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Integration of Multimodal Courtship Display in Female Ring Doves (Streptopelia risoria)

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Abstract

Animal communication, especially in the context of courtship, often incorporates several components from different sensory channels into one multimodal signal with components either containing redundant or nonredundant information. To determine which applies for the male bow-coo display in ring dove courtship, twelve female ring doves were exposed to audiovisual playback in a within-individual, cue occlusion experiment. The playback design consisted of three phases that each lasted two minutes with control phases flanking a test phase presenting one of four conditions: (1) audiovisual courtship, (2) visual courtship combined with vacuum cleaner noise, (3) auditory courtship combined with foliage and (4) control containing neutral stimuli in both modalities. Female behavioral responses were manually scored and in subsequent statistical analyses behaviors were compared between conditions and playback phases. In accordance with previous findings, most sexual behavior occurred in the test phases of the audiovisual followed by the visual condition. Least sexual behavior was found in the auditory condition, whereas perch coos, which are vocalizations akin to contact calls, occurred almost exclusively in auditory and never in test phases of visual conditions. Thus, perch-cooing suggested nonredundancy, whereas sexual behavior pointed towards redundancy of the signal components. More fine-tuned analyses in the future may shed more light on these contradictory findings. The within-individual approach additionally provided evidence that previously suggested effects of inter-individual differences are not stronger than effects of condition. Furthermore, recordings of cooing behavior outside the experiment hinted at only minor influences of the playback on the reproductive state of most females.

1. Introduction

1.1 Theoretical background

The social challenges animals face and the contexts in which they occur can be manifold and one way to address them is by means of communication. For this purpose, animals have evolved to produce and perceive a diverse range of signals serving as information carriers. Encompassing all behaviors that serve the purpose of finding a potential mate and reproducing with them, courtship constitutes one of the most multifaceted contexts of animal communication. This includes attraction of potential mates as well as advertising various aspects of mate quality using a myriad of signals produced in a wide array of sensory modalities. Additionally, courtship signals rarely occur on their own but are rather combined into complex displays consisting of several components (Mitoyen et al. 2019). For example, the multiple colors in manakin plumage may represent individual signals (Doucet et al. 2007) and fruitflies (*Drosophila saltans*) incorporate visual, auditory, chemical and tactile signals in courtship (Colyott et al. 2016). Such composite signals are termed multicomponent when signal components occur in the same sensory modality, but they may also consist of multiple signals transmitted via different channels and are then referred to as multisensory or multimodal (Higham & Hebets 2013).

Traditionally, research in animal communication has focused on single components, thereby neglecting the true complexity at hand. However, in order to obtain a full picture of the processes involved in animal communication, especially in the courtship context, signals and displays need to be studied in their entirety. Recently, this has been increasingly recognized leading to a substantial increase of research in the field of multimodal communication with one of the main interests revolving around the question of why such complexity may be necessary. Many hypotheses regarding the potential functions of multimodal signaling have been formulated, most of them circling around a concept of redundancy versus nonredundancy with signal components either carrying the same (backup signal hypothesis) or different information (multiple messages hypothesis) (Johnstone 1996, Partan & Marler 1999). Rooted in the assumption that information is not perfectly encoded within a signal, the backup signal hypothesis argues that using redundant components increases the amount of information transmitted, thereby increasing the accuracy with which receivers assess the meaning of the signal. Conversely, the multiple messages hypothesis states that several signals may serve to inform about different aspects of mate quality (Johnstone 1996).

There are, however, many other conceivable functions of both redundant and nonredundant messages. For instance, Hebets and Papaj (2005) distinguish three main families of hypotheses: content-based hypotheses, efficacy-based hypotheses and inter-signal interaction hypotheses. The first of the three includes potential functions focused on the information content of composite signals. Consequently, content-based hypotheses are essentially synonymous with the backup signal and multiple messages hypothesis with the exception of the latter being extended to include several other forms of multiple messages. Instead of both signal components advertising some aspect of mate quality, one component may convey different kinds of information such as species identity or signaler location. On the other hand, information contained in either component may be intended for different receivers either of the same or the opposite sex. In the latter case, this may serve to account for different receiver preferences in mate choice, which may vary between individuals of the choosing sex due to differences in age, experience or condition. Younger female satin bowerbirds (*Ptilonorhynchus violaceus*), for instance, pay more attention to the blue decorations at the bower while with age this seems to shift towards the male display as the main focus for making a mating decision (Coleman et al. 2004).

Similarly, different receivers may vary in how they perceive different sensory modalities. For example, female cowbirds have been shown to vary in their signal perception in both auditory and visual channels and consequently in what types of acoustic and visual signals they prefer (Ronald et al. 2018). Hebets & Papaj (2005) place this perceptual variability within the family of efficacy-based hypotheses, encompassing potential functions aimed at increasing the efficacy of signal transmission and reception. Other functions falling into this family of hypotheses, according to Hebets and Papaj (2005), may be to increase the salience of a display given a sensory bias for multimodal integration exists or to overcome different transmission problems by taking advantage of the varying physical properties within multimodal signals. In many Anurans, for instance, vocal sac inflations accompanying vocalizations have been hypothesized to increase localizability of the vocalizing individual at crowded breeding grounds (reviewed in Starnberger et al. 2014). Alternatively, composite signals may serve to prevent obstruction of a signal in a variable and/or noisy environment. This function is also often assorted with the backup signal hypothesis as its definition in itself implies signal components to back each other up and avoid loss of information (Mitoyen et al. 2019). Furthermore, it has been argued that in order to serve as backup for each other, signal components are required to carry the same information (Partan 2013).

The third group of hypotheses after Hebets and Papaj (2005) are the inter-signal interaction hypotheses, describing signal components as influencing each other in their production, detectability, memorability or meaning. For example, mate quality may be determined by judging the signaler's abilities to produce the components simultaneously, in some cases by assessing the synchrony with which signal components are produced. In ring doves (*Streptopelia risoria*), for instance, it was suggested that females showed increased responses when presented with the natural audiovisual courtship display than with artificially shifted or jittered visual and auditory components (Mitoyen et al. 2022). Furthermore, the use of multiple signals may increase learning and memory of a display or the detection and discrimination of signals and senders (also often referred to as receiver psychology hypothesis, Rowe 1999). For instance, the context in which to respond to one component may be determined by another component, which may be the case when the same display is used in several contexts or shown by both sexes. In the big-clawed snapping shrimp (*Alpheus heterochaelis*), males and females perform the open-chela display and experiments presenting male and female pheromones in combination with open chelae indicated the chemical signal to provide the context for interpreting the visual signal, in this case by providing information about the signaler's sex (Hughes 1996). Several more potential functions and related examples are reviewed in Hebets & Papaj (2005) as well as in Candolin (2003) and Mitoyen et al. (2019) focusing specifically on courtship.

A framework based on the redundancy versus nonredundancy concept for the classification of multimodal signals was proposed by Partan and Marler (1999) and classifies multimodal signals depending on receiver responses to the isolated versus the combined signal (Fig. 1). According to this framework, a composite signal will be categorized as redundant when the isolated components elicit the same response as when combined. The response intensity may either remain unchanged (equivalence) or be increased (enhancement) compared to the combined presentation. Nonredundant signal components, on the other hand, will elicit different responses in a receiver when presented in isolation from each other. Consequently, combination of the signals may either retain all responses shown to the isolated signals (independence), elicit the same response given to one of the unimodal signals (dominance), elicit a response suggesting a change in the meaning (modulation) or lead to an entirely new response (emergence) (Partan & Marler 1999, 2005).

Both presented frameworks may be viewed as opposing each other, while they should rather be seen as complementary. It is important to note here that the classification along redundancy and nonredundancy does not necessarily imply every signal component to contain

information. Rather, it should be interpreted as relativization between signal components. For example, receivers may show a certain response to one isolated component, while they do not respond in any way to another component, indicating no information is contained within that signal. This may lead to a rejection of any content-based hypothesis, although classification using the proposed categories is still feasible. Distinct responses given to one signal, but none to another can also indicate components to be nonredundant as the relative information content between the components differs. This may then lead to a classification as modulation when the combined signal also elicits a distinct response. In the scheme of hypotheses discussed by Hebets and Papaj (2005) this may then hint at one component providing the context for interpreting the information contained within the other component and thus suggest an inter-signal interaction. In conclusion, both frameworks are useful, especially when considered in conjunction. In addition, the authors of both frameworks agree that receiver responses to isolated versus combined signals is a useful approach for learning more about the potential functions of multimodal signals (Hebets & Papaj 2005, Partan & Marler 2005).

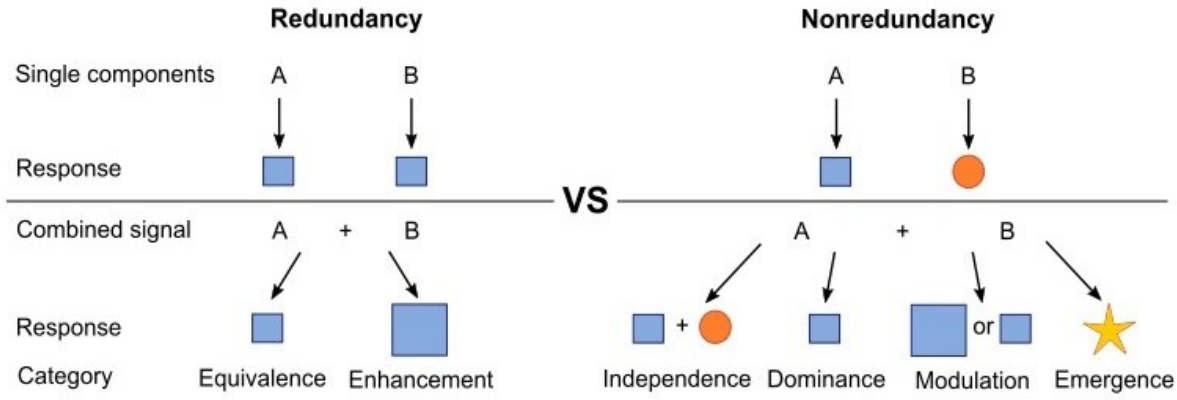


Fig. 1: Schematic of the classification framework for multimodal signals. The components of a multimodal signal are represented by the letters A and B. Receiver responses to the single components as well as to the combined signal are depicted as shapes. Based on comparisons of these responses, a composite signal can be categorized as either redundant or nonredundant and subsequently assigned to one of six categories. Adapted from Partan & Marler (1999).

