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Abstract

Courtship plays a crucial role in reproduction and often consists of multicomponent displays that contain various courtship behaviors. This is the case in budgerigars (*Melopsittacus undulatus*), a small parrot species originated in Australia. Males of this avian species sing and show courtship behaviors to attract females. Behaviors included in courtship context are not only directed at females, but also at male individuals. Same-sex sexual behavior has already been observed in over 130 avian species, although it is far from being clear what function it has. The first step to examine this is to study if female-directed courtship displays differ from those that are directed to males. In my thesis I used video recordings of two independent colonies and coded following courtship behaviors based on Brockway's ethological studies from the 1960s: nudging, pumping, bill-hooking, head-shaking, head-bobbing and courtship feeding. To show if the sex of the receiver affects courtship sequences, I first used the sequence duration and used Bayesian methods to fit a multi-level model. The model suggests strong evidence for the absence of an effect but the reliability of the model was influenced, maybe because of missed explanatory variables like a potential bonding between interaction partners or the imbalance of my data. Exploratory research was conducted on other structural parameters using descriptive and frequentist statistics, resulting in a significant relation between the sex of the receiver and the probability distributions of observed behavioral transitions. In conclusion, generalizations about an audience effect on the visible courtship behavior in budgerigars are limited, further studies on the level of bonding between individuals could help to examine if an existing pair bond has a greater effect on the structure of those courtship displays than the sex of the receiver.

Introduction

Courtship is very common in the animal kingdom, plays a crucial role in reproduction and can often be observed occurring directly before copulation (reviewed by Mitoyen, Quigley & Fusani, 2019). Behaviors during courtship are displayed by an individual to attract, to mate and to eventually reproduce with an individual of the opposite sex (Bastock, 1967). Additionally, performing courtship behaviors might serve as means to identify species and sex membership to conspecifics (reviewed by Fusani, 2008). Organisms must have the ability to recognize members of their own species and to differentiate between the sexes to successfully produce offspring (Mitoyen et al., 2019). Furthermore, courtship is important for pair bond formation and to advertise mate quality in many species, especially in birds such as the budgerigar covered in this study (Brockway, 1964; Fusani, 2008).

Also known as the Undulated Parrot or Warbling-Grass-Parrakeet, the budgerigar (*Melopsittacus undulatus*) is native to the continent of Australia and is one of the smallest parrot species (Russ, 1927). As budgerigars are extraordinarily sociable and several pairs can be housed together in one aviary (Brockway, 1964), I was able to observe captive budgerigars and examine their courtship behavior. Like most of the parrots, budgerigars usually display social monogamy by building pair bonds and showing biparental care (Brockway, 1964b; Forshaw, 2002). At least in captivity, budgerigars breed readily throughout the year when nestboxes are provided (Brockway, 1964b).

Courtship is usually female-directed and male-initiated (reviewed by Mitoyen et al., 2019), as is the case in budgerigars. Male budgerigars perform courtship behaviors to be chosen by females for reproduction (Brockway, 1964). This is also named female choice, a part of sexual selection and a widespread phenomenon in the animal kingdom

(Darwin, 1871). The female's eggs are energetically expensive and therefore females aim to select the males of highest quality to ensure the survival of their offspring (Darwin, 1871). Energetically costly morphological traits of males and courtship behavior displayed by males often increase the male's reproductive success, which indicates that females assess mate quality by such factors (Darwin, 1871).

In budgerigars, courtship behaviors can also be observed between members of the same sex, especially between males (Abassi & Burley, 2012; Brockway, 1964; Brockway 1974). Same sex courtship activities have been often ignored by researches, likely because researchers have tended to treat such interactions as mistakes (Bagemihl, 1999). Female-directed (FD) courtship displays can increase the male's reproductive success (Brockway, 1964), but the goal of male-directed (MD) courtship is not clear, as same-sex courtship cannot lead to reproduction. This leads to my research question: Does the sex of the receiver (i.e. the audience) have an effect on the visible courtship behavior in budgerigars and do female-directed courtship displays show structural differences to male-directed ones? Answers to these questions could allow the possibility to draw inferences about potential functions of male-directed courtship displays.

Across species, courtship is composed of complex displays and elaborate ornaments in some cases that may increase the male's reproductive success (Darwin, 1871). In some species, display intensity is related to the mating success, for example, female red deers prefer male roars with lower formant values (Charlton et al., 2007). A species that performs elaborate courtship dances is the male golden-collared manakin (*Manacus vitellinus*) from the order Passeriformes (Fusani et al., 2007). These dances, called jump-snap displays, are combined with mechanically produced sounds (Fusani et al., 2007). This kind of courtship is also an example of multimodal displays that are

common in avian species, meaning that concomitant signals occur in different sensory modalities (reviewed by Mitoyen et al., 2019).

Budgerigars courtship behavior is an example of multimodal and multicomponent courtship displays. On the one hand, budgerigars vocalize to attract mates producing courtship songs. On the other hand, they perform specific movements in courtship context that are visible for potential mates (Brockway, 1964). Signals used for communication are composed of components, in budgerigar courtship there are auditory and visual components (Tobin et al., 2017; Brockway, 1964). My study focuses on one sensory modality, the visual one. Visual courtship displays of budgerigars are often composed of multiple components (Brockway, 1964; Brockway, 1974). Multicomponent displays are courtship displays where components occur in the same sensory modality (Rowe, 1999). While the different modalities of multimodal signals can display different aspects of a male's quality, for example the bower quality and the coloration of the plumage is related to mating success in the satin bower-bird (Doucet & Montgomerie, 2003), in multicomponent displays it is still not clear what role each component plays (reviewed by Mitoyen et al., 2019). Auditory and visual signals used for communication and consequently in courtship are composed of components, one component is for example the head-bobbing occurring during courtship in budgerigars (Brockway, 1964). However, multicomponent signals can be detected, memorized and discriminated better in contrast to single-component displays, particularly when they are performed in multiple sensory modalities (reviewed by Rowe, 1999). Budgerigars are impressive in their ability to learn new vocalizations throughout life (Hile et al., 2005). It is not surprising, that the research in budgerigars concentrates mainly on their song in all its facets (see for instance: Hile et al., 2005; Mann et al., 2021; Tobin, Medina-García, Kohn and Wright, 2017).

To my knowledge, there are only a few studies covering the visual modality in courtship of birds (see e.g.: Brockway, 1964; Abbassi & Burley, 2012; Polverino et al., 2012) and I found no study that compared FD and MD visible courtship displays in budgerigars. Brockway's ethological studies include detailed descriptions of budgerigar's FD courtship behavior (Brockway, 1964). Abbassi and Burley investigated MD courtship, by examining male reproductive success dependent on the budgerigars' relative participation in same-sex activities (Abbassi & Burley, 2012). Polverino and colleagues observed that budgerigars sometimes direct behaviors included in courtship towards inanimate objects like perches and that budgerigar's courtship behaviors are often modified by spatial limitations (Polverino et al., 2012). The intention of my study was therefore to examine both FD and MD visible courtship behavior of budgerigars.

In order to be able to distinguish courtship behaviors from other behaviors, the nature of other behaviors must additionally be considered. I found detailed descriptions of both reproductive and non-reproductive behavior of budgerigars in Brockway's ethological studies (1964; 1964b; 1974) that helped me to discriminate between relevant behaviors included in courtship (see *Methods*) and behavior occurring in non-reproductive context, which were not analyzed in this study. Non-reproductive behavior ranges from reciprocal preening to scratching, stretching, shaking, yawning, foot & bill care and movements involved in agonistic context (Brockway, 1964b). Behaviors included in budgerigar's courtship can often look similar to movements involved in non-reproductive context, especially movements involved in agonistic interactions. For example, bills collide during agonistic encounters in bill thrusting and during courtship in nudging (Brockway, 1964b; Brockway, 1964). In general, budgerigars are rarely observed interacting in agonistic contexts (Brockway, 1964b). However, when they do perform agonistic behaviors, female budgerigars are the more prominent part in initiating

aggressive behavior to their conspecifics, either to members of the opposite or the same sex (Brockway, 1964b; Hile et al., 2005). As opposed to bill thrusting, bill gaping occurs when the bill is held open during the whole agonistic interaction with another individual. An agonistic encounter typically ends up with bill gaping and is followed by one individual turning away (Brockway, 1964b). The held open bill during an encounter indicates agonistic behavior, while the bill is typically shut during nudging movements in courtship. Nudges are more often repeated than colliding movements in bill thrusting, which helps to discriminate between agonistic and courtship behavior (Brockway, 1964b; Brockway, 1964).

