greater precision could be considered more desirable by females, artificial songs might offer more consistent, clear and well structured vocalisations than natural

males, signaling a higher quality mate. This could make artificial songs more appealing for females compared to natural songs that may exhibit more variations or imperfections.

Ultimately, we can say that these artificial stimuli are sufficiently interesting for the birds, which means we can test for grammar preference with artificial stimuli.

4.3. Experiment 3

Budgerigars show remarkable skills regarding their vocal recognition and processing. They are able to imitate a broad range of sounds, incorporating new auditory information into their already established vocal repertoire (Brittan-Powell et al., 1997). Budgerigars also exhibit advanced auditory abilities, including the ability of phase-matched tapping (Hasegava et al., 2011), perception of lexical stress patterns (Hoeschele and Fitch, 2016), and discrimination of diverse artificial sounds (Dooling et al., 1989). Furthermore, they are able to generalize patterns learned in artificial grammar tasks, showing some cognitive flexibility in auditory learning and processing that points to advanced mechanisms for both their vocalization and auditory perception (Spearings and Ten Cate, 2016). Additionally, in recent years there is a growing number of studies that show that animal vocalisations, especially bird vocalisations, have distinct rules and syntax, even comparing their vocalisations to human language. Mann et al. (2021) have shown that budgerigar songs are organized by consonant- and vowel-like segments. In Experiment 2 we could show that the artificial stimuli were more interesting for female birds than natural vocalisations. All these incredible findings lead to the assumption that budgerigars would prefer artificial songs with a likely segment order over those with random segment order in Experiment 3. This would support the idea that animal vocalisation, including budgerigar songs, share organisational principles with human language, where basic units are arranged in specific orders to convey meaning. However, contrary to the expectations, the birds did not show any preference for likely or random segment order. They show an overwhelmingly significant preference for the silent option over both given stimuli. Even when looking at females only, they stayed significantly longer on silent than any other stimuli set. These results seem to add to the trend that was observed in Experiment 1 and 2, where especially male birds

prefer the silent option more than each of the given stimuli. In Experiment 3 even the female birds preferred silence while they were very curious about artificial stimuli in Experiment 2. Of course, there could have been errors in the setup or noise interference while the experiment was done. Considering that the setup was not changed between Experiment 2 and 3 this probably has not been the case. As for noise interference there can not be a definitive answer because the birds were left alone during the experiment to prevent said interference. However, the testing was done over several days and there was not any construction work or other noisy work done during testing time. The birds did not just sit on one of the perches the entire time of the experiments. The data shows that most of them frequently change position, spending time on all three options.

Beside these plausible explanations, there could be problems with the given stimuli sets. The stimuli sets could sound unnatural, unfamiliar or unrecognizable. Birds with specialized communication systems could be highly attuned to certain patterns of sounds. If the artificial songs did not serve any apparent social function the birds might have ignored or avoided the songs. However, budgerigars have been shown to have a wide flexibility in their auditory recognition system, mimicking and learning new sounds over their whole life (Hile et al., 2000; Brittan-Powell et al., 1997). In Experiment 2 female birds showed interest in new artificial sounds which indicates a certain curiosity for novel stimuli. Maybe some of the birds participated in too many experiments. It is possible that the artificial songs in Experiment 3 were not sufficiently novel or interesting so that the birds lost interest quickly. In this case, a greater variance of artificial sound stimuli or a different set of birds would lead to stronger effects. Conducting the different experiments in a counterbalanced order could also control for interest declining as experiments progress.

In Bellmann et al. (in prep.) budgerigars seem to like stimuli of intermediate complexity, which could also have an effect with the stimuli used in this study. The artificial songs could have been insufficient or even too challenging for the birds.

In our experiments we used a speaker outside the testing chamber to play a familiar colony background sound recorded beforehand. Silence might have been perceived by the birds as a baseline for a safe environment, in which they felt more comfortable. In an experimental situation, the absence of sound could be less stressful for the birds, especially if they do not see any conspecifics. The same argument made in Sections 4.1 and 4.2 could also be a possible explanation. The

birds hear familiar flock sounds from the background speaker which would reflect a natural group situation better than new and possibly strange stimuli.

But yet, the results of this study could also mean that segment order lacks functional significance for the birds, unlike in human language. Instead of encoding meaning through specific arrangements of sound segments, budgerigar songs may primarily serve to showcase vocal complexity. This interpretation would highlight a possible key distinction between human and non-human vocal behaviour - even if animals produce consonant- and vowel-like segments, they may not organize them to carry structured meanings as humans do.

4.4. Methods

As described in 4.1, 4.2 and 4.3, especially the male birds did show an overwhelming preference for the silent option in our experiments. These findings align with Wagner et al. (2020), where budgerigars showed the same preference for silence over consonant or dissonant stimuli. The experimental setup in this study is exactly the same as in Wagner et al. (2020) with at least some birds being the same individuals. Considering the literature of preference experiments, discussed before, it might have been a problem with our used setup and birds. However, this is unlikely because the experiments of Haiduk et al. (in prep.; female birds listened significantly longer to rhythmic stimuli compared to arhythmic), Bellmann et al. (in prep.; budgerigars prefer stimuli with intermediate complexity) and some results in this very study showed significant effects. Another possibility is, like mentioned above, that our birds are used to this kind of preference experiments and that the given stimuli are not interesting enough anymore. Considering that in Experiment 2 the female birds did listen to artificial sounds significantly longer would suggest otherwise. Additionally, these kinds of results would change if the current stock of birds is increased and new birds are added to our colonies. In Bellmann et al. (in prep.) new birds were added to our colonies which may have led to an increased interest in the provided stimuli.