1.2 Experimental implementation

The experimental approach which does exactly that, exposing receivers to the signal components individually as well as in conjunction, is called cue isolation. In the past, live animals were used as displaying individuals in such experiments, prompting elaborate experimental designs and apparatuses for achieving isolation of the signaling channels. Some spiders, for example, incorporate visual and vibratory signals in their courtship, which can be separated by using either opaque or transparent walls between male and female for controlling visual input

and discontinuous or continuous substrates to control the transmission of vibratory signals (reviewed in Uetz & Roberts 2002). Similarly, in ring doves the auditory and visual components of the male courtship display were separated by arranging cages holding females around another center cage holding the displaying male. Cages were separated by different kinds of visual partitions such that females either heard and saw the male, heard the male but only saw themselves in a mirror or only heard the male (Friedman 1977). However, presentation of the visual component alone was not feasible with this experiment design, leaving the picture of the function of either component incomplete.

Rapid advances in technology have led to a steep increase of acoustic and video playback methods employed in studies of animal behavior (Rosenthal 2019). Playback studies involve the presentation of pre-recorded or artificially created stimuli aiming at simulating the real world in order to evoke and analyze responses of focal individuals. This has also appealed to researchers conducting cue isolation experiments as it allows for the creation of more standardized stimuli and clean separation of the visual and auditory channels. However, the technology usually employed in such experiments is developed specifically for human perception, which can differ quite substantially from that of other species, especially in the visual domain (Fleishman et al. 1998, Fleishman & Endler 2000). Color perception is a case in point as many animals perceive wavelengths outside the range of human perception. Specifically, many bird species have photoreceptors sensitive to wavelengths below 400 nm (ultraviolet, UV), which standard monitors usually used for video playback are not designed to display (Fleishman & Endler 2000, Rosenthal 2019). Thus, in playback experiments it has to be considered that colors do not represent the real world to the study animals. Also pigeons may perceive wavelengths in the UV range, but no distinct evidence exists for ring doves. In fact, an experiment investigating female responses to just the shadow of a courting male was sufficient in inducing ovulation, indicating any further visual information to be of lesser importance (Lambe & Erickson 1973). Another important aspect to consider in playback experiments is to ensure the video is played at a sufficiently high frame rate (or image presentation rate, IPR). Many animals, especially those that move by means of flight such as birds, have higher visual temporal resolution than humans and may perceive video playback as jerky rather than smooth if the frame rate is too low (Fleishman & Endler 2000, Ware et al. 2015). In pigeons, motion quality was shown to be essential in evoking a sexual response in both males and females with frame rates of 60 fps yielding the biggest response (Ware et al. 2015). Despite this and other still remaining issues of the video playback method such as depth perception and lack of reciprocal interactions between sender and receiver, among others (Fleishman & Endler 2000), several experiments

have successfully employed video playback in birds (e.g. Bird & Emery 2008, Guillette & Healy 2017).

A study that successfully combined the cue isolation approach with playback methods in birds was conducted using pigeons (*Columba livia*) (Partan et al. 2005). Recordings of the male bow-coo display, an important component of courtship in many Columbiforme species consisting of an auditory and a visual component, were presented to six females. Playback included either the full bimodal display or each of the two components individually. Longer durations of circle walking and higher numbers of tail spreading, two behaviors indicating sexual interest, but fewer preening events were observed in stimulus than in control intervals, indicating females responded to the playback. Furthermore, audiovisual playback evoked more sexual behavior than both unimodal conditions and an interaction between interval and condition was found for vocalizations with most coos observed in stimulus intervals of the auditory condition. Given that female responses represented similar behaviors in all conditions, but were increased in intensity in the audiovisual condition, the authors concluded that the male display likely contained redundant information. Specifically, there seems to be an enhancement effect when signal components are presented in conjunction (Partan et al. 2005).

1.3 Courtship in ring doves

Similar to pigeons, male ring doves (*S. risoria*) also perform an audiovisual bow-coo display during early courtship phases in a relatively stereotypical way, making it ideal for investigating multimodal signaling. The ring dove is a domesticated, monogamous and monomorphic species, whose courtship and reproductive system have been thoroughly researched in the past (reviewed in Cheng 1979). During courtship, the pair traverses a predictable series of behavioral and physiological changes that also influence each other (Lehrman 1964).

At the beginning of this courtship sequence, the male, upon encountering a female, starts performing the bow-coo display. As the name suggests, this display consists of a visual component, a bowing movement, and an auditory component, a cooing vocalization. In response to this, the female's estrogen level begins to rise (Korenbrot et al. 1974) and she may engage in excessive self-preening, a behavior previously interpreted as displacement preening, especially when concentrated to the wings (Craig 1909, Goodwin 1956, Cheng 1973). The male may then begin to chase the female (also referred to as "charging" or "circling") while assuming a distinct body posture. Overall, his body appears directed along a horizontal line, his back slightly hunched, wing feathers expanded and his tail either forming an extension with his back

or dragged on the ground behind him. Occasionally, he may utter a short vocalization resembling a human laugh, in the literature sometimes referred to as “kah” call (Craig 1909). In-between bouts of circling, the male may stop to join the female in self-preening and eventually will engage in billing as if feeding her. This may be repeated several times until the female assumes the sex crouch position, lowering herself down until her chest comes in contact with the ground and extending her wings over her back, ready for copulation (Cheng 1973).

As courtship progresses, the male begins to nest-coo, a cooing vocalization given with the head lowered towards the ground and the tail held high. Occasionally, this is accompanied by gentle twitches of the shoulders (wing flips). In most cases, as the name implies, the nest coo is uttered either to indicate a suitable nesting site or at an already established nest (Craig 1909, Miller & Miller 1958, Lehrman 1964). This may motivate the female to join him in nest-cooing, which in turn initiates a decrease in nest-cooing in the male. Female nest-cooing, on the other hand, will continue to increase, accompanied by an increase in progesterone secretion, which is thought to enhance nest-associated behaviors such as nest-cooing, nest building and incubation behaviors (Cheng & Silver 1975). Approximately seven to eleven days after courtship began, the female lays a clutch of two eggs in the span of roughly 48 hours (Lehrman 1964) and both parents take turns in incubating the eggs as well as in subsequent care of the squabs.

1.4 Further research in ring doves

The physiological changes accompanying behavioral changes in the female along the described courtship sequence are influenced by several factors. The presence of male stimuli appears to play an important role in initializing these changes. For example, the amount of courtship a female is exposed to over a certain amount of time seems to be positively correlated with oviduct growth (Barfield 1971). Furthermore, conspecific vocalizations have been shown to be capable of inducing follicular growth in visually isolated female ring doves, although the type of vocalization and the sex of the vocalizing individuals were not controlled (Lehrman & Friedman 1969). However, a female’s own nest-cooing behavior has been demonstrated to also increase physiological responses (reviewed in Cheng 1992). In a study with surgically muted females, for instance, higher follicular development was discovered when females were presented with recordings of their own nest coos than with those of males (Cheng 1986). Consequently, while male stimulation seems to be required for inducing certain behavioral and physiological changes in a female, it is her own vocalizations that further mediate such changes.

Besides the aforementioned bow and nest coo, ring doves' vocalizations also include the perch coo, which gets its name from the upright perching position of the vocalizing bird and is uttered by both sexes. Contrary to the other two coo types, perch coos are normally not associated with a sexual context, but rather seem to fulfill a purpose akin to that of a contact call seeing as it is often given in response to the coos of other birds (Craig 1909) or in the dark (Davies 1974). All three coo types consist of the same basic structure of two elements, a shorter followed by a longer one with an intermittent brief pause (Fusani et al. 1997). Given that these coos seem to be indistinguishable by ear to humans, the body posture accompanying each coo type is essential in determining the difference between coos. However, nest coos have been described as softer and of lower amplitude than the other two coo types (Miller & Miller 1958, Craig 1909) and measurements of temporal structure and amplitude, among other parameters, seem to indeed indicate such differences. For instance, measurements of such parameters in collared doves (*S. decaocto*) revealed nest coos to be on average longer than either of the other two coo types and to exhibit significantly lower amplitudes for the first element of the nest coo (Ballintijn & ten Cate 1999). It remains however unclear whether any informative value is contained within these differences such as signaler identity, sex or signaling context.

Detailed analyses of inter-individual differences in temporal patterns of the bow coo as well as the accompanying visual component have been conducted, aiming at shedding light onto this open question (Fusani et al. 1997). Mainly differences in the auditory component between males were found, indicating information about signaler identity to be conveyed via the coo, while the bow contained information about signaler sex. Thus, these results suggested the bow-coo display to contain nonredundant information. Experiments comparing female physiological responses to the bow-coo components seem to further suggest an important sexual role of the visual component. Females presented with just the shadow of a courting male were more likely to lay eggs than when only hearing his vocalizations (Lambe & Erickson 1973) and follicular growth was increased in females observing a courting male compared to those that just heard him (Friedman 1977). Additionally, highest physiological responses were found in females seeing a male courting them rather than a different female (Friedman 1977), indicating an importance of male-female interactions in courtship (discussed in Cheng 2008).

Taken together, the presented results provide valuable information regarding potential functions of the bow-coo display and both of its components. Expanding on this information, further research on female behavioral responses to male courtship has been conducted in the Dove Lab at the University of Vienna. For example, in a first study females were confronted

with live males and their immediate behavioral responses measured in relation to whether the male courted or not (Mitoyen et al. 2021). Interestingly, females did not vocalize and while higher activity levels (measured as the number of steps taken by the bird) were found to occur with male courtship, no such relationship was detected for self-preening, despite its previously assumed role in courtship (Craig 1909, Goodwin 1958, Cheng 1973). The only sexual behavior that was observed significantly more often during male courtship were tail quivers, rapid up- and down-movements of the tail feathers akin to a vibratory motion (Mitoyen et al. 2021). In fact, quivers have been previously described to show sexual stimulation in other birds (e.g. domestic canaries, Amy et al. 2015; zebra finches, Witte 2006), making a similar function of tail quivers in ring doves conceivable as well.

This finding was further supported by the results of another experiment investigating whether synchronization of the visual and auditory components of the bow-coo display is necessary for eliciting female interest (Mitoyen et al. 2022). As mentioned before, females did respond more to playback recordings of the unaltered display than to those presenting the visual and auditory components shifted relative to each other along a time axis. Additionally, the experiment demonstrated that ring doves did respond in similar ways to the playback as would be expected to live males, showing higher activity levels, more preening events and tail quivers during playback intervals including a male stimulus. Another, more surprising, result was that females also exhibited circling behavior, previously assumed to be a primarily male behavior (Craig 1909), which was also shown significantly more often when presented with male courtship recordings (Mitoyen et al. 2022).