Male-directed Courtship Behavior

To my knowledge, there are only a few studies in evolutionary biology that capture the functions, causes and consequences of courtship behavior directed to the same sex (see e.g.: MacFarlane et al., 2006; MacFarlane et al., 2010; Abbassi & Burley, 2012). While Brockway focused mainly on female-directed courtship behavior (1964), Abbassi and Burley related male-directed courtship to the male's mating success for a first investigation of possible functions concerning same-sex activities in budgerigars (2012). The authors observed that similar courtship behaviors occur in the MD context, as in the FD context (Abbassi & Burley, 2012). What has not yet been studied is, if the sex of the receiver affects the duration of courtship displays and if the structure of MD courtship displays differ from those that are directed to females. Due to this lack in the literature, I wanted to fill this gap by comparing the structure of MD and FD visual courtship displays in my study.

Many posed hypotheses can be found in the literature that give explanations for same-sex courtship activities (reviewed by Bailey & Zuk, 2009). Abbassi and Burley (2012) focused on one hypothesis that may explain same-sex behaviors, the “Courtship practice” hypothesis. This hypothesis predicts an improvement of courtship or copulatory skills as an explanation for same-sex activities. The authors also took a “confidence” variant of the “Courtship practice” hypothesis into account. This variant suggests that practice with conspecifics of the same sex supports individuals to overcome their fear of being rejected by females when making courtship invitations. Abbassi and colleagues rejected the “Courtship practice” hypothesis as male relative participation in same-sex activities had no influence on the mating success, although they authors suggested that this hypothesis is quite plausible because of the social organization in budgerigars. As an alternative explanation for same-sex interactions the authors suggest the “leadership assessment hypothesis” in the role of foraging decisions. Budgerigars are more protected while foraging on the ground in flocks than foraging on their own. Abbassi and colleagues observed that males vary in their propensity to lead the flock to the ground. The authors suggest that MD behaviors included in courtship give the male the opportunity to assess leadership qualities of other males. The reason why budgerigars should follow leaders in foraging over others might be that “preferred leaders” may be predominant food finders or provide a feeling of safety because of extraordinary risk-assessment abilities (Abbassi & Burley, 2012).

Structure of Courtship displays

Visible courtship behaviors are linked to elements of budgerigar’s courtship song (Brockway, 1964; Tobin et al., 2017). Though the structure of MD versus FD visible courtship sequences were not yet been studied, the structure of warble song depending

on the sex of the receiver was already examined by Tobin and his colleagues (Tobin et al., 2017). Warble song is used by budgerigars while courting and specific acoustic structure in bird song can be correlated with specific behavioral functions (Tobin et al., 2017). The authors found that FD warble element types are more consistent in their sequential organization than MD warble in budgerigars. Females may prefer consistency in warble song to assess a male's overall quality or cognitive abilities. The authors additionally calculated structural parameters like the total duration of a warble bout, the total number of elements in warble bouts and the Shannon diversity index for analyzing the structure of warble song depending on the sex of the receiver. Concerning these parameters, the authors found no structural differences between FD and MD warble bouts (Tobin et al., 2017).

Previous studies observed that similar courtship behaviors occur in the FD and in the MD context (Abbassi & Burley, 2012). As MD courtship cannot lead to reproduction as FD courtship in budgerigars, it is still not clear what the function of MD behavior is and if visible courtship displays between males last equally long and are organized similarly compared to male-female courtship displays in budgerigars. I hypothesize that the sex of the receiver has an effect on the duration of visible courtship displays and that there are structural differences between FD and MD courtship in general, as visible courtship behaviors are linked to elements of budgerigar's courtship song and previous studies found an effect on the vocal part of courtship in budgerigars (Brockway, 1964; Tobin et al., 2017). Although studies found no effect on the warble song duration, there could be differences in visible courtship duration if FD and MD courtship displays have different functions. To examine my hypothesis, I studied recordings of two bird colonies and labeled 6 different courtship behaviors based on Brockway's ethological studies (Brockway, 1964; Brockway, 1974). In order to determine whether the sex of the receiver

affects the structure of courtship displays or not, I extracted FD and MD courtship sequences initiated by 9 male budgerigars from the behavioral observations. To predict structural differences between FD and MD courtship sequences, I considered similar parameters like Tobin and colleagues (2017) such as the total duration and total number of behavioral elements in a sequence, the Shannon diversity index and the proportion of each courtship behavior type in a sequence. Brockway additionally suggests that the sequential organization of courtship displays in budgerigars is complex and transitions of courtship behaviors within a display are not clear (Brockway, 1964). She claimed in 1974 that pumping never precedes nudging and another courtship behavior, bill-hooking, never precedes nudging or pumping. Because of previously mentioned complexity in the transitions of courtship behaviors, I described the behavioral transitions within a sequence to show if there are differences in FD versus MD courtship.

I used the total duration and other structural parameters of a courtship sequence to compare FD and MD courtship displays, because the courtship structure can vary greatly (reviewed by Mitoyen et al., 2019). Courtship duration can range a lot, for example budgerigar's behaviors like nudges, pumps and head-bobs that occur in courtship sequences can vary greatly in their number and rapidity (Brockway, 1964). Brockway described in her ethological studies durations of single behaviors (1964), but to my knowledge it was not yet examined how long courtship displays in budgerigars last, either FD or MD ones. Due to this, I wanted to draw generalizations on the courtship sequence duration with a mixed model. Because of the within-individual variation in the sequence durations and singularity issues in my mixed model, I decided for a chi square test of independence for the behavioral transitions and to use non-parametric, paired statistical tests for the other structural parameters to give an insight into structural differences of FD versus MD courtship displays.

Material and Methods

Courtship Behavior of the Budgerigar

For the analysis of the audience effect on the structure of visible courtship displays I used video recordings to code courtship behaviors of the budgerigar (see *Table 4*). Descriptions of these behaviors are based on Brockway's ethological studies (Brockway, 1964; Brockway, 1974), the detailed version can be found in the *Appendix*.

Table 1. Ethogram.

Courtship behavior (coded as state events)	Description (including start and stop of behavior)
Head-shaking	Shaking limited to the head Start: Movement of head Stop: Head in straight position again
Head-bobbing	Head moves up and down in circular movement Start: first move of head (up or down) Stop: Head turns away
Nudging	Head darts out sharply, bills touch sometimes Start: Facing and approaching to another individual Stop: Gaze averted
Pumping	Head and neck move up and down, no circular movement Start: beginning of head movement (up or down) Stop: Gaze averted
Bill-hooking	Bird pulls on tip of maxilla of another bird, performed on one side or both sides of maxilla Start: Facing and approaching to another individual Stop: Gaze averted
Courtship feeding	Bills of two birds are arranged for food exchange Start: Bills touch each other Stop: bill contact ends

The discrimination between the sexes was important for my observations. In order to correctly differentiate between the sexes of adult individuals, I considered the sexual dichromatism of cere, leg and the foot color. On the one hand, ceres, legs and feet of adult males are bluish. On the other hand, the cere of adult females vary from faded to dark brown, while legs and feet are pinkish (Brockway, 1964).

Data

Using the video recordings, I coded 6 courtship behaviors (courtship feeding, head-bobbing, nudging, pumping, bill-hooking, head-shaking) initiated by male budgerigars.

In total I coded 72 videos that were recorded by three different individuals in the time span from April 2017 to July 2021. The 72 video durations ranged from 36 seconds to 12 minutes and 3 seconds. The total observation time amounts to approximately 8 hours (8h, 6min, 41s).

Two independent colonies were recorded. Colony 1 consists of 15 individuals in total across all recording times, the number of recorded individuals varied during data acquisition because individuals would die or new individuals would be added to the colony to keep the sex ratio balanced. Colony 2 is comprised of 6 individuals with a balanced sex ratio. The colonies were independent, housed in two separated, non-adjacent rooms at the University of Vienna in the Department of Cognitive Biology. They had no visual, acoustic or physical contact to each other. In May 2021, both colonies moved to the Acoustics Research Institute (ARI) of the Austrian Academy of Sciences. Even during the move, the two colonies had no visual, acoustic or physical contact to each other (or to any other budgerigars).