One of the first papers where the idea of a third “silence” option is discussed is Hoeschele and Bowling (2016). They argue that a two sided preference paradigm would not necessarily show preference for one stimuli type, but possibly an

avoidance of the other type. On one hand, having three options complicates the experimental methods, produces more complicated results and might be more difficult to replicate. On the other hand it allows researchers to discern more complex preferences in birds than before. Future studies with this new approach have the potential to significantly enhance our understanding of vocalisation and acoustic preference.

The fact that the birds spent more time on silence might also have been a way to give the bird a better chance of detecting potential predators in their immediate vicinity, and that the birds only go for sound stimuli that really have importance. Evans et al. (2018) reported that birds alter their foraging behavior in response to increased ambient noise. In noisy environments, zebra finches heightened their vigilance, likely because the loud environment impeded their ability to assess predation risk. This resulted in reduced foraging efficiency, as the birds spent more time scanning for threats. Additionally, as suggested by Rubene et al. (2023), the presence of silence or quieter conditions may enhance other sensory inputs, improving foraging efficiency and security by allowing birds to utilize both auditory and visual cues more effectively. Therefore, the combined effect of noisy environments on zebra finches highlights the importance of auditory information in foraging and anti-predator behaviors, with disturbances potentially leading to suboptimal foraging decisions and increased risk perception.

4.5. Conclusion and future research directions

This study sheds light on how budgerigars perceive and respond to different types of vocal stimuli, contributing to our understanding of the importance of grammatical structure in budgerigar vocalisations. While their songs show structural similarities to human language, the birds did not constantly prefer familiar, natural or well-structured sounds over silence - possibly hinting that the birds do not use those structures in the same way as humans. Instead, their behaviour seemed influenced more by curiosity and novelty than by familiarity.

To investigate whether segment order carries meaning for budgerigars - as it does in human language - we first assessed their interest in novel vocalisations (Experiment 1). When given the choice between familiar and novel, unfamiliar

stimuli, budgies showed no preference for the familiar sounds, indicating an openness to novel sounds. Building on this, we compared responses to artificial versus natural vocalisations (Experiment 2), finding that budgies, if anything, preferred the artificial stimuli. This suggests that artificial vocalisations are sufficiently engaging to test more structure features, such as grammatical patterns. However, when presented with sound sequences that were either likely or random, budgies showed no preference (Experiment 3). This lack of differentiation suggests either that they habituated across experiments or that segment order itself is not meaningful to them. If the latter is true, it may indicate that, unlike in human language, budgie vocalisation prioritizes acoustic complexity or performance over structure meaning. Thus, even though budgerigars produce consonant- and vowel-like segments, they may not use these elements to encode meaning in the way humans do - supporting the possibility that humans are unique in applying complex meaning to their natural vocalisations.

Future Studies on auditory preference testing artificial stimuli with different segment orders in budgerigar songs have a number of promising directions in which to explore our knowledge of auditory perception and the underlying mechanisms. One area of particular importance is the exploration of temporal structure in budgerigar vocal preferences - particularly how rhythm and timing influence perception. Previous work, such as Hoeschele and Bowling (2016), has highlighted the importance of temporal patterns and auditory segmentation in vocal learning. Building on this, we propose using artificially generated stimuli that can be precisely manipulated in their segment order, timing and structure. This would allow us to test how features like tempo and repetition, usually often used in animal vocalisations, affects their preference. For example we could investigate whether songs with regular beats or consistent timing are more attractive than irregular ones, or whether repeated segments draw more attention. Further, examining the contextual variables, such as social dynamics and level of development (juvenile vs. adult), that might influence song preference could reveal how environmental and interactive factors impact auditory discrimination such as the auditory or visual presence or absence of conspecifics inside the testing chamber or the social context between those individuals (a similar point is made by Fujii et al., 2022). Testing these variables could help to understand why the birds in our study did not consistently respond to the vocalisations presented. Finally, the impact of song complexity on preference

needs to be explored methodically, particularly how variation in segment length and arrangement may affect the attractiveness of artificial songs to budgerigars. We know that Budgerigars are very sensitive to different budgerigar “warble” sequences (Tu and Dooling, 2012) and that their songs contain elements that resemble consonant- and vowel-like patterns (Mann et al., 2021). Future research could search for features and sequences that budgerigars might be most sensitive for using artificially modified songs or completely artificially created sounds to get deeper understanding for the similarities of animal communication and human speech.

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7. Appendix

7.1. Experiment Data

Table 1: Experiment Data from Experiment 1 (seconds).