First efforts in determining the meaning of the two components of the male's bow-coo display have been conducted in a master's project by Daniela Biegler (2021), who presented audiovisual playback in a between-individual approach to a total of 21 female ring doves separated into three groups. Each group of birds was shown either the unchanged bimodal display or one of the two unimodal components, broken up by short playback breaks throughout the whole 15-min trial. Rather than using the usual cue isolation approach, unimodal courtship stimuli were not presented entirely on their own, but together with occluding stimuli (vacuum cleaner in the visual, plants in the auditory condition) in order to create a masking effect for the respectively missing component. This cue occlusion approach was used to create a more ecologically valid experimental paradigm as it has been pointed out that separation of the components may not usually occur in nature without a reason. The results of the experiment indicated once again the effectiveness of the playback method with circling and self-preening occurring

significantly more in the stimulus intervals than the playback breaks. However, neither activity level and circling nor vocalizations differed significantly between the three groups, although shorter circling durations and most perch coos were observed in the auditory condition. The only significant effect was found in the preening rate, which was significantly lower in the auditory condition as well. Given that circling was observed in all three groups, the bow-coo display was concluded to contain redundant information, with the combination of signal components likely creating an enhancement effect.

In a follow-up study in the form of another master's thesis by Conny Bourgmeyer (2022), further analyses on the same video material were conducted, this time focusing on tail and wing quivers as well as wing flips. While both wing and tail quivers did not occur significantly more often during playback intervals and did not differ between conditions, substantial inter-individual differences became apparent. This motivated another follow-up study using a within individual approach, which served as a pilot to the present thesis (Hacek 2022). Based on the experiment design employed in Partan et al. (2005), this study presented six female ring doves with recordings of either the full multimodal bow-coo display or with the unimodal components paired with the respective occlusion stimulus. The playback was divided into three phases of equal length (2 min each), namely a pre- and post-test phase showing neutral audiovisual stimuli and the test phase presenting one of three conditions (audiovisual, visual, auditory) or the control, which included the same neutral stimuli as those in the pre- and post-test phases. Again, higher activity levels in the test phases compared to the control phases (pre- and post-test phase) were found, but did not differ between conditions. Furthermore, there was significantly more sexual behavior in the audiovisual than the auditory condition and most perch coos were observed again in the auditory condition, though not to a statistically significant degree. Contrary to previous results (Biegler 2021), the within-individual approach indicated a modulation effect with the visual component likely modulating the meaning of the auditory component (Hacek 2022).

1.5 Hypotheses and predictions

The aim of the present thesis was to add to the current knowledge about the meaning of the bow-coo display in ring doves. Following the same setup as in the pilot, two principal questions were addressed. First, I wanted to determine whether the signal components of the male bow-coo display conveyed redundant or nonredundant information. Based on the results obtained in the pilot study as well as on the observation that different types of ring dove vocalizations are most easily discernable by the body position of the signaler, I hypothesized that the

components of the bow-coo are nonredundant with the visual modulating the meaning of the auditory component. Consequently, I predicted that females would show most sexual behavior, including preening and quivering, in the audiovisual condition, closely followed by the visual condition. Furthermore, I predicted perch coos to be observed more in the auditory condition, while overall activity measured as number of steps would not differ significantly between conditions.

Second, I asked whether female responses depended solely on experimental condition or on differences inherent to the individuals themselves and predicted that while individual differences do influence female behavior, experimental conditions have the stronger effect. I did, however, refrain from formulating distinct hypotheses on what drives these individual differences as this would be largely speculative at this point.

2. Material and methods

In the present study, a cue occlusion experiment was conducted presenting female ring doves (*Streptopelia risoria*) with playback of male courtship either containing the full audiovisual display, the auditory or the visual component only. This approach was based on a study with pigeons (*Columba livia*) executed by Partan and colleagues (2005) and adapted from a pilot study conducted in 2022 in the same lab as the present study (Hacek 2022). Each individual was exposed to each condition twice, surmounting to a total of 8 experiment sessions per bird. Experiment days were interspersed with rest days to ensure a baseline reproductive level in the females. I participated in planning and preparing the experiment, habituated the birds to the setup and the isolation cages and ran the experiment. Subsequently, I analyzed the obtained video material and conducted statistical analyses.

2.1 Ethics statement

Approval for the procedures employed in this experiment (no. 2022-010) was given by the Animal Ethics and Experimentation Board of the Faculty of Life Sciences, University of Vienna. Keeping conditions closely followed national guidelines. Food, grit and water were provided ad libitum and multiple perching opportunities were offered in both the outdoor aviaries as well as the isolation cages for environmental enrichment. During isolation, individuals were visually but not acoustically separated from each other. Isolation cages were cleaned daily from the start of the isolation phase until the end of the experiment. Body weight was closely monitored through daily measurements to detect potential weight changes as this may indicate stress, but no such changes have been detected over the course of the experiment.

The birds of this study were used to human presence and to being handled. People newly introduced to the doves underwent careful training to ensure correct handling. All subjects were habituated to the isolation cages as well as the experimental setup for several days prior to the experiment. Any sign of severe fear or stress during testing (e.g. flying in the setup) led to premature discontinuation of the test trial to prevent injuries (see below for more detail).

2.2 Subjects

The ring dove (*S. streptopelia*) is a domesticated relative of the African collared dove (*S. roseogrisea*) and has been extensively studied in the past, mainly regarding courtship and reproductive physiology (e.g. Lehrman 1964, Barfield, 1971, Cheng 1973, Friedman 1977). The subjects of the present study were 12 female ring doves, four of which had been acquired from breeders in Austria in 2017 and 2018, and three from a French breeder in 2019. The remaining

five individuals were hatched between May and August 2022 and reared at the Konrad Lorenz Institute of Ethology (KLIVV) in Vienna, Austria. At the KLIVV, breeding pairs are kept in separate aviaries with their offspring until they are fully fledged, after which the young birds are introduced to same-sex groups. Subjects were between at least six years and twelve months old at the time of the experiment, though the exact age of the birds acquired from external breeders cannot be determined due to lack of detailed documentation. Sexual maturity is reached at around six months after hatching (Miller & Miller 1958), meaning all birds were matured at the time of the experiment. For reasons of simplicity, I will henceforth refer to the seven females acquired between 2017 and 2019 as “older” birds and the five females hatched in 2022 as “younger” or “young” birds.

Almost all subjects had been moved from the KLIVV to the University of Vienna Biology Building (UBB), where the current study was conducted, at least a year prior to the start of the experiment and thus were given sufficient time for adjusting to the new environment. Only four of the females were moved to the UBB in May 2023, but their overall demeanor seemed relaxed and well-adjusted by the time the experiment commenced. At the UBB as well as the KLIVV, individuals were housed in same-sex groups in outdoor aviaries equipped with various perching and sheltering opportunities at different heights. Food, water and grit were accessible at all times. During the time prior to the experiment male and female groups were kept in outdoor aviaries on opposite sides of the UBB to ensure minimal exposure to male stimuli. However, due to strong winds and relatively high amplitude of male cooing, acoustic isolation was not entirely achievable. Group sizes varied from four to six individuals per compartment and directly adjacent compartments were visually and acoustically connected.

All females had little to no previous reproductive experience and no prior successful breeding attempts. For the younger females, male contact had been restricted entirely to their fathers and brothers during early life stages, after which they were never housed with other male conspecifics. However, it has been stated that females may start exhibiting male-like behaviors when kept in isolation from the opposite sex for an extended time period (Craig 1909). Such observations have also been recorded in our colony. On one occasion, a female was observed to seemingly court and even copulate with one of the other females. The individual in question was not included in the present study, though other individuals from the same aviary that might have been courted by that female were. Nevertheless, there is no reason to believe that any of the subjects in this study had formed a stable pair with another female.

Six of the older subjects had previously participated in similar experiments, during which they were exposed to either live males displaying to them, male playback much similar to that in the present experiment or otherwise manipulated male courtship playback (Mitoyen et al. 2021, Biegler 2021, Mitoyen et al. 2022). Three of these six had participated in all three of those experiments, while the remaining three had only participated in the latter two. Therefore, these subjects differed in their experiences from the remaining six individuals not just in the amount of exposure to male courting, but were also already familiar with the experiment setup. Additionally, seven of the twelve females had undergone a process of habituation to the setup in August 2022, when the experiment was originally planned to be carried out but had to be postponed due to technical failure. These individuals included five of the older and two of the younger birds. All individuals were habituated to the setup again in preparation for the current experiment as it is not clear for how long memory is retained in this species.

Although breeding efforts may be decreased during fall and winter, the breeding cycle of the ring dove as a domesticated species is thought to continue throughout the whole year (Craig 1909). This seems to be true for our colony as freshly laid eggs have been continuously found throughout the winter of 2022/23. Nevertheless, to minimize the possibility of females not showing interest in the experiment, the start of the experiment was chosen to be in July. It was not possible to start earlier due to precautionary anti-parasite treatment of the birds in the preceding weeks that could have altered female responses to the experiment.

2.3 Experiment setup

The testing setup (Fig. 2) comprised two connected cubic compartments (50 x 50 x 50 cm) framed by aluminum strips with either black fabric or mist netting mounted on them and was constructed by a former doctoral student of the lab (Mitoyen et al. 2022). One of the compartments served as temporary confinement for the subjects during testing sessions (subject compartment), while the other compartment (playback compartment) contained the monitor (24-inch ASUS VG248QE, refresh rate 120 Hz) and the loudspeaker (Fostex FE108ez) displaying the visual and auditory components of the playback. The monitor was positioned at a distance of approximately 21 cm from the subject compartment to ensure visual stimuli appeared as natural as possible in terms of size. The loudspeaker was located behind the monitor and black sound absorbing fabric was wrapped around the top, back and side walls of the playback compartment to keep any further potential distractions from the monitor at a minimum and increase

sound quality of the auditory stimuli. To prevent subjects from entering the playback compartment while maintaining proper view of the visual stimuli, mist netting was mounted between compartments.