Video Recording & Equipment

All individuals were recorded in their aviaries (Colony 1 aviary: $2.5 \times 2 \times 2$ m; Colony 2 aviary: $2 \times 1 \times 2$ m). Both colonies were housed in separate rooms lined with acoustic foam padding (Basotect 30 Plain) which served to reduce outside noise and echo in the room. Videos were recorded with 30 to 60 frames per second with a GoPro Hero 4 or a GoPro Hero 8. Videos that were recorded with the GoPro Hero 4, the camera was installed on the top of a Sennheiser directional shotgun microphone (Mann et al., 2021). A microphone was used here in addition to the video camera, because these videos stem from acoustic analysis projects (see for example: Mann et al., 2021). After the move in May 2021, 15 of the total 72 videos were recorded in the Acoustics Research Institute (ARI) of the Austrian Academy of Sciences. I used a GoPro Hero 8 which recorded 60 frames per second. The ranging frame rates do not affect the results of my study, because even the duration of the observed shortest behavior (head-shaking) could be detected at 30 frames per second, as I observed that this behavior lasts 0.1 second on average. All recorded budgerigars were familiar with the presence of a human with recording equipment in their social environment (Mann et al., 2021). The purpose of this habituation was to record the colony showing behavior that comes as close to their naturalistic performance as possible. Videos were recorded from different angles of the cage to capture as many individuals performing courtship behavior as possible.

I used the program BORIS for coding the courtship behaviors. BORIS (Behavioural Observation Research Interactive Software) is a free, open-source program for video- and audio-coding (Friard & Gamba, 2016). BORIS was well suited for my study because it allows users to create a project-based ethogram, to code the start and stop frames of state events and to define subjects within the project (Friard & Gamba, 2016). To detect the frequency and correct duration of courtship behaviors, I only included courtship

behaviors in the coding process where I was sure that I captured the entire courtship display. Each of the coded behaviors was recorded as a state event including start and stop frame (Martin & Bateson, 1993).

Sequence Division

Courtship behaviors initiated by 9 male budgerigars were coded as described in my ethogram. One male from Colony 2 was excluded from analysis because I did not observe him performing courtship behavior. For the analysis of courtship displays, I needed to extract sequences from the longer behavioral observations.

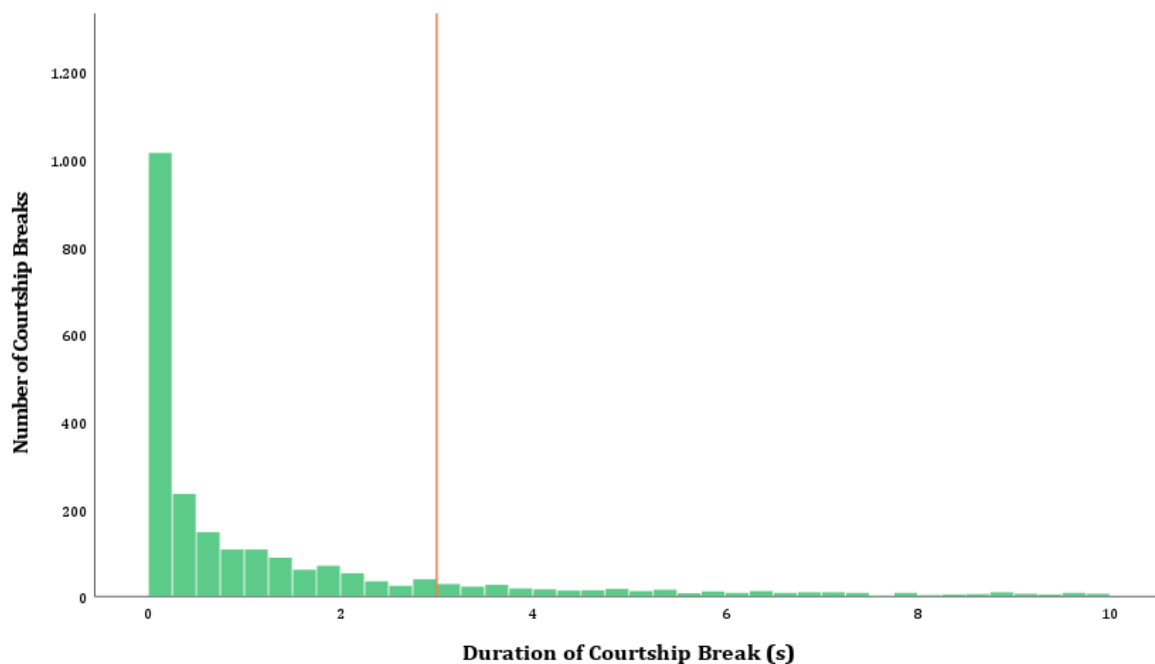


Figure 1. Histogram of courtship breaks (N = 2284 of 9 male individuals) plotted with their duration.

I calculated the pause durations between observed courtship behaviors for each male. The pause duration ranges from 6 milliseconds to over 10s. To distinguish objectively between pauses within a sequence and pauses that divide two sequences from another, I plotted these courtship breaks (N=2284 breaks; see *Figure 1*) and followed a method

similar to Farabaugh and colleagues when extracting syllables from warble songs (Farabaugh, Brown & Dooling, 1992). Behaviors belong to one sequence, if the break between one behavior and the next is less than or equal 3 seconds. I chose 3 seconds as a cut-off (see *Figure 1*) because it is the closest integer that contains approximately 89% of the data, with 89% as a reasonable estimate in the Bayesian framework (see for example: Makowski, Ben-Shachar, Lüdecke, 2019; Makowski, Ben-Shachar, Chen, & Lüdecke, 2019). As such, when a male budgerigar shows no courtship behavior for longer than 3 seconds, I considered the sequence to have ended.

Statistical analysis

I conducted the analysis with R version 4.1.1, SPSS version 1.0.0.1406 and Excel version 2018 (R Core Team, 2021; IBM Corp., 2017; Microsoft Corporation, 2018). The sequence durations were calculated with Excel, using the difference between the end of the last behavior and the start of the first behavior in a sequence (i.e. containing all behaviors and courtship breaks in a sequence).

Bayesian Model

To draw generalizations about the effects of the audience on the structure of visible courtship displays, I fit a Generalized Linear Mixed Model (GLMM). I used a mixed model because each individual has more than one observation in the dataset. I used the R package `lme4` (Bates et al., 2015) and used sequence duration as the response variable and the sex of the receiver as a predictor variable. I log-transformed the duration data so that the residuals would be normally distributed. I included individual as a random effect. I started with a maximal model; so, I included random slopes, random intercepts, and the

correlation between them. I removed the correlations between both random intercepts and slopes to reduce the complexity in my model, but this did not solve the issues with singularity. Further simplifying of the random effect structure by removing the random slopes was not an option since in this model the slope is the difference between male- and the female-directed group. It does not seem biologically valid to allow the FD courtship displays (the intercept) to vary by individual, while not permitting the difference between the male and female directed courtship displays (the slope) to vary by individual.

Because I could not further simplify the model, I decided to use Bayesian methods to estimate the model parameters. Bayesian methods permit prior knowledge, called “priors”, to narrow the range of possible estimates (van Doorn et al., 2021) and are recommended to deal with singularity issues (Bates et al., 2015). I used the R package `brms` to fit the model (Bürkner, 2017). I defined weakly informative priors by setting the log-transformed durations of both the FD- and MD-group as normally distributed, centered around 0 (exponentiated = exp.: 1 second) and with a standard deviation of 1.5 (exp.: 4.48 seconds) (Bürkner, 2017). I also set the intercept (the mean of the reference group, here the FD courtship duration) to 0 to give both groups (FD and MD) the same prior structure. There is no reason that there is more uncertainty in courtship duration for the MD group than for the FD group in this case. Additionally, two non-flat priors (`student_t(3, 0, 0.5)`, `class = 'sd'`; `student_t(3, 0, 1)`, `class = 'sigma'`) were chosen by the `brms` package and I left them in the default setting.

Back to the original scale and showing realistic, non-log-transformed values, the prior distribution of both FD and MD courtship duration is centered around 1 second with a standard deviation of approximately 4.48 seconds. Two standard deviations would come up to around 20 seconds of courtship, this is probably longer than I would expect, but is still narrow enough to rule out unreasonable estimates. Typically, the priors should

be chosen before seeing the data (van de Schoot et al., 2014) but published information about Nudging/Pumping durations (that last about 1 to 2 seconds) in Brockway's ethological studies (Brockway, 1964) is consistent with my own knowledge about the typical range of budgerigar courtship durations. I left the two non-flat priors to the defaults, as I found no other sources than Brockway's in the literature that give information about courtship duration in budgerigars and the priors were broad enough to reflect this uncertainty.