	Familiar		Unfamiliar		Silence	
	Sum of time		Sum of time		Sum of time	
female	**69929**	**36,22%**	**69480**	**35,99%**	**53652**	**27,79%**
Lemon	10753	58,65%	5144	28,06%	2436	13,29%
Melanzani	261	1,01%	7290	28,29%	18220	70,70%
Mida	13896	66,35%	5292	25,27%	1755	8,38%
Pebbles	13127	63,12%	6134	29,49%	1536	7,39%
Pistachio	5312	27,67%	6761	35,22%	7124	37,11%
Smaug	7217	33,61%	14254	66,39%	0	0,00%
Storm	6576	45,08%	7063	48,42%	947	6,49%
Summer	2569	12,44%	3741	18,11%	14347	69,45%
Yara	4102	33,22%	5653	45,78%	2593	21,00%
Ziggy	6116	32,26%	8148	42,98%	4694	24,76%
male	**13464**	**13,65%**	**24272**	**24,60%**	**60920**	**61,75%**
Atlas	3041	14,25%	9787	45,87%	8510	39,88%
Darwin	1014	7,23%	119	0,85%	12888	91,92%
Elvis	2302	8,32%	7014	25,35%	18351	66,33%
Fourier	4876	26,45%	6094	33,06%	7463	40,49%
Hobo	2231	12,97%	1258	7,32%	13708	79,71%
All Birds	**83393**	**28,59%**	**93752**	**32,14%**	**114572**	**39,28%**

Table 2: Experiment Data from Experiment 2 (seconds).

	Natural		Artificial		Silence	
	Sum of time		Sum of time		Sum of time	
female	**41079**	**29,90%**	**47842**	**34,82%**	**48463**	**35,28%**
Lemon	3060	15,66%	5117	26,18%	11365	58,16%
Mida	8575	42,18%	9773	48,07%	1981	9,74%
Pebbles	1131	5,22%	19519	90,16%	999	4,61%
Pistachio	7260	43,90%	5267	31,85%	4009	24,24%
Smaug	7209	33,84%	6981	32,77%	7116	33,40%
Storm	8863	80,40%	471	4,27%	1689	15,32%
Strom	4586	83,34%	332	6,03%	585	10,63%
Summer	395	1,84%	382	1,78%	20719	96,39%
male	**14590**	**14,17%**	**18502**	**17,97%**	**69872**	**67,86%**
Atlas	2083	9,78%	2279	10,70%	16933	79,52%
Darwin	6978	34,57%	7314	36,24%	5892	29,19%
Elvis	973	4,15%	3117	13,30%	19346	82,55%
Fourier	1781	8,85%	3320	16,50%	15019	74,65%
Hobo	2775	15,48%	2472	13,79%	12682	70,73%
All Birds	**55669**	**23,16%**	**66344**	**27,60%**	**118335**	**49,23%**

Table 3: Experiment Data from Experiment 3 (seconds).

	Likely		Random		Silence	
	Sum of time		Sum of time		Sum of time	
female	**28763**	**21,55%**	**25277**	**18,94%**	**79435**	**59,51%**
Lemon	4554	33,63%	1197	8,84%	7790	57,53%
Mida	5323	35,46%	9101	60,63%	587	3,91%
Pebbles	4227	18,39%	3831	16,66%	14931	64,95%
Pistachio	2105	8,05%	1214	4,64%	22826	87,31%
Smaug	7293	52,71%	6542	47,29%	0	0,00%
Storm	2888	28,93%	922	9,23%	6174	61,84%
Strom	2185	50,06%	2180	49,94%	0	0,00%
Summer	188	0,68%	290	1,05%	27127	98,27%
male	**5156**	**9,54%**	**11082**	**20,51%**	**37806**	**69,95%**
Fourier	4587	16,37%	10697	38,18%	12730	45,44%
Hobo	569	2,19%	385	1,48%	25076	96,33%
All Birds	**33919**	**18,09%**	**36359**	**19,39%**	**117241**	**62,52%**

Table 4: Median and Mean time per perch-visit (seconds)

	Female		Male	
	Mean time	Median time	Mean time	Median time
Experiment 1				
familiar	167.29	4	57,54	6
unfamiliar	144,45	5	112,37	7
silence	92,19	9	198,44	43
Experiment 2				
natural	70,58	2	9,79	0
artificial	71,83	2	51,25	5
silence	54,21	1	150,26	15
Experiment 3				
likely	42,99	1	90,46	9
random	58,92	2	194,42	6
silence	226,31	37	389,75	65

Table 5: Number of perch-visits in Experiment 1 (seconds).

	Familiar in sessions				Familiar in sessions total	Unfamiliar in sessions			Unfamiliar in sessions total	Silence in sessions				Silence in sessions total	total number of visits
Subject	1	2	3	4		1	2	3		1	2	3	4		
f	165	114	138	1	418	95	158	226	479	159	189	232	2	582	1479
Lemon	7	7	13	/	27	3	4	137	144	7	3	46	/	56	227
Melanzani	3	16	3	1	23	4	4	4	12	35	1	6	2	44	79
Mida	13	2	1	/	16	16	2	1	19	14	3	1	/	18	53
Pebbles	2	1	9	/	12	1	1	6	8	0	1	5	/	6	26
Pistachio	21	71	79	/	171	20	102	58	180	26	144	90	/	260	611
Smaug	0	0	3	/	3	1	1	0	2	0	0	0	/	0	5
Storm	5	0	19	/	24	3	20	7	30	0	0	11	/	11	65
Summer	20	13	11	/	44	24	11	6	41	63	33	62	/	158	243
Yara	2	3	/	/	5	3	12	0	15	1	4	0	/	5	25
Ziggy	92	1	0	/	93	20	1	7	28	13	0	11	/	24	145
m	72	59	103		234	58	52	106	216	92	61	154		307	757
Atlas	30	20	58	/	108	30	19	59	108	36	20	66	/	122	338
Darwin	0	13	0	/	13	0	12	0	12	0	13	1	/	14	39
Elvis	5	4	18	/	27	4	3	18	25	10	4	17	/	31	83
Fourier	10	11	5	/	26	2	18	6	26	7	7	42	/	56	108
Hobo	27	11	22	/	60	22	0	23	45	39	17	28	/	84	189
total number of visits	237	173	241	1	652	153	210	332	695	251	250	386	2	889	2236