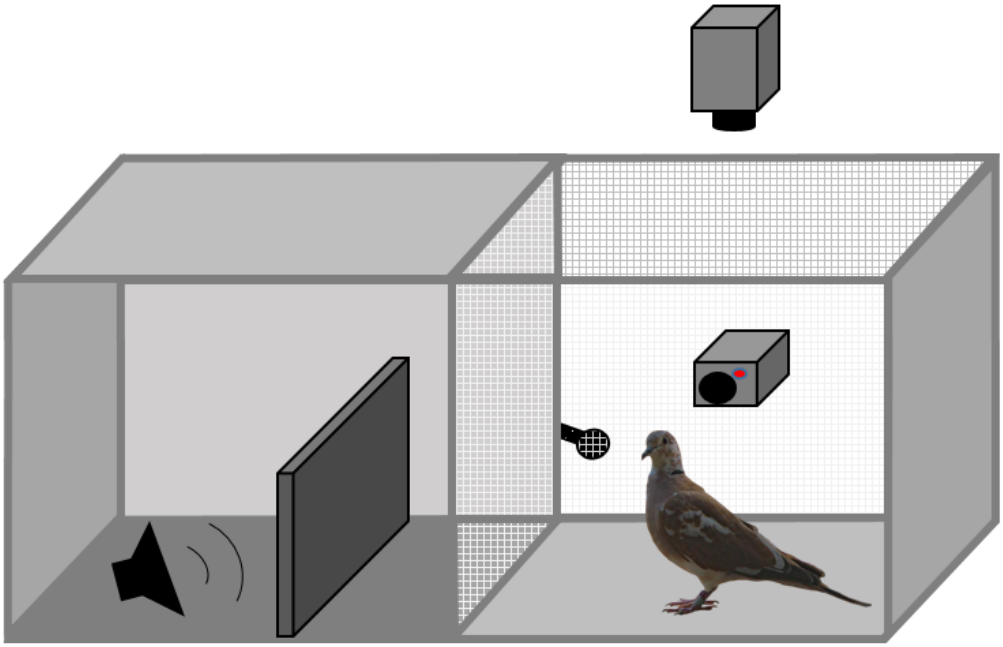


Fig. 2: **Experiment setup from the side.** Depicted are the screen and loudspeaker producing the playback (left) as well as the side and top view cameras and the microphone recording the female's behaviors (right). Hatched areas indicate sides covered with mist netting, solid areas indicate sides covered with black fabric or flooring.

Female visual responses were recorded by two synchronized video cameras (Basler acA1920-155uc) at 60 frames per second, one filming the female from the side (approx. 60 cm from subject compartment) and the other one from above. Only video material of the side-view camera was used in subsequent video scoring. A third camera of the same model was pointed at the monitor. This footage was used for identifying the timing of the three playback phases. Auditory responses were recorded via a Sennheiser ME66 K6 microphone positioned to the left of the playback compartment and as close to the subject compartment as possible without being visible to the female. Suitable illumination was provided by a soft box diffuse light (Neewer LED max. 45W) located behind the side-view camera and 7 LED spotlights fastened on the top frame of the subject compartment.

This setup as described was located within two layers of curtain suspended from a wooden frame, with white curtain facing towards the setup and black, sound absorbing curtain facing away from it. In this way, a smaller chamber within the experiment room was created, allowing

for better control over lighting and acoustic conditions for audio and video recordings. Additionally, acoustic foam was attached to the walls, although it was not possible to cover the area entirely.

Outside this chamber, but within the experiment room, a gaming PC (graphics card: AMD Radeon Pro WX 4100, 4GB GDDR5; operation system Ubuntu) used for controlling the recording of female responses as well as the playback was located. Video material was recorded using the Motif Video Recording System (loopbio gmbh, Vienna, Austria) and Audacity (© 1999-2023 Audacity Team) was used to record auditory responses. Furthermore, the playback was coordinated by an Octave script written by Cliodhna Quigley using Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) run on the same computer.

2.4 Stimuli and playback

2.4.1 Stimulus acquisition

In total, six stimuli of three categories (courtship, occlusion, neutral) were presented to the subjects, always combining a visual with an auditory stimulus (Tab. 1). First efforts to obtain courtship recordings for later stimulus creation have been conducted by Daniela Biegler during her Master's thesis work in 2021 by exposing males to live females and recording male responses. However, only two males produced sufficient amounts of courtship, one of which was a parent to three of the subjects in the present study. Given that this left us with material of just one suitable stimulus male, additional efforts to obtain new stimulus material were undertaken in the spring of 2023. Similarly, only one male courted with sufficient frequency. This forced us to use courtship stimuli recorded in slightly diverging lighting conditions, introducing a potential confounding factor. To keep any potential impact of this divergence on female responses at a minimum, all testing conditions showing the visual component of the male display (i.e. audiovisual and visual conditions) were matched with neutral stimuli recorded in the same lighting conditions. For this purpose, new recordings of the empty subject compartment (neutral visual stimulus) were recorded under the same conditions as the new courtship stimulus. Furthermore, to guarantee familiarity of the subjects with the visual occlusion stimulus, plants from their home aviaries were transferred to the subject compartment and a short recording was obtained, which was also combined only with the new neutral visual stimulus in pre- and succeeding playback phases. Through this approach, noticeable changes in the visual appearance of the stimuli during phase transitions within test trials were prevented. Courtship sequences from the reused courtship material had been selected and cut by the bachelor students who conducted the pilot to the present study in 2022 and consisted of two 60-second sequences of

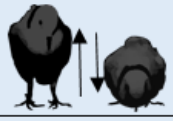
courtship with a total of 33 full bow-coos. To ensure comparability of courtship stimuli, I selected two 60-second sequences of the newly acquired recordings containing 35 full bow-coos. Both stimuli included non-courtship sequences (walking, looking around) to create stimuli as close to natural courtship as possible.

All visual stimuli were recorded at 120 frames per second to avoid flicker perception by the females and video size (45.5 x 18 cm) was chosen based on male movement inside the setup throughout the playback. The neutral auditory stimulus (low intensity white noise) was recorded in the experiment room by simply recording the ventilation sound in the room, while the auditory occlusion stimulus (vacuum cleaner noise) was obtained in 2021 by Daniela Biegler. All auditory stimuli were recorded at 48 kHz. Auditory courtship stimuli of both males were displayed at the same sound levels (68-80 dB), while the maximum level of the auditory occlusion stimulus (vacuum cleaner noise) was slightly lower (68-75 dB). We decided against increased sound levels to avoid causing distress in the subjects.

2.4.2 Playback design and conditions

The design of the playback was based on the study conducted by Partan and colleagues (2005) with female pigeons (*C. livia*) and consisted of three phases: the pre-test, test and the post-test phases. All three phases were of 2 minute duration, resulting in a total playback duration of 6 minutes. Both the pre- and the post-test consisted of the neutral stimuli (i.e. low intensity white noise and a recording of the empty subject compartment). In the test phase, one of four conditions, each consisting of a visual and an auditory component, was presented (Tab. 1). The audiovisual condition contained the full bimodal bow-coo display, while the auditory component (the coo) was paired with the visual occlusion stimulus (plants) and the visual component (the bowing movement) was combined with the auditory occlusion stimulus in the auditory and visual conditions, respectively. Occlusion stimuli served the purpose of creating a more ecologically relevant experiment design by providing a potential explanation for the missing signal component. This approach has been applied successfully in previous studies of the Dove Lab (Biegler 2021, Hacek 2022).

Tab. 1: The four conditions presented in the test phase of the experiment. Each condition consisting of a visual and an auditory component. Colors indicate stimulus category: blue = courtship stimulus; orange = occlusion stimulus; grey = neutral stimulus.

Modality / Condition	visual	auditory
audiovisual		
visual		
auditory		
control	empty compartment	low intensity white noise

2.5 Procedure

2.5.1 Habituation

Throughout a period of five consecutive days in early July 2023, all individuals underwent a period of repeated introduction to the testing setup as well as the isolation cages. Subjects were caught from the aviaries in the morning, transferred to the isolation cages (48 x 46.5 x 51cm) and released back to the aviaries once habituation was completed for the day. Thereby, we avoided catching the birds multiple times a day in the high July temperatures, which would have caused them considerable stress and exhaustion. Food, water and grit were provided ad libitum in the isolation cages and multiple perching opportunities were offered as enrichment. Isolation cages were cleaned daily over the course of the entire habituation and experimental periods. Birds were regularly exposed to the noise of the vacuum cleaner during the whole isolation period, as cleaning included vacuuming both the floor of the room as well as the cages themselves, but seemed unbothered by it. The room where the birds were kept was temperature-controlled at about 21 °C and an automated light/dark cycle was set to 14/10 hours. Light absorbing curtains were hung over the windows, though some natural light might have still shone through small slits as it was not possible to fasten the curtains tightly to the windows. However, the natural light cycle during that period was similar to the one set for the room, thus likely not drastically influencing the subject's circadian cycle. Females were visually,

but not acoustically separated from each other, thus providing at least some social contact with each other.

In order to habituate the subjects to the experiment setup, they were transferred into the setup individually and slowly familiarized with the neutral and occlusion stimuli. At the beginning, no stimulus was presented until the doves seemed fairly relaxed, upon which first stimuli were introduced. At first, just the visual stimuli were presented to draw attention to the monitor while simultaneously avoiding to induce fear. The birds seemed unfazed by that, so we proceeded with the acoustic stimuli, starting with the less intense white noise and lastly progressing to the vacuum cleaner noise. Number of habituation rounds per day and individual as well as the duration were also gradually increased, ultimately ranging from 1 to 5 times per day and 3 to 6 minutes per habituation round. This was also aligned with individual requirements as some birds seemed to need more time to adjust to the setup than others. In total, females were habituated between 8 to 11 times during the five day period.

2.5.2 Experiment

Isolation started four days before the planned start of the experiment. However, one female laid eggs twice during the four days prior to the experiment, forcing us to postpone the start by two days. Eggs were removed immediately upon discovery and the delay was to ensure the female had returned to a baseline hormonal state (Cuthbert 1945). This was unfortunately not possible when another female laid eggs on days 11 and 12 of the experiment. Due to the progressed stage of the experiment and the female's continued interest in the playback, excluding her from the experiment was not deemed necessary.

The experiment was conducted over the course of 15 days from mid to end of July 2023. Each female underwent one experiment trial per testing day and was presented with all four conditions twice over the whole experimental period. The resulting 8 testing days were alternated with rest days during which no experiment trials were conducted to prevent females from progressing in their reproductive cycle. The order in which individuals were tested was randomized for each testing day using a custom written Octave script. Randomization of experiment conditions presented to each individual per testing day was also done using Octave, but included two important restrictions. Firstly, control conditions were not presented on consecutive testing days to prevent the subjects from losing interest in the playback. Secondly, audiovisual conditions were presented only after both the auditory and visual condition of the respective male stimulus had been presented to a given female in a previous trial. This served the purpose

of excluding the possibility that any reactions to unimodal conditions were the result of the female already having formed a mental representation of the full display, thus influencing her response in the unimodal conditions.