With the `brms` package I ran a prior predictive check with 1 chain and 5000 iterations using the programming language *Stan* (Bürkner, 2017; Stan Development Team, 2017) to make sure the priors gave reasonable estimates. Prior predictive distribution plots of both the FD- and MD-group can be found in the *Appendix* (see *Figure 2*). Model diagnostics and post predictive checks can be found in the section *Results*.

I used Bayes factor to compare the full- and the null-model for a quantification of an audience effect in the sequence duration (van Doorn et al., 2021). The Bayes factor is the likelihood of the full-model given the data over the null-model given the data, by including the prior information. A value over 1 represents more support for the full-model and with a value under 1 more support is gained for the null-model (van Doorn et al., 2021). Bayes factors over 10 and under 0.1 respectively are considered to indicate strong evidence for favoring one model (van Doorn et al., 2021). In contrast to the full-model, the null-model is missing the predictor variable of interest (here the sex of the receiver). If the output of both models looks similar, the resulting Bayes factor would favor the null- over the full-model (van Doorn et al., 2021). And this would suggest that the sex of the audience has no effect on the response variable (here the sequence duration).

Descriptive and Frequentist Statistics

To further compare the structure of FD and MD courtship sequences, I took the following additional parameters: the total number of single behaviors counted in a sequence, the action and pause duration (combined together it reveals the sequence duration), and the Shannon-Index. The action duration is the total time of active courtship performance within a sequence, meaning the sum of the duration of every single behavior occurring in a sequence. The pause duration within a sequence was calculated as the difference of the sequence duration and the action duration, meaning the total time of inactivity in a sequence. I calculated the proportions of each courtship behavior type in a sequence and the Shannon-Index, an index used for the estimation of the diversity in a sequence.

I described the transitions of courtship behaviors occurring in a sequence to show structural differences of FD versus MD courtship. Each behavioral transition within a sequence was documented for 378 FD sequences and 156 MD sequences performed by 9 male individuals. To show how probable one behavior is followed by the next, I took all 36 possible transitions of the 6 coded courtship behaviors into account, repetitions included. If one assumes that each of the 36 transitions is equally likely to occur, the probability of each transition would be expected by 2.8%.

Due to time constraints and because very little research has been conducted on budgerigar courtship displays, I used simpler statistical tests to evaluate the other structural parameters including the behavioral transitions. To support the description of the total number of single behaviors counted in a sequence, the action and pause duration and the Shannon-Index, I conducted paired Wilcoxon signed-rank tests. Concerning the behavioral transitions, I used a chi square test for independence with an alpha level of 0.05 to see if the distribution of FD and MD behavioral transitions in general differ from

each other. To indicate which transitions could be responsible for the difference in probability distributions, I tested all transition types for each condition with the calculation of the binomial probability. The binomial probability states how probable the observed number of transitions for one transition type conforms exactly to the expected value in a specific number of trials. I used an alpha level of 0.05 (Bonferroni-correction: 0.0007); binomial probabilities which undercut the Bonferroni-corrected value were marked as statistically significant. These data will permit us to form clearer hypotheses about budgerigar courtship behavior in subsequent experiments.

Results

After dividing the behavioral observations, they result in 534 sequences in total. Those 534 sequences were initiated by 9 of 10 males, 378 of them were FD and 156 MD (see *Table 4*). Individuals varied in the number of interaction partners (see *Table 5* in *Appendix*).

Table 4. Male budgerigars with the number of sequences observed, divided in sex of the receiver.

Initiator	Number of Sequences	
	FD	MD
Afina	62	9
Bender	40	2
Darwin	49	7
Elvis	28	5
Hedwig	1	16
Mercury	197	38
Puck	1	40
Topaz	0	27
Woody	0	12
Total	378	156

Sequence Duration and Bayesian Model

I calculated the mean sequence duration for the 9 male individuals, dependent on the sex of the receiver (see *Figure 3*). The data was imbalanced because 5 males showed more sequences directed to females, 2 males more to males and 2 other males courted only each other (see *Table 4*). The FD mean sequence duration ($N = 7$) ranged from 0.9 s to 6.57 s with a median score of 3.92 s. The MD mean sequence duration ($N = 9$) showed a median score of 3.32 s and ranged from 0.96 s to 4.43 s.

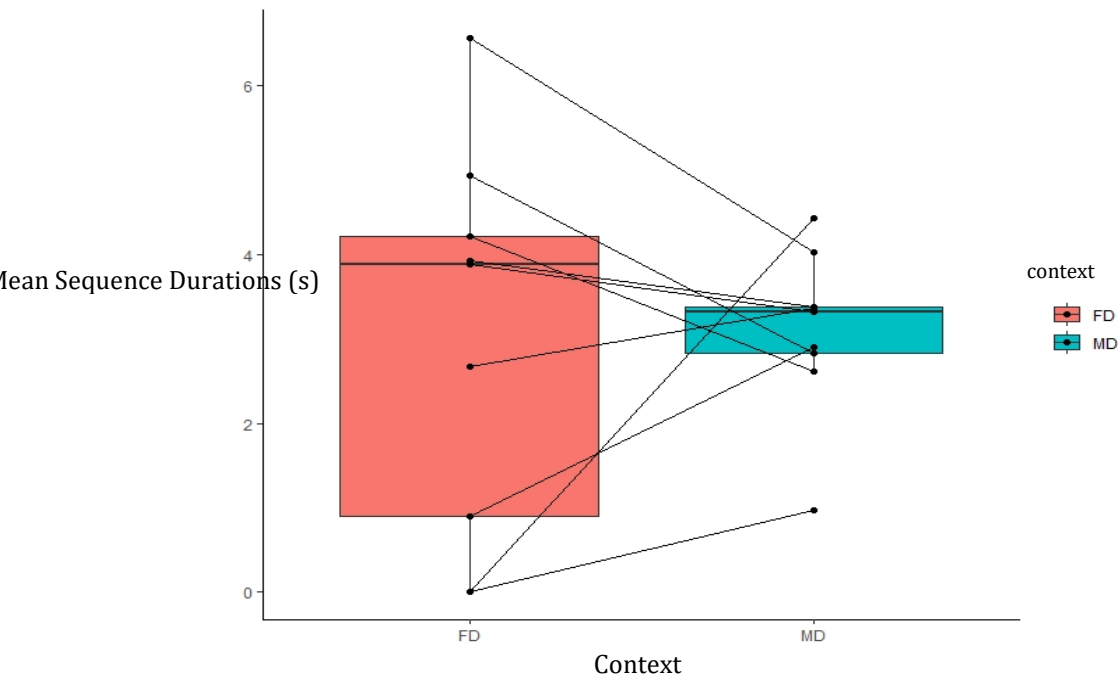


Figure 3. Boxplot of the mean sequence duration (in s; $N_{FD} = 7$; $N_{MD} = 9$) from 9 male individuals grouped by the sex of the receiver (FD = female-directed; MD = male-directed).

To see if there is an audience effect on the duration of a sequence, I fit a GLMM. The model was singular, it could not estimate any individual differences for the intercept, i.e. the mean of the “reference”-group (here the FD courtship). Due to these singularity issues, I used Bayesian methods to fit the model. In the Bayesian model, I used Hamiltonian Monte Carlo Markov Chains (4 chains) to estimate the model parameter posterior distributions. I did not get any warnings about divergences, the convergence was calculated with the *PSR* (Potential Scale Reduction Factor). The chains reached an appropriate convergence criterion ($PSR = 1.00$) in 5000 iterations. Due to this, I also checked *Rhat*, which did not go beyond 1.00.

Posterior predictive checks were conducted by visual inspection of posterior sample plots. In the figure below (Figure 4) the observed data (y) was plotted with the posterior estimates from the model (y_{rep}). The same was done with the mean and standard

deviation (see *Appendix*, Figure 5). The model stability was estimated using the function `loo`, the model shows no “high-leverage” points (see *Appendix*, Figure 6).