Table 6: Number of perch-visits in Experiment 2 (seconds).

	Natural in sessions				Natural in sessions total	Artificial in sessions				Artificial in sessions total	Silence in sessions				Silence in sessions total	total number of visits
Subject	1	2	3	4		1	2	3	4		1	2	3	4		
f	207	194	181		582	155	414	97		666	242	548	104		894	2142
Lemon	17	2	10	/	29	3	5	22	/	30	1	4	29	/	34	93
Mida	3	3	48	/	54	4	4	22	/	30	4	1	11	/	16	100
Pebbles	1	0	2	/	3	1	1	3	/	5	1	0	2	/	3	11
Pistachio	114	172	51	/	337	124	401	40	/	565	139	534	48	/	721	1623
Smaug	14	0	0	/	14	0	0	1	/	1	0	2	0	/	2	17
Storm	46	0	58	/	104	11	0	0	/	11	11	0	0	/	11	126
Strom	0	16	0	/	16	0	2	0	/	2	0	1	0	/	1	19
Summer	12	1	12	/	25	12	1	9	/	22	86	6	14	/	106	153
m	49	73	1359	10	1491	56	75	218	12	361	77	123	255	10	465	2317
Atlas	6	44	106	/	156	5	43	127	/	175	6	50	167	/	223	554
Darwin	13	1	1195	1	1210	14	0	0	2	16	13	0	0	1	14	1240
Elvis	5	7	4	9	25	14	6	23	10	53	1	6	5	9	21	99
Fourier	0	7	6	/	13	1	10	22	/	33	7	39	5	/	51	97
Hobo	25	14	48	/	87	22	16	46	/	84	50	28	78	/	156	327
total number of visits	256	267	1540	10	2073	211	489	315	12	1027	319	671	359	10	1359	4459

Table 7: Number of perch-visits in Experiment 3 (seconds).

	Likely in sessions				Likely in sessions total	Random in sessions				Random in sessions total	Silence in sessions				Silence in sessions total	total number of visits
Subject	1	2	3	4		1	2	3	4		1	2	3	4		
f	125	384	85	75	669	118	134	108	69	429	135	112	28	76	351	1449
Lemon	14	1	6	18	39	9	4	9	4	26	13	10	0	13	36	101
Mida	9	326	38	10	383	7	66	74	20	167	6	39	0	7	52	602
Pebbles	10	20	0	10	40	9	20	0	10	39	13	21	0	12	46	125
Pistachio	74	30	18	35	157	80	31	18	33	162	87	35	20	40	182	501
Smaug	0	3	0	/	3	1	0	0	/	1	0	0	0	/	0	4
Storm	7	0	19	/	26	1	0	3	/	4	1	0	3	/	4	34
Strom	0	2	0	/	2	0	10	0	/	10	0	1	0	/	1	13
Summer	11	2	4	2	19	11	3	4	2	20	15	6	5	4	30	69
m	14	8	24	11	57	12	7	27	11	57	23	13	48	13	97	211
Fourier	3	3	3	4	13	3	3	4	4	14	2	4	4	6	16	43
Hobo	11	5	21	7	44	9	4	23	7	43	21	9	44	7	81	168
total number of visits	139	392	109	86	726	130	141	135	80	486	158	125	76	89	448	1660

7.2. Additional Pictures

Figure 10.: Picture of how the Sound files were recorded before the experiments. The songs were recorded with a Sennheiser directional shotgun microphone. A GoPro Hero 4 was mounted on the microphone to identify the individuals vocalising (similar to Mann et al. 2021)

Figure 11.: Picture of the hexagonal testing apparatus at the Animal care facility (Universität Wien Althanstraße), surrounded by the three speakers.

Figure 12.: Picture of the Inside view of the Testing Apparatus. The perches each are equipped with an infrared emitter and sensor, in front of a speaker.