Testing usually started in the morning between 8:45 and 9:00 am and was completed between 11:10 and 11:45 am. These times were chosen based on the natural circadian cycle of the ring doves, which is characterized by higher activity levels in the morning that decrease by midday (Craig 1909). Originally, it was planned to start testing at an earlier time, however, after loud unheralded handiwork in a neighboring room forced us to interrupt the experiment for about 45 minutes after only two trials on the first testing day, we decided to also delay starting times slightly on the following days. At the start of each testing trial, the individual was placed inside the subject compartment and given a brief moment to adjust before the playback was started. Trials were started as soon as the subject seemed calm. However, in three cases birds nonetheless began showing signs of panic in form of repeated flying bouts during the test phase of the playback, always in visual conditions presenting the vacuum cleaner stimulus as auditory occlusion. In two of those cases, birds were not able to calm themselves down within 60 seconds of the test phases, thus leading to discontinuation of the trial. In the third case, the bird stopped flying, but seemed frozen for the rest of the test phase, thus likely not paying attention to the male on the monitor. All three subjects were tested once more after the last trial of the day had been completed and seemed much calmer, even responding to the playback. I analyzed only the second recording for each of these three instances.

In order to determine the degree to which the experiment may have influenced the subjects' reproductive state and thus their responses in subsequent test trials, their behavior inside the isolation cages was recorded for 30 minutes after completion of the last testing trial using two Hero4 GoPros. This was also done on rest days at the same time of day, always starting between 11:38 am and 12:02 pm with one exception when technical issues with the GoPros resulted in a delayed start (12:22 pm). On the 28th of July after the last GoPro recording had been obtained, birds were released from isolation.

2.6 Data preparation and analyses

2.6.1 Video scoring and data preparation

In total, 97 complete test trials were recorded, of which 96, eight for each individual, were subsequently scored using Loopy (http://loopb.io, loopbio gmbh, Vienna, Austria). One video was excluded as it constituted the case in which the female showed no response to the playback as an apparent result of stress (mentioned above), while the repeated test trial was

included. Audio and video recordings were joined by experiment day and subject before scoring commenced. I conducted video coding of all 96 recordings in accordance with a previously established ethogram. A selection of the scored behaviors relevant for data analysis is described in Table 2 and the remaining behaviors that were scored but not statistically analyzed can be found in Table A1 of the Appendix.

In order to get the obtained data into a format suitable for data analysis, data wrangling was carried out in R (version 4.3.2, R Core Team 2023) and R Studio (version 2023.12.0+369, Posit Team 2023) using the R packages *dplyr* (Wickham et al. 2023a), *tidyr* (Wickham et al. 2023b) and *stringr* (Wickham 2022). In a first step, columns including the age class (younger, older) and the origin (Austrian breeder, KLIVV, French breeder) were added for each female and all scored behaviors were assigned to one of the three playback phases during which they occurred. These were determined by an algorithm written by Cliodhna Quigley, which used luminance differences between frames of subsequent phases to identify start and stop frames for each phase. In control conditions, where the video did not change in the test phase, start and stop frames of the test phase were calculated based on the medians of all pre-test or post-test durations, which were added to either the start of the pre-test phase or the newly calculated start frame of the test phase, respectively. This approach guaranteed phase durations to be around the same length, although, pre-test durations in general turned out to be up to half a second longer than post-test durations. Seeing as this is only a small divergence, we decided against scaling phase durations for the sake of simplicity.

Video scoring was conducted on the full length of each recording as it was not possible to determine the exact start and stop of the playback during scoring. Consequently, behaviors scored before the playback had started or after it had ended were discarded from the data-frame, unless their duration overlapped at least in part with the playback. In such cases, behavioral durations were adjusted so that either start or stop frames aligned with those of the playback, such that only the parts of behaviors not coinciding with the playback were cut off. In a few instances, behavioral durations ran through more than one playback phase, which was dealt with in two separate ways depending on the subsequent use of the data.

Tab. 2: Ethogram of scored and statistically analyzed behaviors. For additional behaviors scored during video coding, see Table A1. Adapted from Biegler, 2021.

Category	Behavior	Definition
Event Movement	step	The dove lifts one of her feet off the ground and sets it down again within one second in the same or a different spot. Each step is counted as an individual event.
Body Position	circle	The dove walks while assuming a distinct body posture, i.e. the back is slightly hunched and her head held low forming an almost horizontal line with the back, her wing feathers are slightly spread either on one or both wings and the tail and/or wings may be dragged across the floor. These characteristics may differ slightly between individuals, but the overall appearance is the same. The dove may move in a circle, but not necessarily so.
	sex crouch	The dove lowers herself down so that her chest may almost or completely touch the floor. Her tail is raised but slightly hunched. Her shoulders are raised, thereby extending the wings. Her wings may twitch slightly and her eyes may be closed fully or halfway.
	rudimentary crouch	The dove assumes a position akin to the sex crouch, though its characteristics are not fully pronounced. The wings are not extended like in the sex crouch, but may twitch in a similar fashion.
	nest coo position	The dove stands with her tail held high and her head lowered down, forming a line with the rest of her body, although she might move her head around a bit. Both feed are on the ground, but she may stand on the tips of her toes. Her wings may twitch at frequencies slower than the quivers (wing flip), but are not extended like in the sex crouch. The dove may vocalize while in this position.
Preening	wing preen	The dove touches her wing with her beak or runs it along her wing feathers.
	other-preen	The dove touches or runs through the feathers of any area of the body that is not the wings with her beak.
Quivers	quiver	The wing and/or tail feathers are set into rapid motion similar to vibration. This can occur while the dove is moving or stationary. Quivers of the wing feathers may additionally be accompanied by an extension of the wings.
Duration Vocalization	perch coo	The dove produces a cooing sound while assuming a perching position, i.e. her head is held higher than her tail and both feet are in full floor contact.
	nest coo	The dove produces a cooing sound while assuming a nest coo position, i.e. her tail is held high and her head lowered down, forming a line with the rest of her body, although she might move her head around a bit. Both feed are on the ground, but she may stand on the tips of her toes. Her wings may twitch at frequencies slower than the quivers (wing flip), but are not extended like in the sex crouch.

For count data analysis, behavioral durations were assigned to the phase they originated in with the exception of very long duration behaviors, which were defined as behaviors longer than 90 frames (1.5 seconds) after visually inspecting a histogram of all behavioral durations. These long-lasting behaviors were also assigned to the phase they started in, unless at least 85% of their whole duration occurred in the following phase. Given that there were only a few cases of phase-overlapping durations, this 85% threshold was chosen after visual inspection of the relevant cases. Once all behaviors were assigned to the respective phase, the occurrence of all behaviors was summed by subject, experiment day and playback phase to obtain the dataframe of count data for subsequent statistical analyses of event behaviors.

For duration data analysis, phase-overlapping behaviors were split between phases so that the partial durations were assigned to the phase they were observed in. This, however, was not done for vocalizations as it seemed unnatural to split them, given they usually occur as discrete units under natural conditions, and were instead assigned to the phase they originated in. Subsequently, durations for each behavior were again summed per subject, experiment day and playback phase to obtain the dataframe used for analysis of behavioral durations. In addition, a composite variable of sexual behavior durations was created, which included the durations of preening (total duration), quivering, circle walking, sex and rudimentary crouching, nest coo position and nest-cooing (see Tab. 2) and served the purpose of obtaining a full picture of sexual responses accounting for the fact that different females may show sexual interest in different ways. Despite the fact that preening was initially scored separately for the body area that was preened (i.e. wing vs. other body areas), total preening duration was used because visual inspection of count data did not suggest any distinct differences between wing and other-preening (Fig. 3). Due to the fact that some of the behaviors making up the sexual behavior variable could potentially occur at the same time, we excluded duration overlaps to avoid artificially increasing the actual duration of sexual behavior. In a similar manner, all quiver occurrences coinciding with vocalizations were identified and excluded from the dataframe as it remains unclear whether quivers are actually caused by body movements accompanying vocalizations.

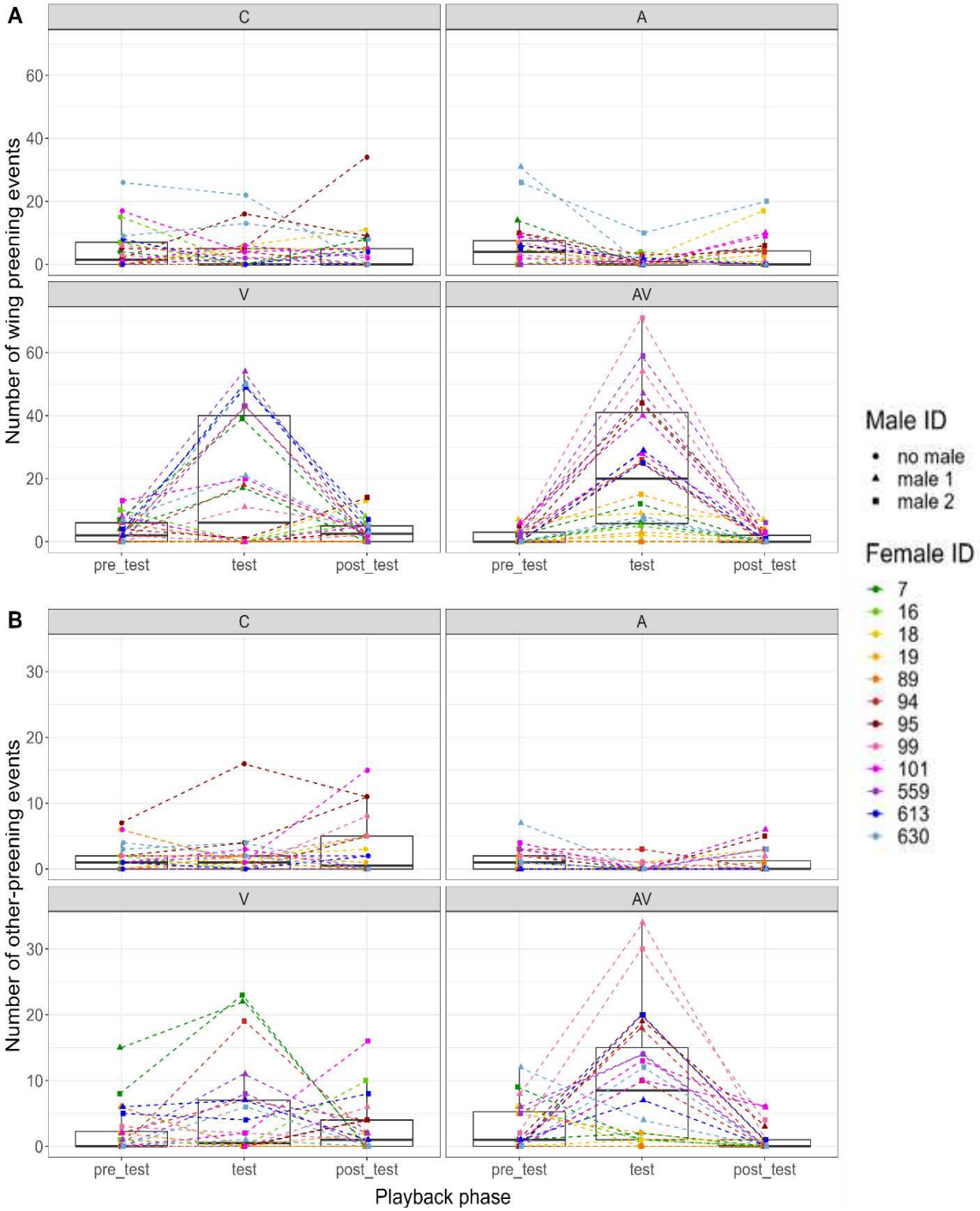


Fig. 3: Boxplots of the number of preening events across conditions per playback phase, separated into wing and other-preening. A) Number of wing preening events. **B)** Number of other-preening events. Boxplots depict first and third quartiles as well as the median, and whiskers represent values within an inter-quartile range (IQR) times 1.5. Points represent individual observations per female and experiment trial. Color indicates female ID, shape represents male ID/absence of male stimulus (control conditions). Letters indicate condition: C = control, A = auditory, V = visual, AV = audiovisual.