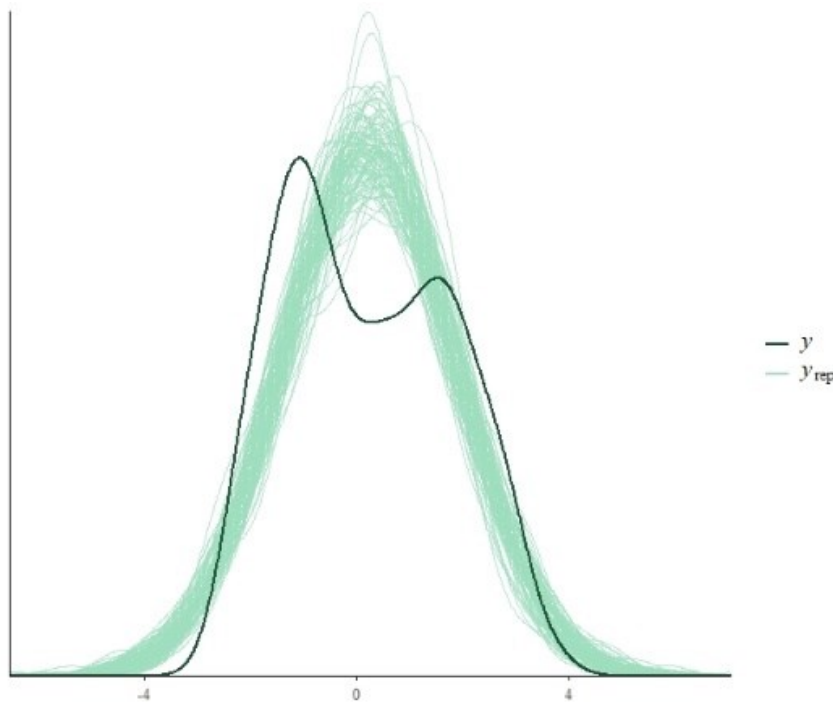


Figure 4. Posterior predictive check ($N_{\text{samples}} = 100$; y = actual data; y_{rep} = model posterior estimates); the bimodal peaks in this graph indicate that the model estimates cannot predict the entire observed data and are less reliable for general statements.

The final model follows Gaussian distribution and was sampled with 4 chains, each with 5000 iterations. Data includes 534 observations (i.e. sequence durations) from 9 male individuals, durations (log-transformed) were grouped by the sex of the receiver.

Table 6. Posterior Estimates (for log-transformed and exponentiated duration) divided by context.

Context	PCE (log)	PCE (exp.)	Estimation Error (log)	Estimation Error (exp.)	95% - CI (log)	95% - CI (exp.)
FD	0.27	1.3	0.12	1.13	0.04 – 0.49	1.04 – 1.63
MD	0.07	1.07	0.16	1.17	-0.24 – 0.41	0.79 – 1.51

The posterior coefficient estimate (PCE) for the female-directed, log-transformed sequence duration amounts to 0.27 (exp.: 1.3) with an estimation error of 0.12 (exp.: 1.13), and for the MD log-duration to 0.07 (exp.: 1.07) with an estimation error of 0.16 (exp.: 1.17) (see *Table 6* below, *Figure 7* in *Appendix*). 95% - credible interval (CI) for FD log-duration ranges from 0.04 to 0.49 (exp.: 1.04 to 1.63) and for MD log-duration from -0.24 to 0.41 (exp.: 0.79 – 1.51) (see *Figure 8*). The estimates of the two groups (FD & MD durations) show an overlap. The 95%-credible interval (or Posterior Probability Interval *PPI*) for the FD- is smaller than for the MD-context, which can also be seen in *Figure 8*, resulting in a more pronounced peak in the posterior estimates for FD.

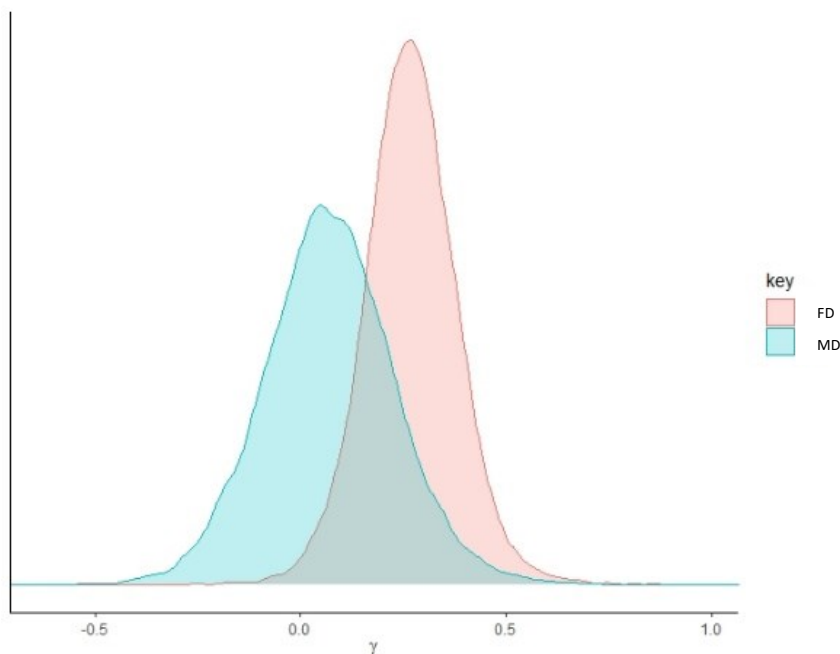


Figure 8. Posterior coefficient estimates: graph shows that estimates from both conditions overlap.

A full-null model comparison using the function `loo_compare` results in an estimated Bayes factor of 0.04263 which means that the data is 25 times more probable under the null hypothesis (that there is no effect) than under the alternative hypothesis.

Other Structural Parameters

Apart from the total duration of a sequence, some other structural parameters were calculated for each of the 534 sequences: the total number of courtship behaviors, the action and pause duration, the Shannon Diversity Index and the proportions of each courtship behavior type in a sequence. For these parameters their range and percentiles were considered to give an insight into potential structural differences in FD sequences compared with MD sequences (see *Table 7* as excerpt; detailed version: see *Table 8* in *Appendix*).

For testing any differences in these parameters, I calculated the median value for 7 male individuals for FD and MD courtship sequences and conducted paired tests by using Wilcoxon signed rank tests with a significance level of 0.05 to compare the two conditions (see *Table 9* in *Appendix*). 2 males were excluded in these tests because they showed no FD sequences. One parameter, the proportion of courtship feeding, was excluded from testing as the median value for both FD and MD sequences for all 7 individuals was 0. I can draw information from the data about structural differences depending on the sex of the receiver, but these results refer only to a small sample of budgerigars and I have to draw generalizations cautiously.

The total number of behaviors showed with 41 a lower range in FD sequences than in MD sequences with 66 but a higher value (7) in the third percentile (= Q_3) than 5 in MD sequences. The Wilcoxon signed rank test showed no significant difference in median scores for this parameter ($p = 0.7874$; $n = 14$).

The pause duration range was smaller in FD sequences compared to MD sequences, 23.39 to 32.25, but showed a higher value in Q_3 of 3.04 than 1.30 in MD sequences. A Wilcoxon Signed-Ranks test indicated that the median score of MD

sequences (Mdn = 0) was not significantly lower than those of FD sequences (Mdn = 0.08) ($p = 0.5541$; $n = 14$).

The Shannon Diversity Index was marked with a higher range of 1.64 in FD sequences than of 1.28 in MD sequences. Wilcoxon signed rank test results of no significant differences in median scores for this parameter ($p = 0.8551$; $n = 14$).

FD sequences showed a not significantly lower median score of 0.5 in the proportion of nudging, compared to MD sequences with a median of 0.73 (Wilcoxon test: $p = 0.2719$; $n = 14$).

When looking at the third percentile, the proportion of head - shaking was higher in FD sequences with a value of 0.25, while MD sequences had a value of 0 in Q_3 . The other measurements did not vary in this case.

Table 7. Excerpt of descriptive statistics for structural parameters (detailed version, see *Appendix*).

	<i>Number of Behaviors</i>	<i>Pause Duration (s)</i>	<i>Shannon Index</i>	<i>Prop. of Nudging</i>	<i>Prop. of Head-shaking</i>
Range					
FD	41	23.39	1.64	1.00	1.00
Range					
MD	66	32.25	1.28	1.00	1.00
Q₁					
FD	1	0.00	0.00	0.00	0.00
Q₁					
MD	1	0.00	0.00	0.00	0.00
Q₂ / Median					
FD	2	0.08	0.00	0.5	0.00
Q₂ / Median					
MD	2	0.00	0.00	0.73	0.00
Q₃					
FD	7	3.04	0.69	1.00	0.25
Q₃					
MD	5	1.30	0.67	1.00	0.00

Behavioral Transitions

In total there were 1822 FD transitions and 638 MD transitions. I hypothesized that the sex of the receiver affects the structure of courtship sequences, among other parameters the behavioral transitions. All theoretically possible transitions were observed at least in FD or MD sequences (see Table 10 & Table 11), except from head-shaking followed by courtship feeding.