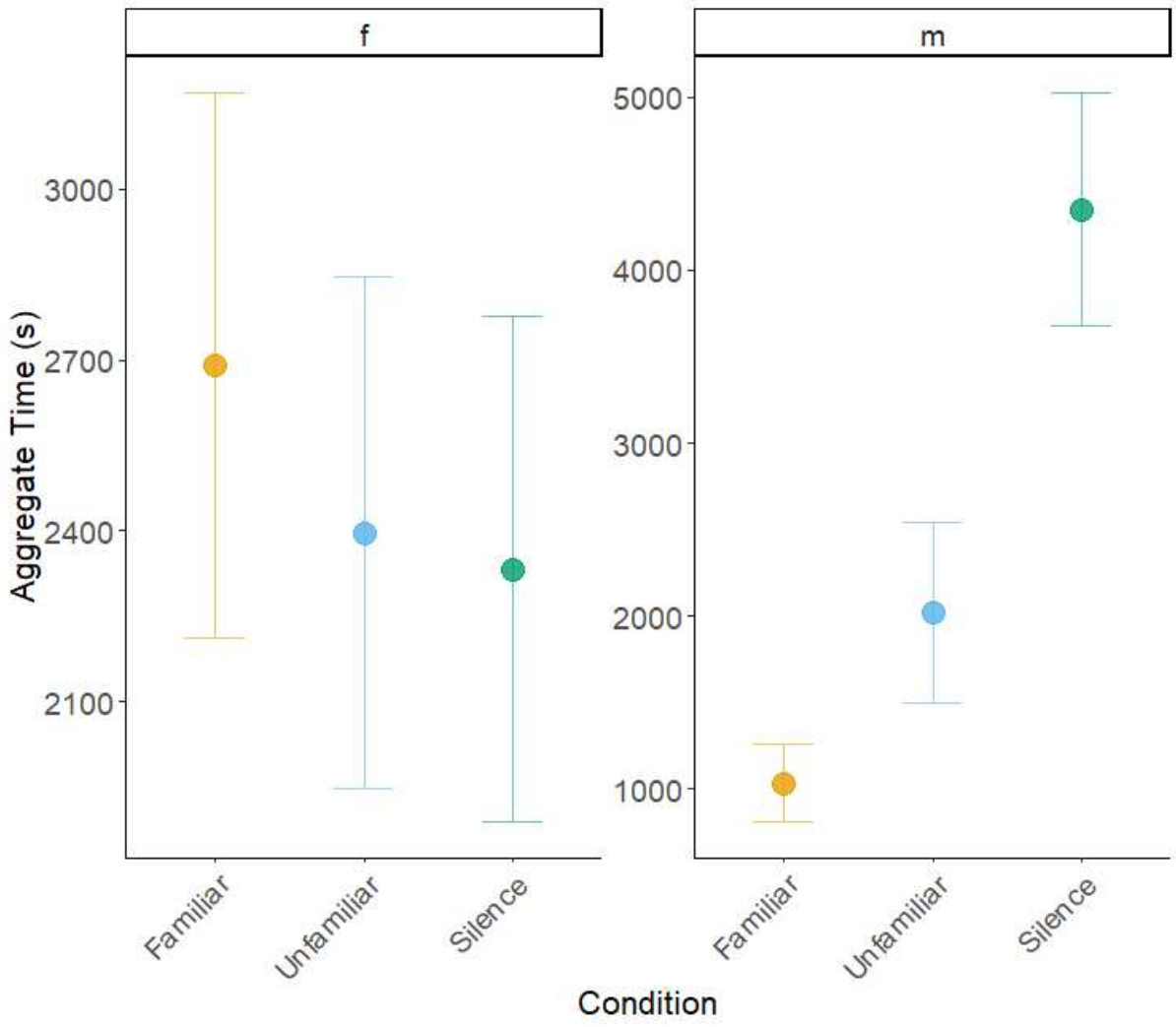

Figure 13.: Aggregated time birds spent listening to familiar, unfamiliar and silence stimuli in Experiment 1, including standard error. n=15 (5 male and 10 female).