Additionally, the GoPro recordings of female behavior in the isolation cages were scored by Beatriz Paiva, a visiting Erasmus intern. Coos were coded for each female whenever it was possible to identify the vocalizing individual with certainty, which was not always the case due to a relatively large area being covered by only two cameras. For the same reason, vocalizations were generalized as coos, because it was not possible to visually categorize them as either nest or perch coos. Again, data wrangling was conducted in R using the aforementioned packages. Number of coos were summed per female and isolation day, categorized into rest and testing days and subsequently plotted using the R package *ggplot2* (Wickham 2016).

2.6.2 Data Analysis

All statistical analyses were conducted in R version 4.3.2 (R Core Team 2023) and R Studio version 2023.12.0+369 (Posit Team 2023). For investigating the effect of condition on female behavior, Generalized Linear Mixed Models (GLMMs) were fitted using the package *glmmTMB* (Mollie et al. 2017) with a beta distribution and logit link for continuous (duration data) and a negative binomial distribution for discrete (count data) response variables, as the use of Poisson distributions lead to substantial overdispersion. The control condition was excluded from these models as the lack of any male stimulus in control conditions created an imbalance in the data for the male identity variable. As response variables, the number of steps, preening events and quivers as well as the proportion of sexual behavior out of 120 s (duration of each playback phase) were used. Additionally, proportions were transformed to fit a range between 0 and 1, which was required for a beta distribution. Condition, playback phase and male identity were included as fixed effects as well as an interaction between condition and playback phase. Female identity was added as random effect to account for repeated testing. Using a custom function written by Roger Mundry (doi: 10.5281/zenodo.7670524), random slopes for condition, playback phase and male identity were identified, dummy coded and centered. All identifiable random effect slopes were included in the model. To avoid model convergence issues, correlations between random slopes and intercepts were removed. Thus, the general structure for the full model looked as follows:

$$\text{behavioral response} \sim \text{condition} * \text{playback phase} + \text{male ID} + (1 + \text{V condition} + \text{AV condition} + \text{test} + \text{posttest} + \text{male.2} \,||\, \text{female ID})$$

Model diagnostics were conducted using additional custom functions provided by Roger Mundry (doi: 10.5281/zenodo.7670524) for assessing potential overdispersion, plotting best linear unbiased predictors to ensure they followed a normal distribution as well as for estimating

model stability by sequentially dropping random effect levels and comparing the resulting estimates. Collinearity between predictors was determined via variance inflation factors (VIFs) using the R package *car* (Fox & Weisberg 2019) with the same response variables and fixed effects excluding the interaction between condition and playback phase within a standard linear model. Normal distribution of model residuals was visually inspected and deemed reasonable for all models. Subsequently, full models were compared to reduced models lacking the interaction between condition and playback phase. This procedure was repeated in the same way for each model and no further model comparisons were needed due to the obtained results. Sample size encompassed 12 individuals with three conditions (A, V and AV), each presented once for each male stimulus and separated into three phases per experiment trial.

For the model of activity level (measured as number of steps), overdispersion, which refers to a bigger variability in the data than expected, was checked. The obtained dispersion parameter indicated slight underdispersion (dispersion parameter = 0.86), leading to potentially conservative p-values. No issues of collinearity (max. VIF = 1) were found on the basis of variance inflation factors. Best linear unbiased predictors were visually inspected, confirming a reasonably normal distribution. Model stability, furthermore, was confirmed through stepwise exclusion of random effect levels.

The full model for preening showed underdispersion as well with a dispersion parameter of 0.66, which was again deemed acceptable as it only leads to potentially conservative p-values. A maximum VIF of 1 indicated no collinearity issues and best linear unbiased predictors appeared largely fine except for moderately big ranges for the random slopes of the V condition and the post-test phase within individuals, likely attributable to large inter-individual differences. Model stability testing demonstrate minor issues with model convergence, but the results indicated reasonable stability nonetheless.

For the model including number of quivers as response variable, no overdispersion was detected (dispersion parameter = 0.92) and distribution of best unbiased linear predictors appeared reasonable, although the ranges of the random slopes of the test as well as the post-test phase within individuals was quite large, again pointing towards large inter-individual variation. However, there was no indication for this to cause any further problems for the model. No collinearity between predictors was found (max. VIF = 1). The model, additionally, appeared fairly stable with the exception of the V condition as well as the interaction between the V condition and the post-test phase.

The full model including composite sexual behavior as response variable returned a dispersion parameter of 0.68, indicating underdispersion. The distribution of best linear unbiased predictors was visually assessed and largely seemed acceptable with the exception of the random slope of the AV condition within subjects exhibiting a rather large range. Collinearity was not an issue as indicated by a maximum VIF of 1 and the model proved to be stable considering the small sample size.

For all models, some interactions between condition and playback phase were always significant and therefore post hoc investigations using Tukey tests with adjusted p-values were conducted for determining contrasts between levels in the interaction term. This was done using the R package *emmeans* (Lenth 2024).

Numerous attempts were made to fit GLMMs also for the behavioral responses of number of perch coos and circling events, but failed each time due to extreme underdispersion, issues of model convergence and low model stability. It was outside the scope of this Master's thesis to conduct further efforts in finding a suitable model structure. However, because visual representations of the data clearly suggested significant effects (see Fig. 12 and 14 in the Results section), the data of all three playback phases were added together for each female and experiment day and non-parametric Friedman tests as well as subsequent paired Wilcoxon signed-rank tests were applied to further investigate the potential effects of condition using the R package *rstatix* (Kassambara 2023a).

All plots were created using *ggplot2* (Wickham 2016), *ggpubr* (Kassambara 2023b) and *cowplot* (Wilke 2023) as well as *ggeffects* for plotting post-hoc testing results (Lüdecke 2018). Additionally, for some plots the data needed to be further prepared to suit the type of plot, which was achieved using the packages *plyr* (Wickham 2011), *reshape2* (Wickham 2007) and *scales* (Wickham & Seidel 2022).

3. Results

In a within-individual approach, 12 female ring doves were exposed to audiovisual playback of male courtship. The playback design was adapted from Partan and colleagues (2005) and consisted of three phases (2 min each): two control phases (pre- and post-test phase) flanking a test condition showing one of three experimental conditions containing playback of a male conspecific (A = auditory, V = visual and AV = audiovisual) or a control condition presenting no conspecific. Each female was shown each condition twice over the course of eight experiment days interspersed with rest days during which no testing took place. Additionally, while in isolation, female vocalizations were recorded every day over the whole experimental period (including experiment and rest days) for half an hour. These recordings were scored by Beatriz Paiva, whereas all 96 recordings obtained during the experiment were coded by me. For subsequent statistical analyses reported below, only behaviors that were displayed by at least half of the birds were considered.

3.1 Model results

3.1.1 Activity level

The number of steps was scored as a proxy for activity level. This behavior was expressed by all tested birds in all playback phases of all conditions with the exception of one post-test phase of a control condition, adding up to a total of 14,762 steps over the whole experiment. Most steps occurred in the auditory test phase (mean = 88.75, sd = 66.24, N = 24 [12 birds x 2 trials]), while the lowest numbers of steps occurred in the test (mean = 37.75, sd = 34.82, N = 24) and the post-test phase of the control condition (mean = 31.92, sd = 27.37, N = 24) as well as in the test phase of the visual condition (mean = 33.71, sd = 34.82, N = 24). Medians and data ranges are displayed in boxplots in Fig. 4A. For a detailed summary of the means and standard deviations of all count behaviors, see Table A2 in the Appendix.

To investigate whether these differences were significant, a GLMM was fit using number of steps as response variable and including condition, playback phase and stimulus male as well as an interaction term between condition and playback phase as fixed effects plus female ID as random effects including all identifiable random slopes. This full model was significantly better than a reduced model lacking the interaction term but otherwise identical to the full model ($\chi^2 = 17.71$, df = 4, $p = 0.001$). As this indicates that including the interaction term provides the best model, further analyses were conducted with the full model. The interaction between the V condition and the test phase was significant and a trend emerged for the interaction of the

AV condition and the test phase. Additionally, significant results were found for the main effect of test phase but not for any of the other main effects (Tab. 3, Fig. 4B).

Tab. 3: Model output for the model of activity level, measured as number of steps.

Explanatory variables	Estimates (95% CI)	SE	z value	p value	
(Intercept)	3.74	0.19	19.85	< 0.001	***
V condition	-0.07	0.21	-0.35	0.73	
AV condition	0.09	0.17	0.51	0.61	
Test phase	0.54	0.19	2.76	0.006	**
Post-test phase	0.17	0.18	0.92	0.36	
Male ID	-0.001	0.08	-0.02	0.98	
V condition : test phase	-0.84	0.25	-3.34	< 0.001	***
AV condition : test phase	-0.42	0.24	-1.71	0.09	.
V condition : post-test phase	0.16	0.25	0.66	0.51	
AV condition : post-test phase	0.01	0.24	0.04	0.96	

Significance codes: < 0.1; * < 0.05; ** < 0.01; *** < 0.001. Reference categories are “A” for “condition” and “pre-test” for “playback phase”. N(observations) = 216, N(subjects) = 12

Subsequent post hoc tests contrasting conditions across playback phases showed significantly higher activity levels in the test phase of the A than the V conditions (post-hoc: E = 0.91, SE = 0.21, p = 0.0001; p-values adjusted for multiple comparisons using Tukey correction) and lower activity levels in the test phase of the V than AV conditions (post-hoc: E = -0.58, SE = 0.21, p = 0.02) (Fig. 5A). Furthermore, a contrast of activity within playback phases across conditions showed significantly lower activity levels in the pre-test phase than in the test phase of the A condition (post-hoc: E = -0.54, SE = 0.20, p = 0.02), while significantly more steps occurred in the post-test phase than the test phase of the V condition (post-hoc: E = -0.63, SE = 0.20, p = 0.005) (Fig. 5B).