A chi square test of independence was conducted with an alpha level of 0.05 to test if there is an association between the sex of the receiver and the distribution of the transitions. One transition type (head-shaking followed by courtship feeding) was not observed in my study, so I took the chi square test statistics and the critical value depending on the degrees of freedom to give a statement about the statistical significance. The test statistics was greater than the critical value ($100.8 > 49.8$), which means that there was a statistically significant difference between the distributions of FD and MD transitions, $X^2(35, n = 2460) = 100.8$.

The repetition of nudging showed the highest, statistically significant difference from 2.8%, with +35.4 in FD and +39.5 in MD sequences (both receiver sexes with a binomial probability of $p < 0.0001$). Nudging tended to be the most common first member in a transition-pair in general for both receiver sexes. The transition from nudging to courtship feeding was statistically significant less common than expected for both receiver sexes (see Table 10 & Table 11; both receiver sexes with a binomial probability of $p < 0.0001$). The transition from nudging to pumping was with 3.6% more common than expected in FD sequences and with 1.6% less common than expected in MD sequences but both were statistically not significant (see Table 10 & Table 11).

The repetition of pumping occurred less common than expected for both receiver sexes (see *Table 10 & Table 11*; both receiver sexes with a binomial probability of $p < 0.0001$).

The transition from pumping to bill-hooking occurred statistically significant less common than expected in FD sequences (see *Table 10*). Pumping followed by head-shaking was statistically significant less common than expected concerning both receiver sexes (see *Table 10 & Table 11*). The transition from pumping to head-bobbing was statistically significant less common than expected concerning both receiver sexes (see *Table 10 & Table 11*; both conditions with a binomial probability of $p < 0.001$).

Bill-hooking followed by pumping, to courtship feeding and to bill-hooking itself was statistically significant less common than expected for both receiver sexes (see *Table 10 & Table 11*; both receiver sexes with a binomial probability of $p < 0.0001$). The transition to head-bobbing was statistically significant less common in FD and MD sequences (see *Table 10 & Table 11*; both receiver sexes with a binomial probability of $p < 0.0001$). The transition to nudging occurred statistically significant more common than expected for MD sequences (see *Table 11*).

Head-shaking followed by pumping or bill-hooking occurred less common than expected concerning both receiver sexes (see *Table 10 & Table 11*; both receiver sexes with a binomial probability of $p < 0.0001$).

The transition from head-bobbing to head-shaking and to head-bobbing occurred less common than expected for both receiver sexes (see *Table 10 & Table 11*; both receiver sexes with a binomial probability of $p < 0.001$).

The transition courtship feeding to bill-hooking and the repetition of courtship feeding were less common than expected concerning both receiver sexes (see *Table 10* & *Table 11*; both receiver sexes with a binomial probability of $p < 0.001$).

Table 10. Transition probability matrix for FD courtship behaviors, occurring percentages & binomial p -value in brackets; binomial cut-offs: $p < 0.0001 \rightarrow$ red, $p < 0.0007 \rightarrow$ orange, $p < 0.01 \rightarrow$ yellow, $p > 0.01 \rightarrow$ green.

Probability of Next Behavior in FD courtship							
Initial Behavior in FD courtship		Nudging	Pumping	Bill-hooking	Head-shaking	Head-bobbing	Courtship feeding
	Nudging	35.4% (<0.0001)	3.6% (0.0063)	5.8% (<0.0001)	4.1% (0.0004)	1.8% (0.0017)	0.2% (<0.0001)
	Pumping	4.0% (0.0006)	5.6% (<0.0001)	0.5% (<0.0001)	1.0% (<0.0001)	0.2% (<0.0001)	4.3% (<0.0001)
	Bill-hooking	2.8% (0.0566)	0.8% (<0.0001)	0.3% (<0.0001)	1.7% (0.0007)	0.6% (<0.0001)	0% (<0.0001)
	Head-shaking	3.8% (0.0026)	1.2% (<0.0001)	0.5% (<0.0001)	8.5% (<0.0001)	1.7% (0.0007)	0% (<0.0001)
	Head-bobbing	2.2% (0.0170)	0.5% (<0.0001)	0.5% (<0.0001)	0.3% (<0.0001)	0.3% (<0.0001)	2.3% (0.0213)
	Courtship feeding	0.6% (<0.0001)	3.1% (0.0424)	0% (<0.0001)	0.3% (<0.0001)	1.3% (<0.0001)	0.1% (<0.0001)

Table 11. Transition probability matrix for MD courtship behaviors, occurring percentages & binomial p -value in brackets; binomial cut-offs: $p < 0.0001 \rightarrow$ red, $p < 0.0007 \rightarrow$ orange, $p < 0.01 \rightarrow$ yellow, $p > 0.01 \rightarrow$ green.

Probability of Next Behavior in MD courtship							
Initial Behavior in MD courtship		Nudging	Pumping	Bill-hooking	Head-shaking	Head-bobbing	Courtship feeding
	Nudging	39.5% (<0.0001)	1.6% (0.0153)	8.6% (<0.0001)	3.3% (0.0674)	2.0% (0.0524)	0.5% (<0.0001)
	Pumping	2.0% (0.0524)	8.9% (<0.0001)	0.8% (<0.0001)	0.5% (<0.0001)	0.3% (<0.0001)	3.4% (0.0545)
	Bill-hooking	6.3% (<0.0001)	1.1% (<0.0001)	0.2% (<0.0001)	1.1% (0.0018)	0.8% (0.0002)	0.3% (<0.0001)
	Head-shaking	2.7% (0.0955)	0.3% (<0.0001)	0.2% (<0.0001)	3.7% (0.0310)	0.8% (0.0002)	0% (<0.0001)
	Head-bobbing	2.4% (0.0808)	0.3% (<0.0001)	1.3% (0.0041)	0% (<0.0001)	0.3% (<0.0001)	1.4% (0.0084)
	Courtship feeding	0.5% (<0.0001)	2.8% (0.0949)	0.5% (<0.0001)	0.3% (<0.0001)	0.9% (0.0007)	0.5% (<0.0001)

Discussion

This project addressed the question whether the sex of the receiver (i.e. the audience) affects the structure of visible courtship behavior of budgerigars. First, I tested the effect on the sequence duration by fitting a multi-level model with Bayesian methods. The model posterior estimates from both FD (female-directed) and MD (male-directed) overlap, suggesting that an absence of an effect on the duration of courtship is more probable than the presence of an effect. This is in line with studies of the audience effect on the warble song structure of budgerigars, where Tobin and colleagues did not find any significant effects in compositional measures like the total duration and the proportions of element types (Tobin et al., 2017). Nevertheless, posterior predictive plots show bimodal peaks in the actual data; the imbalance of my dataset or the missing of explanatory variables like the bonding level between colony members might be responsible for that. The posterior estimates of the model could not explain the entire actual, observed data in my study and the model outcomes are therefore less reliable. Due to this uncertainty, generalizations about an audience effect on the duration of courtship sequences in budgerigars are limited.

To avoid issues at testing the other structural parameters, I described and supported them by conducting frequentist statistics. This serves to give further insights into the structural differences between FD and MD courtship sequences. I found several differences in the behavioral transitions. There was a statistically significant relation between the sex of the receiver and the probability distributions of the transitions. My data points were not independent, so the calculated chi square test serves as demonstration of testing an effect of the receiver sex on behavioral transitions. The significant difference found in the transitions is linked to findings of Tobin and colleagues

on the sequential organization of warble element types. The authors found out that there is less variation in elemental ordering of FD warbles (Tobin et al., 2017) but the calculation of the diversity index during my study results of no statistically significant difference in variation of FD and MD sequences.

Concerning the compositional measures like the proportion of courtship behavior types, the number of behavioral components in a sequence or the sequence diversity, I found several differences when describing these other structural measures of FD and MD sequences. While these differences were not statistically significant, the tests run on these data do not provide any insight as to whether the null hypothesis (means that there is no difference) is more likely than the alternative hypotheses or whether the study is underpowered, and the effect size is too small for the sample size. However, the direction of the differences in the sample are consistent with other findings in the literature and are discussed in more detail below.

FD sequences tend to contain more behavioral components, but statistical tests showed no significant difference between the two conditions. This finding is consistent with research suggesting that males want to impress females with multiple-component displays that are energetically more costly than single-component displays and give females the chance to assess their quality (Byers, Hebets & Podos, 2010). The duration of pauses in a sequence was mostly longer in FD-context. Abbassi and colleagues claimed that males often hesitate in interaction with potential mates, and this could indicate insecurities or a “fear” to be rejected by the female (Abbassi & Burley, 2012). The longer pauses in FD sequences could arise from these insecurities of the male. These insecurities could be mitigated by practicing with other males supporting the “confidence” variant of the courtship practice hypothesis (Abbassi & Burley, 2012). Another structural difference I found was the proportion of head-shaking, though statistical results were not significant.