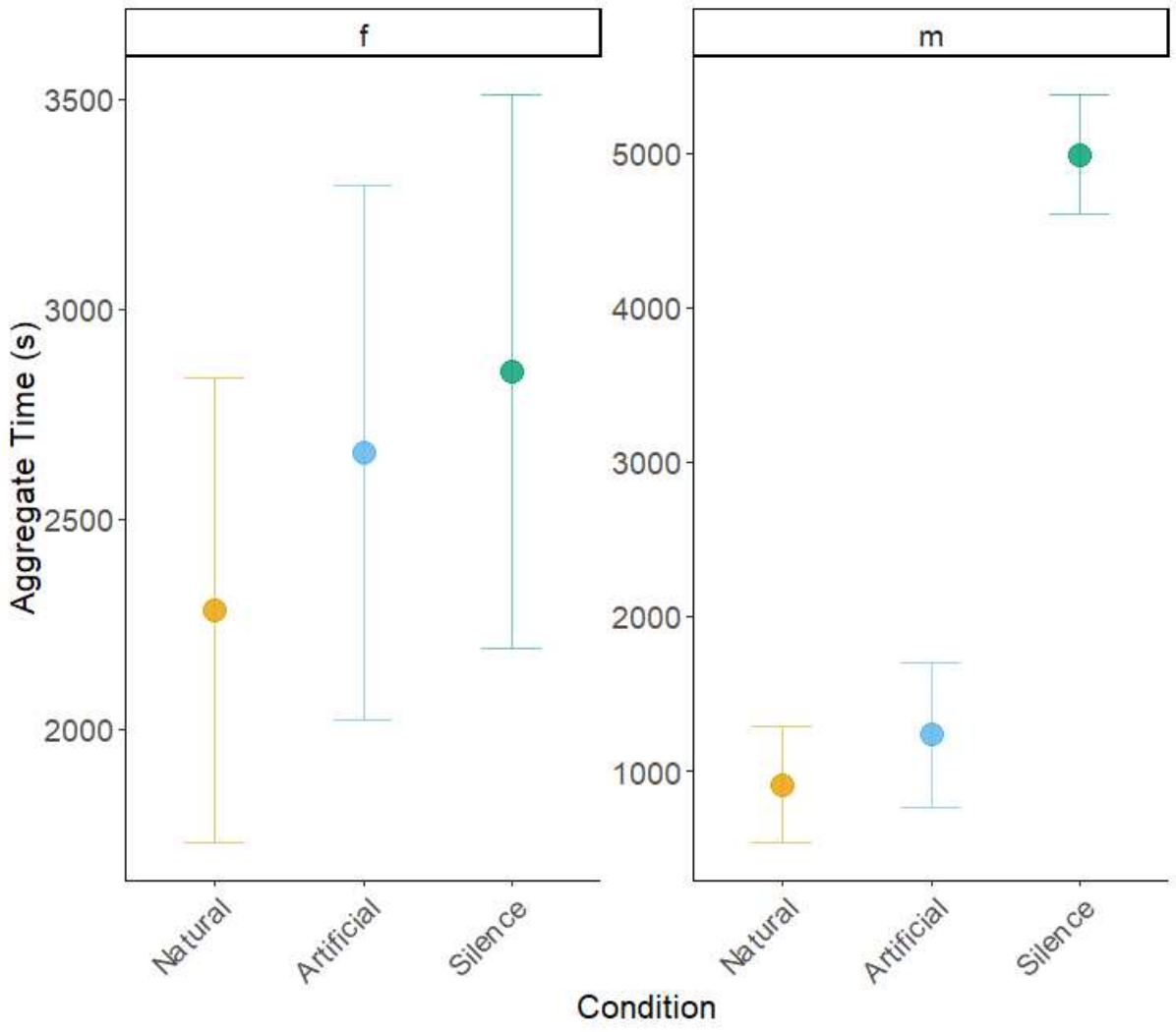

Figure 14.: Aggregated time birds spent listening to Natural, Artificial and silence stimuli in Experiment 2, including standard error. n=13 (5 male and 8 female).