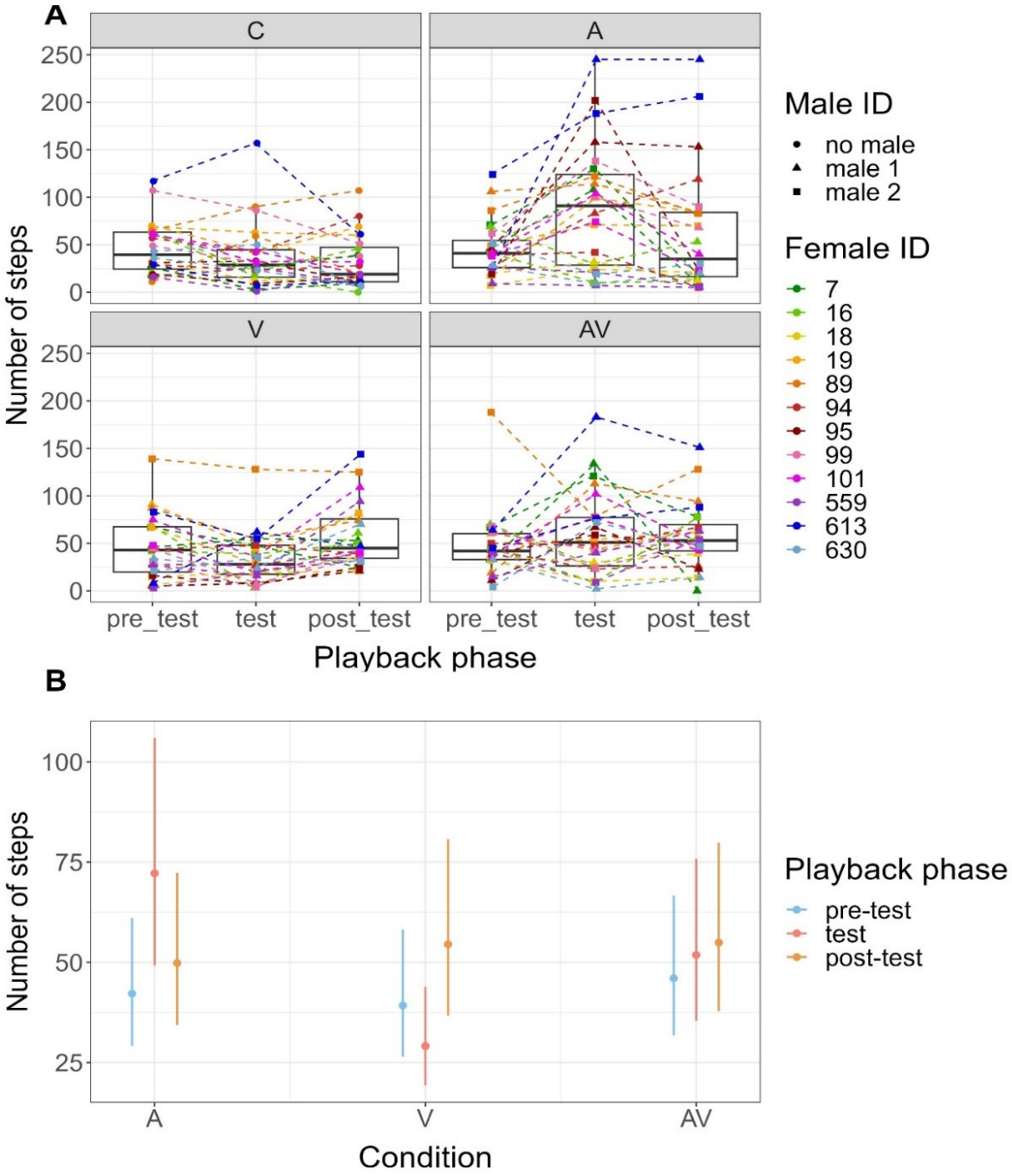


Fig. 4: Activity level measured as number of steps. A) Boxplots of the number of steps across conditions per playback phase using the data obtained through video scoring. Box-and-whisker plots depict the median as well as the first and third quartiles (represented by the box) and the values within the inter-quartile range (IQR) times 1.5 (represented by the whiskers). Points are overlaid to display observations per individual and experiment trial, with shapes representing male ID as well as absence of any male stimulus. Colors indicate female ID and letters represent conditions: C = control, A = auditory, V = visual, AV = audiovisual. **B)** Plots of model predictions for the number of steps per condition using the model results with dots representing the predicted response and error bars depicting 95% confidence intervals. Colors indicate playback phases.

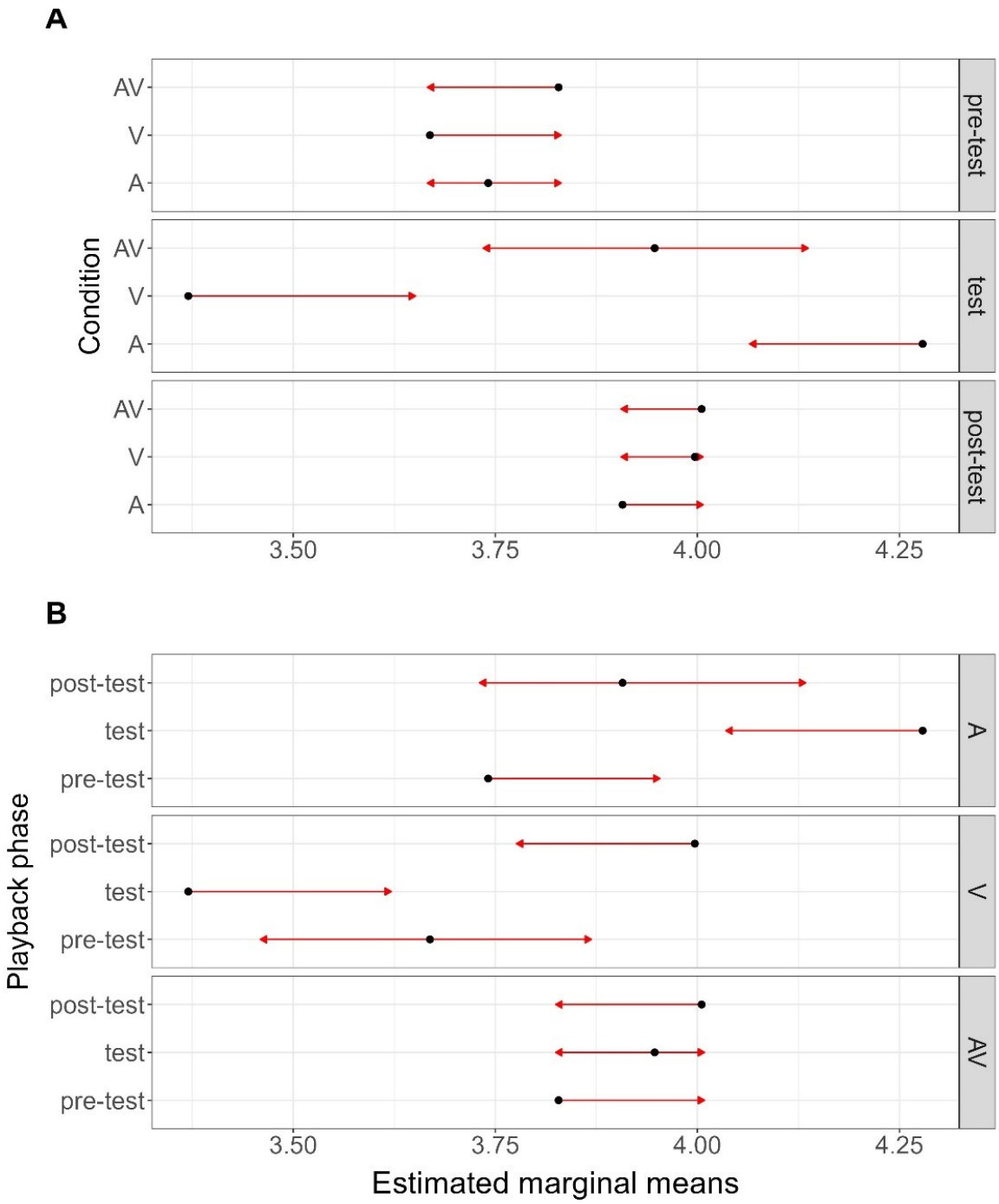


Fig. 5: Contrasts between condition and playback phase of number of steps resulting from post hoc testing. A) Contrasts across conditions grouped by playback phase. **B)** Contrasts across playback phases by condition. Dots represent estimated marginal means (EMMs) per contrast level, red arrows indicate comparisons between EMMs. Lack of overlap between arrows of the same group indicates significant differences between the respective conditions or phases.

3.1.2 Preening

Total number of preening was analyzed as a sum of all scored wing and other-preening events as no distinct differences between the two body areas emerged through visual inspection (Fig. 3). Most preening events occurred in the test phase of the audiovisual conditions (mean = 32.96, sd = 30.07, N = 24), followed by the test phase of the visual condition (mean = 22.00, sd = 25.82, N = 24), although quite some variability became apparent (Fig. 6A). The fewest preening events occurred in the auditory test phase (mean = 1.21, sd = 2.36, N = 24) and the post-test phase of the audiovisual condition (mean = 2.21, sd = 2.96, N = 24) (Tab. A2).

The full model including an interaction term of condition and playback phase was significantly better than the reduced model lacking the interaction (χ^2 = 40.09, df = 5, p < 0.001). Significant effects emerged for the interaction of the test phase with the V condition and the AV condition, respectively, as well as for the main effect level of test phase. Trends were found for the main effect levels of post-test phase and male ID (Tab. 4, Fig. 6B).

Tab. 4: Model output for the response variable total preening number.