Head-shaking is a sign of courtship invitation and serves to appease females, as they respond less aggressively to this behavior than to others (Brockway, 1964). In my study head-shaking was more prominent in FD sequences than in MD sequences. My results go in a direction that would support Brockway's findings and together with future studies examining the structure of budgerigar courtship displays I might be able to find support for this observation.

Nudging was the most prominent component observed in the courtship sequences in both FD and MD sequences. This prominence is reflected in the nudging repetitions that occurred significantly more often than expected in courtship sequences, regardless of the receiver sex. The common repetition of nudging observed in my study is in line with Brockway's observations, as she claimed that nudges occur in bouts (Brockway, 1964). I cannot draw inferences to the general population of budgerigars, but these repetitions may serve to attract the attention of a colony member or a potential mate, as multicomponent signals can raise the probability to be perceived by the receiver (Mitoyen et al., 2019). Nudging actions might additionally function to appease the more aggressive females, giving the male a better chance to mount (Brockway, 1964). These repetitions of nudges go along with the repetitive nature of many male mating displays and like any repetition of movements they are energetically more costly than single-component displays (Byers, Hebets & Podos, 2010). Repetitions in general could therefore serve to show the male's quality, giving males a higher chance to be selected by females for reproduction (Byers, Hebets & Podos, 2010). The prominence of nudging in the MD condition could serve as practice for FD courtship which is predicted by the courtship practice hypothesis, while nudging and its repetitions might serve to increase the chance to be seen as a 'preferred leader' by the other flock members which is predicted by the leadership assessment hypothesis (Abbassi & Burley, 2012).

The imbalance of my data set (less than 30% of the sequences were MD) is reflected in the posterior distribution of the actual model and could affect the posterior estimates. Estimated parameters for group FD are less uncertain than other values, because of the smaller range and the taller, pronounced peak in the plot of the posterior distribution (Zyphur et al., 2015). Additionally, the estimated Bayes factor suggests strong evidence for supporting the null hypothesis. This factor cannot be taken to draw all-or-nothing conclusions, as it is the updating factor from prior odds to posterior odds (Doorn et al., 2021). The posterior estimates and the Bayes factor are modified by the priors and can change once the priors are specified (Doorn et al., 2021). The Bayes factor represents, therefore, the relative predictive success of two or more models given the priors, here the null or the full model (Etz et al., 2017).

A greater number of FD sequences in the data set should be expected since courtship is primarily directed towards females, serving to initiate reproduction (reviewed by Mitoyen et al., 2019). It is far from clear what function MD courtship in budgerigars has. Nevertheless, 30% of all courtship sequences is a quite considerable percentage. Same-sex interactions have been documented in over 90 bird species (McFarlane et al., 2010) and budgerigars engage in those interactions more often than many other birds do (Brockway, 1974). Brockway suggested that male budgerigars typically direct courtship behaviors to other males, when females are unavailable (Brockway, 1974). However, the data presented here contradict this observation. For example, two males used for this study (Puck & Hedwig from Colony 1) were observed to initiate courtship nearly exclusively with other males despite this colony was composed of 6 females and 6 males (Puck & Hedwig included). These observations may indicate a preference for the same sex or an insecurity to make courtship overtures to potential mates (Abbassi & Burley, 2012). The courtship practice hypothesis predicts that males

court other males to overcome this insecurity, and that MD courtship serves as practice for FD courtship and is not “real” courtship itself (Abbassi & Burley, 2012) which might explain the majority of MD sequences in Puck & Hedwig’s case.

In addition, two males from the other colony (Topaz and Woody from Colony 2) were observed only courting each other despite being housed with 3 females. These males seem to have a homosexual relationship to each other, as I did not observe them courting any females or any other males. Because of this, it is not clear if their MD courtship should be treated like standard MD courtship for males that also court females or whether it should belong in the same category as FD courtship. The data from Topaz and Woody could therefore reduce the reliability of the model itself because their courtship might have to be categorized differently.

It is also possible that courtship displays are influenced primarily by whether or not two individuals are pair bonded (regardless of whether the bond is hetero- or homosexual) and these bonded displays have a different structure to those displayed by unbonded partners. Courtship serves to initiate reproduction in a large number of species (reviewed by Fusani, 2008) and is needed for pair-formation which occur often in budgerigars of opposite sexes and rarely as homosexual formations (Brockway, 1964). Sequences directed to a bonded partner could affect the outcomes of the used model but defining pairs during the setting of my study was unfortunately not possible. The lack of nestboxes reduces pairbond formation (Brockway, 1964; Brockway, 1974) and I rarely observed mounting attempts and copulations during my data acquisition. The number of copulations (extra-pair copulations occur only rarely in budgerigars) and interactions like preening and courting each other, and the relative time two budgerigars sit closely side by side indicates an existing pair bond (Brockway, 1964; Brockway, 1974; Trillmich, 1976). Providing nestboxes would help to measure these parameters and evaluate a pair

bond between colony members in further studies. In this way it can be examined if the structure of courtship displays is additionally or even stronger affected by the pair bond.

In conclusion, I found an audience effect on the visible courtship of budgerigars, but generalizations are limited. A chi square test of independence results of a significant relation between the sex of the receiver and the probability distributions of the behavioral transitions. As the datapoints in my study were not independent, I will perform permutation tests for the behavioral transitions in further steps to control independence. The description of some compositional parameters indicates a direction of a structural difference between FD and MD courtship, though conducted frequentist statistics showed no significance. The Bayesian model outcome suggests more support for the absence of an effect on the duration of courtship sequences, but the model reliability was reduced. Explanations for these reliability problems could be the imbalance of my dataset or the influence of the bonding level between colony members. I suggest that pair bond formations might play a role in the structure of courtship displays and the consideration of this bonding level in further experiments will give more clarification about the audience effect on the visible courtship of budgerigars.

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Appendix

Detailed Ethogram

Following behavioral descriptions are mainly based on Brockway's ethological studies (Brockway, 1964; Brockway, 1974), additional information includes a reference source. Behaviors are described in the traditional context, as Brockway described behaviors included in courtship as male-initiated and female-directed. Similar behaviors can be observed in male-directed context (Abbassi & Burley, 2012).

1) *Courtship feeding*: this courtship behavior begins with regurgitating food via head-bobbing movements, after that the male's bill is proffered to the female. When the bills are arranged at longitudinally right angles, food exchange follows. Courtship feeding serves to tighten the pair bond. Females are often less receptive to male courtship activities in the beginning. Courtship feeding could be useful for calming down aggressive females, the male could get nearer this way and is maybe able to mount the female.

2) *Head-Bobbing*: A head-bob is characterized by circular movements of the head (by moving the head up and down rapidly), in most of the cases it appears vertical in real-time (Abbassi & Burley, 2012). Withdrawing and pulling motions of the head are combined in this movement (Brockway, 1964).

"Nudging-Pumping actions":

3) *Nudging*: During nudging, the male darts out his head sharply toward the female and sometimes hits the dorsal surface of her maxilla with his own. When the bills make contact with each other, the male's bill is slightly opened. The sound while striking can be easily heard. Brockway claimed that nudging occurs in bouts, with no other behaviors intervening. The mean speed of nudging is about one nudge every 0.48 seconds, the mean

number varies from 3 to 4 in every bout. Nudging can be confounded with head-bobbing, but the emphasis of the movement is here different. In nudging it orients to the bill of another, therefore outward, and in head-bobbing it orients on withdrawal. A bout of nudging ends up with the male facing the female in right angles.

4) *Pumping*: Similar to head-bobbing, the head and neck move up and down often during pumping. Both body parts are held horizontally during this movement. The male is orienting vis à vis from the female, they are then near or almost in contact with the female. After pumping or sometimes during the last few pumps of a series of pumps, the male faces the female in right angles. Brockway claimed that this indicates an element of escape. Per bout the number of pumps fluctuate between 2 and 6 and the speed varies from 0.18 to 0.33 seconds from every one pump.

5) *Bill-hooking*: The male turns his bill at right angles to the female and pulls on the tip of her maxilla with his own. It is a quick action and is usually conducted successively on both sides of her bill. After bill-hooking, the male faces away from the female.

6) *Head-shaking*: Head-shaking is a lateral motion of the head. When it is performed by a female to a male, it represents a consensual signal or a courtship invitation. The male then has a lower risk of physical rebuff when approaching (Hile, 2005; Brockway, 1964; Brockway, 1964b). These discrete, deliberate signs are necessary, because females are the more dominant sex in social context (Trillmich, 1976).