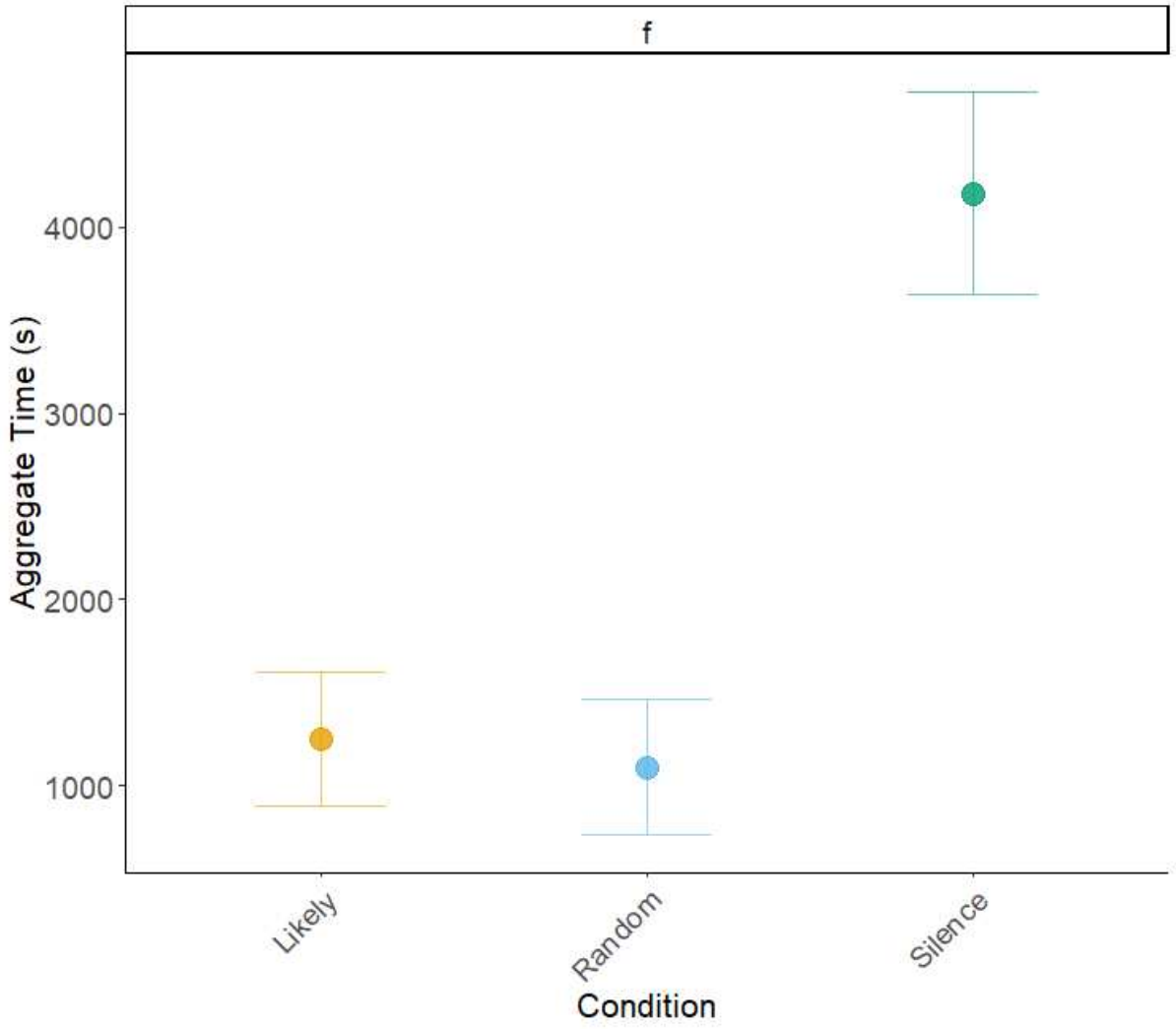

Figure 15.: Aggregated time female birds spent listening to artificial songs with likely or random segment order and silence stimuli in Experiment 3, including standard error. n=8.

7.3. Deutsche Zusammenfassung

Ergebnisse jüngerer Studien zeigen, dass der Gesang von Wellensittichen (Melopsittacus *undulatus*), ähnlich wie menschliche Sprache, in bedeutungslose Segmente zerlegt werden kann. Mit diesen Segmenten können durch Kombination Sinnvolle Muster gebildet werden. Studien, bei denen Analysetechniken der menschlichen Sprache eingesetzt wurden, ergaben, dass diese Vögel ihre Gesänge ähnlich strukturieren: Konsonanten-ähnliche Laute finden sich häufiger am Anfang von Artikulationen und vokal-ähnlichen Laute häufiger am Ende (Mann et al. 2021). Gutscher et al. (2019) konnten nachweisen, dass sich Wellensittich-Gesänge in kleine Segmente zerlegen lassen, die sich wiederum zur Erzeugung realistischer synthetischer Laute verwenden lassen.

Ziel dieser Studie ist es, die auditive Wahrnehmung von Wellensittichen zu bestimmen. 15 Wellensittiche (5 Männchen und 10 Weibchen) aus zwei verschiedenen Kolonien werden in 3 Experimenten getestet, um ihre akustischen Vorlieben zu untersuchen. In Experiment 1 konnten die Vögel zwischen bekannten (eigene Kolonie) und unbekannten (fremde Kolonie) unbearbeiteten Wellensittich-Gesängen wählen. Insgesamt verbrachten die Vögel ähnlich viel Zeit auf jeder Option. Männchen bevorzugten die “Silent” Option (in der keiner der beiden Gesänge abgespielt wurden) gegenüber bekannten, allerdings nicht gegenüber fremden Gesängen. Die Weibchen bevorzugten keine der drei Optionen mehr als die anderen. In Experiment 2 wurde den Vögeln die Wahl zwischen natürlichen und künstlich erzeugten Wellensittich-Gesängen angeboten (basierend auf Gutscher et al., 2019). Männliche Wellensittiche zeigten eine Vorliebe für Stille (Silent). Weibchen hingegen verbrachten mehr Zeit mit künstlichen als mit natürlichen Gesängen. In Experiment 3 konnten die Vögel zwischen künstlichen Gesängen mit einer Wahrscheinlichen (natürlichen) und einer unwahrscheinlichen (zufälligen) Segmentreihenfolge wählen. Die Wellensittiche bevorzugten nicht die wahrscheinliche gegenüber der zufälligen Reihenfolge der Segmente. Sie verbrachten aber signifikant mehr Zeit auf der “silent” Option, bei der keine Laute abgespielt wurden, gegenüber beiden Stimuli-Sets. Die Ergebnisse entsprachen nicht in vollem Umfang den Erwartungen. Die Methode erweist sich aber als geeignet für diese Art von akustischen Präferenz-Experimenten. Die Ergebnisse anderer Studien deuten darauf hin, dass das Problem bei den verwendeten Vögeln

liegen könnte - Wahrscheinlich aufgrund von Gewöhnung an diese Art von Experimenten - und unterstreicht die Notwendigkeit weiterer Forschung, insbesondere unter Verwendung neuer, nicht habituierter und naiver Individuen. Die Stimuli für Präferenztests müssen für die Vögel ausreichend interessant sein, damit sie sich auf Experimente wie diese Studie einlassen.

7.4. LLM R Script

```
# Libraries ####
library(gridExtra)
library("lme4")
library(emmeans)#for lmer
library(car)  #for lmer
library(effects) #for lmer
library(xtable)
library(ggplot2)
library(forcats)
library(dplyr)
library(sjPlot)
library(Matrix)

# Set path here ####
#clean space
ls()
rm(list=ls())
directory = ''
#Path
data1 = read.csv(("Path_to_file_P1_combined.csv"), header = T, sep = ',')
data2 = read.csv(("Path_to_file_P2_combined.csv"), header = T, sep = ',')
data3 = read.csv(("Path_to_file_P3_mitM_combined.csv"), header = T, sep = ',')

#Aggregating, just for checking. Do not use for analysis.
#data1 <- with(data1, aggregate(time~subject+condition+session+sex, FUN="sum"))
#data2 <- with(data2, aggregate(time~subject+condition+session+sex, FUN="sum"))
#data3 <- with(data3, aggregate(time~subject+condition+session+sex, FUN="sum"))



# DATA PREP ####

#Needed for LMM
data1$condition <- as.factor(data1$condition)
data1$sex <- as.factor(data1$sex)
data1$session <- as.numeric(data1$session)
data1$subject <- factor(data1$subject)
data1$condition <- fct_relevel(data1$condition, "Familiar","Unfamiliar","Silence")
```

```
data2$condition <- as.factor(data2$condition)
data2$sex <- as.factor(data2$sex)
data2$session <- as.numeric(data2$session)
data2$subject <- factor(data2$subject)
data2$condition <- fct_relevel(data2$condition, "Natural","Artificial","Silence")

data3$condition <- as.factor(data3$condition)
data3$sex <- as.factor(data3$sex)
data3$session <- as.numeric(data3$session)
data3$subject <- factor(data3$subject)
data3$condition <- fct_relevel(data3$condition, "Likely","Random","Silence")

#Clean up, remove 0-sec trials
data1 <- data1 %>%
  filter(time > 0)
data2 <- data2 %>%
  filter(time > 0)
data3 <- data3 %>%
  filter(time > 0)



# MODELS ####

# LMM, Both sexes
mbird_P1 = lmer(time ~ condition*sex+session+(1|subject), REML = TRUE,
         control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
         contrasts = list(condition='contr.sum'),
         data1)

mbird_P2 = lmer(time ~ condition*sex+session+(1|subject), REML = TRUE,
            control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
            contrasts = list(condition='contr.sum'),
            data2)

mbird_P3 = lmer(time ~ condition+session+(1|subject), REML = TRUE,
            control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
            contrasts = list(condition='contr.sum'),
            data3)

# Optional LMM, Males (if interaction sex*condition in mbird)
```

```
data1_male <- data1[data1$sex == "m",]
mbird_P1_XY = lmer(time ~ condition+session+(1|subject), REML = TRUE,
                   control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
                   contrasts = list(condition='contr.sum'),
                   data1_male)

data2_male <- data2[data2$sex == "m",]
mbird_P2_XY = lmer(time ~ condition+session+(1|subject), REML = TRUE,
                   control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
                   contrasts = list(condition='contr.sum'),
                   data2_male)

data3_male <- data3[data3$sex == "m",]
mbird_P3_XY = lmer(time ~ condition+session+(1|subject), REML = TRUE,
                   control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
                   contrasts = list(condition='contr.sum'),
                   data3_male)


# Optional LMM, Females (if interaction sex*condition in mbird)
data1_female <- data1[data1$sex == "f",]
mbird_P1_XX = lmer(time ~ condition+session+(1|subject), REML = TRUE,
                   control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
                   contrasts = list(condition='contr.sum'),
                   data1_female)

data2_female <- data2[data2$sex == "f",]
mbird_P2_XX = lmer(time ~ condition+session+(1|subject), REML = TRUE,
                   control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
                   contrasts = list(condition='contr.sum'),
                   data2_female)

data3_female <- data3[data3$sex == "f",]
mbird_P3_XX = lmer(time ~ condition+session+(1|subject), REML = TRUE,
                   control = lmerControl(optimizer = 'bobyqa', optCtrl = list(maxfun = 10000)),
                   contrasts = list(condition='contr.sum'),
                   data3_female)


# MAIN ANALYSIS ####
```

```
#Select model
model = mbird_P3 # mbird; mbird_P2; mbird_P3 # Optional: mbird_XY mbird_XX

# ANOVA
Anova(model, type=3)
summary(model)
#capture.output(summary(model) ,file="stats.csv") # Save output as csv
xtable(coef(summary(model)))

#POST HOC
emt = emmeans(model, pairwise ~ condition); summary(emt)

# PLOTTING ####
#PLOT: MODEL FIT
plot_model(model, type = "pred", terms = c('condition'))+
  theme_minimal()+
  ylab("Estimates (s)")
ggsave(paste0(directory, 'FIG_estimates.png'), width = 7, height = 5)

#PLOT: MODELED DATA (i.e., trials)
#install.packages('ggokabeito')
library(ggokabeito) # color-blind friendly colors; Reference:[1].

ggplot(data3, aes(condition, time, group=condition, color=condition, fill=condition))+theme_bw()+
  stat_summary(fun.y=mean, geom="point", size = 5, alpha=0.8)+
  theme_classic()+
#  facet_wrap( ~ sex, scales = "free_y")+ # SEX SEPARATED
  #geom_line(aes(group = subject), color = "grey", alpha = 0.5) +  # Individual subject lines
  scale_color_okabe_ito()+
  scale_fill_okabe_ito()+
   # stat_summary(fun.data = 'mean_cl_boot', geom = "errorbar", width=0, alpha=0.6)+ #plot CI as
error
   stat_summary(fun.data = 'mean_se', geom = "errorbar", width=0.4, alpha=0.6)+          #plot mean
seas error
  xlab("Condition") + ylab("Mean Time (s)")+
  theme(legend.position = 'none',
        text = element_text(size = 16),  # Increase font size
        axis.text = element_text(size = 14),  # Adjust axis text size
        axis.title = element_text(size = 16),  # Adjust axis title size
```

```
        strip.text = element_text(size = 14),
        axis.text.x = element_text(angle = 45, hjust = 1))
ggsave(paste0(directory, 'FIG_modelledData.png'), width = 7, height = 5)
```