Tables

Table 5. 9 initiators in alphabetical order with interaction partners and their number of sequences.

Initiator	Interaction Partner	Number of Sequences	
Afina	Batman	2	
	Elvis	2	
	Mercury	7	
	Ziggy	60	
Bender	Batman	3	
	Lemon	3	
	Mercury	2	
	Yara	28	
	Ziggy	6	
Darwin	Bender	4	
	Lemon	3	
	Mercury	3	
	Pebbles	46	
Elvis	Mercury	2	
	Mida	12	
	Puck	3	
	Ziggy	16	
Hedwig	Mercury	11	
	Puck	5	
	Ziggy	1	
Mercury	Afina	2	
	Batman	123	
	Darwin	11	
	Elvis	3	
	Hedwig	13	
	Mida	9	
	Nebel	2	
	Puck	9	
	Yara	58	
	Ziggy	5	
	Mida	Afina	1
		Elvis	13
		Gandalf	1
Ziggy		1	
Puck	Afina	1	
	Elvis	4	
	Mercury	35	
	Nebel	1	
	acting alone	37	
Topaz	Woody	27	
Woody	Topaz	12	

Table 8. Descriptive statistics for structural parameters.

Structural Parameter	Range FD	Range MD	Q₁ FD	Q₁ MD	Q₂ / Median FD	Q₂ / Median MD	Q₃ FD	Q₃ MD
Number of Behaviors	41	66	1	1	2	2	7	5
Action Duration (s)	20.17	20.86	0.33	0.27	0.72	0.72	2.17	1.78
Pause Duration (s)	23.39	32.25	0.00	0.00	0.08	0.00	3.04	1.30
Shannon Index	1.64	1.28	0.00	0.00	0.00	0.00	0.69	0.67
Prop. of Nudging	1.00	1.00	0.00	0.00	0.5	0.73	1.00	1.00
Prop. of Pumping	1.00	1.00	0.00	0.00	0.00	0.00	0.04	0.00
Prop. of Bill-hooking	1.00	1.00	0.00	0.00	0.00	0.00	0.13	0.16
Prop. of Head-shaking	1.00	1.00	0.00	0.00	0.00	0.00	0.25	0.00
Prop. of Head-bobbing	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Prop. of Courtship Feeding	1.00	0.5	0.00	0.00	0.00	0.00	0.00	0.00

Table 9. Results from Wilcoxon signed rank tests with test statistics (V), exact p -value and effect size (r).

Structural Parameter	V	p	r
Number of Behaviors	9	0.7874	0.153
Action Duration	14	1	0
Pause Duration	10	0.5541	0.256
Prop. of Nudging	7	0.2719	0.446
Prop. of Pumping	0	1	0.378
Prop. of Bill-Hooking	2	1	0.169
Prop. of Head-Shaking	0	0.3711	0.506
Prop. of Head-Bobbing	3	1	0
Shannon Index	4	0.8551	0.138

Figures

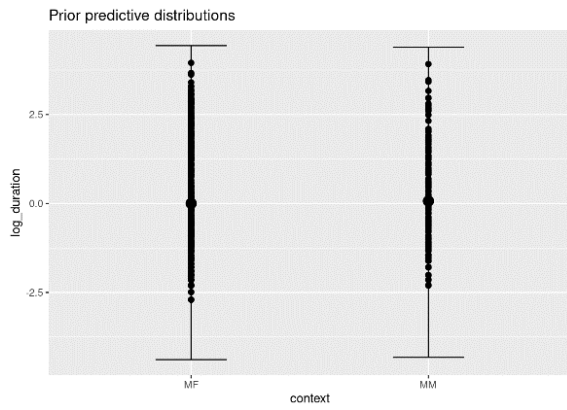


Figure 2. Prior predictive distributions.

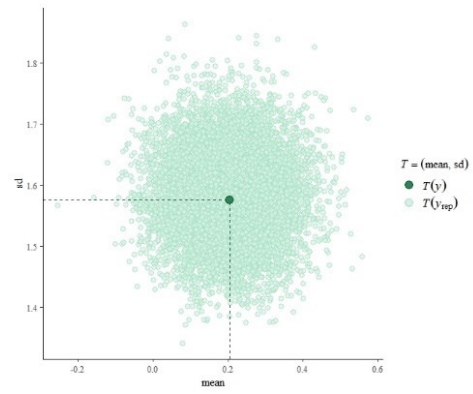


Figure 5. Check for mean & standard deviation.

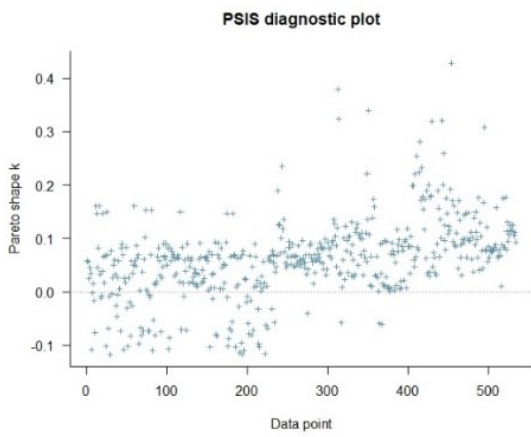


Figure 6. PSIS diagnostic plot.

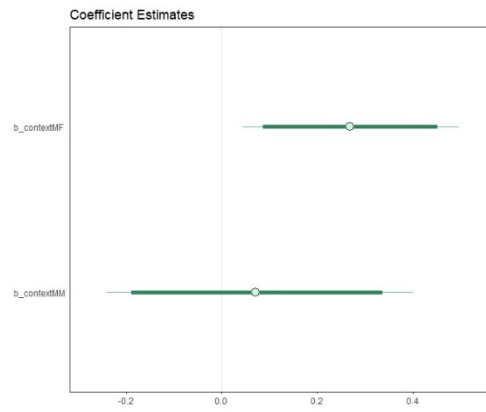


Figure 7. Posterior coefficient estimates.

Zusammenfassung

Eine wesentliche Rolle in der Reproduktion spielt die Balz und häufig besteht diese aus mehreren Verhaltensweisen. Zutreffend ist dies bei Wellensittichen (*Melopsittacus undulatus*), einer Papageienspezies mit Ursprung in Australien. Um Weibchen zu imponieren, leiten hier überwiegend Männchen die Balz ein. Balzverhalten wird aber oftmals auch an Männchen gerichtet. Balzverhalten zwischen Individuen desselben Geschlechts wurde schon in über 130 Vogelspezies beobachtet, jedoch ist dessen Funktion immer noch nicht klar. Die Untersuchung von Balzverhaltensmuster, die jeweils an Weibchen beziehungsweise an Männchen gerichtet sind, ist in diesem Fall wichtig und kann Rückschlüsse auf eventuelle Gemeinsamkeiten oder Unterschiede in der Funktion zulassen. Im Zuge meiner Masterarbeit nutzte ich Videoaufnahmen von zwei Kolonien und codierte folgende Balzverhaltensweisen, basierend auf ethologischen Studien von B. Brockway aus den 1960ern: Schnäbeln, Pumpen, Schnäbel-Ziehen, Kopf-Schütteln, Kopf-Dümpeln und einander füttern. Um zu zeigen, ob das Geschlecht des Empfängers (sprich: des Publikums) einen Effekt auf Balzsequenzen hat, zog ich zuerst die Balzsequenzdauer heran und nutzte bayesianische Methoden, um ein hierarchisches Modell anzupassen. Ergebnisse dieses Modells zeigen eine starke Evidenz, dass das Geschlecht des Publikums offenbar keinen Einfluss auf die Dauer von Balzsequenzen hat, die Verlässlichkeit des Modells wurde aber durch mögliche Einflüsse von Paarbindungen zwischen untersuchten Wellensittichen oder die Unausgeglichenheit meiner Daten beeinflusst. Weitere explorative Untersuchungen zu anderen strukturellen Parametern zeigten eine signifikante Beziehung zwischen dem Geschlecht des Empfängers und der Wahrscheinlichkeitsverteilung der beobachteten Verhaltensübergänge. Schlussendlich kann ich keine Verallgemeinerungen über einen Publikumseffekt auf sichtbare Balzverhaltensweisen bei Wellensittichen treffen. Weitere Studien über Paarbindungen

könnten helfen, um einen womöglich zusätzlichen Effekt dieser Bindung zwischen Wellensittichen auf die Struktur von Balzverhaltensmuster festzustellen.