Explanatory variables	Estimates (95% CI)	SE	z value	p value	
(Intercept)	1.59	0.37	4.24	< 0.001	***
V condition	-0.25	0.49	-0.51	0.61	
AV condition	-0.37	0.45	-0.82	0.41	
Test phase	-1.90	0.50	-3.80	<0.001	***
Post-test phase	-0.85	0.50	-1.71	0.09	.
Male ID	0.38	0.21	1.79	0.07	.
V condition : test phase	2.82	0.65	4.37	< 0.001	***
AV condition : test phase	3.73	0.63	5.95	< 0.001	***
V condition : post-test phase	0.99	0.63	1.56	0.12	
AV condition : post-test phase	-0.22	0.63	-0.36	0.72	

Significance codes: < 0.1; * < 0.05; ** < 0.01; *** < 0.001. Reference categories are “A” for “condition” and “pre-test” for “playback phase”. N(observations) = 216, N(subjects) = 12

Post hoc investigations of contrasts between conditions revealed that females preened significantly less in the test phase of auditory than visual (post-hoc: E = -2.57, SE = 0.55, p < 0.0001) as well as audiovisual conditions (post-hoc: E = -3.36, SE = 0.50, p < 0.0001). A significant difference was additionally found between the post-test phase of V and AV conditions, with more preening events scored in AV conditions (post-hoc: E = 1.33, SE = 0.56, p = 0.046)

(Fig. 7A). Additionally, contrasts between playback phases revealed significantly higher numbers of preening events in the pre-test than the test phase of A conditions (post-hoc: E = 1.90, SE = 0.50, p = 0.0004), whereas an increase from the pre-test to the test phase (post-hoc: E = -1.82, SE = 0.46, p = 0.0002) as well as a decrease from the test to the post-test phase occurred in AV conditions (post-hoc: E = 2.90, SE = 0.54, p < 0.0001) (Fig. 7B).

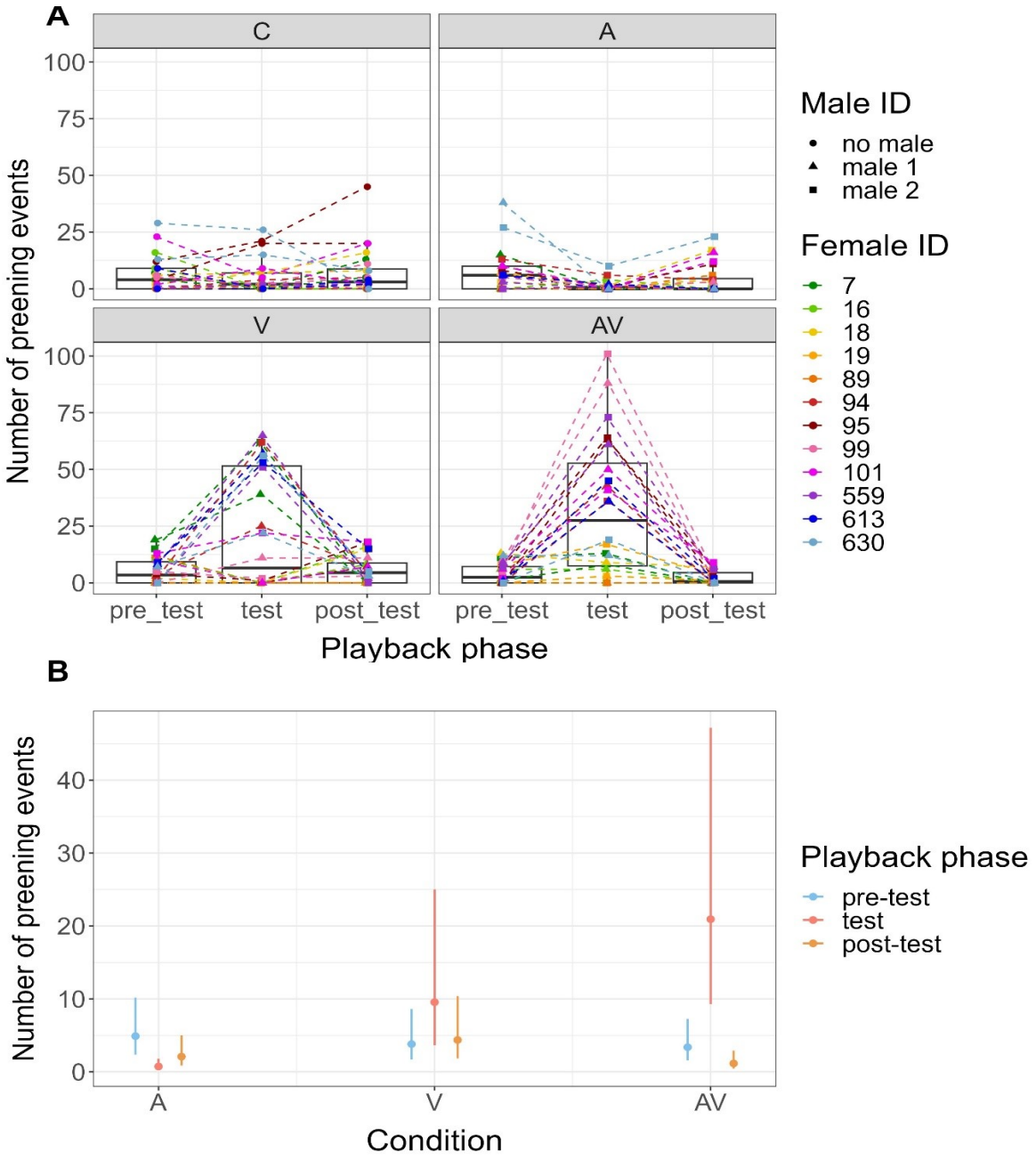


Fig. 6: Number of total preening events. A) Boxplots of the number of total preening events across conditions per playback phase using the data obtained through video scoring. Shapes represent male ID as well as absence of any male stimulus, while female ID is marked by color. Letters indicate condition: C = control, A = auditory, V = visual, AV = audiovisual. **B)** Plots of model predictions for the number of preening events per condition using the model results. Colors indicate playback phases.

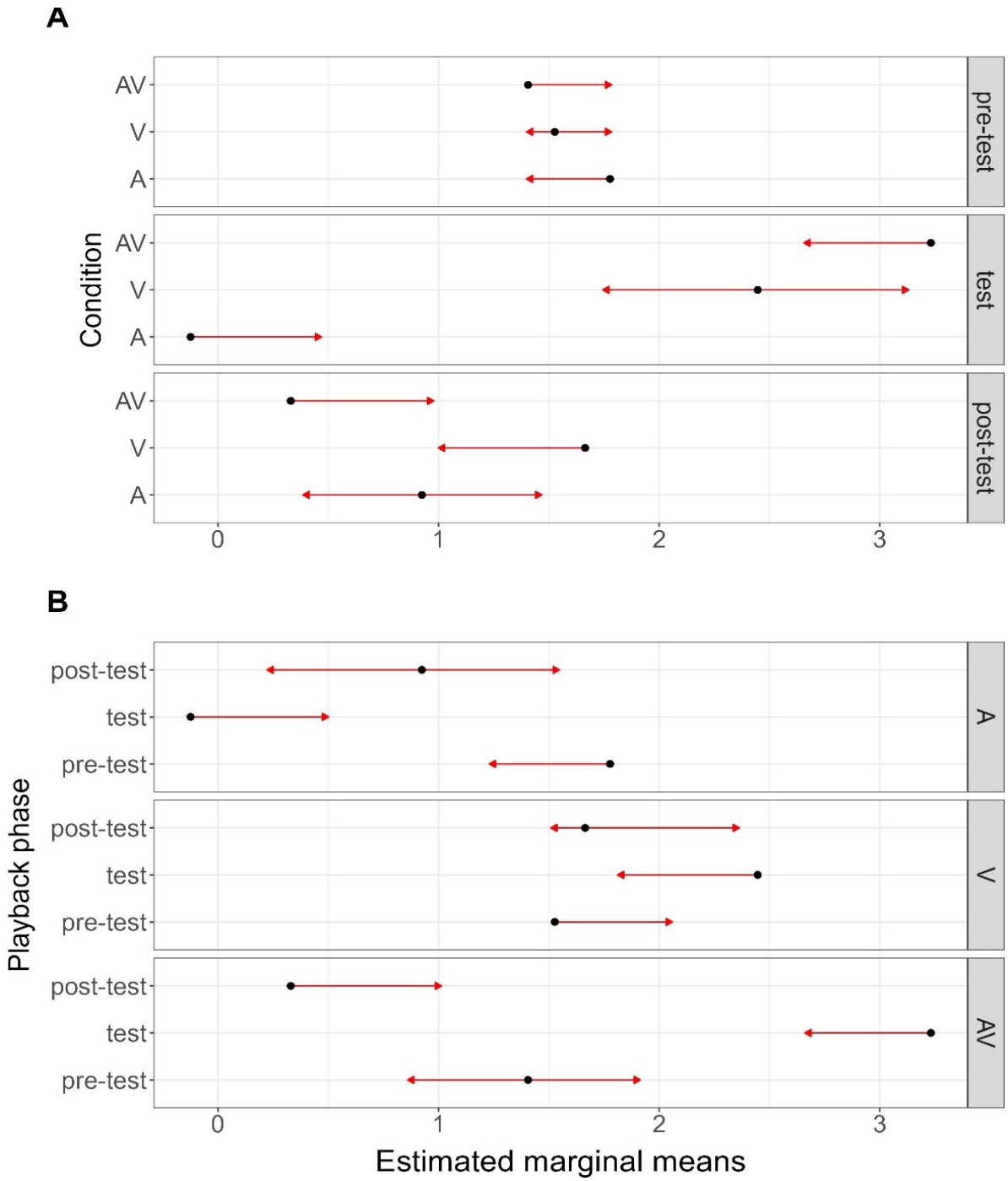


Fig. 7: Contrasts between condition and playback phase of the total number of preening events resulting from post hoc testing. A) Contrasts across conditions grouped by playback phase. **B)** Contrasts across playback phases by condition. Lack of overlap between arrows of the same group indicates significant differences between the respective conditions or phases.

3.1.3 Quivers

For the analysis of the number of quivers, only quivers not coinciding with vocalizations were considered. The highest numbers of quivers were generally observed in the test phases of all conditions showing a male stimulus and exhibited a gradual increase from the auditory (mean = 6.96, sd = 7.53, N = 24) to the visual (mean = 11.58, sd = 7.44, N = 24) and from the visual to the audiovisual condition (mean = 18.17, sd = 11.90, N = 24) (Fig. 8A, Tab. A2). Again, a full model with an interaction between condition and playback phase was compared to a reduced model without the interaction, confirming that the full model was a better fit ($\chi^2 = 21.50$, df = 4, $p < 0.001$). Significant results were obtained for the main effect levels of test and post-test phase, but not for the main effect of condition. Furthermore, the interaction between the AV condition and the post-test phase was significant and a trend for the interaction of the V condition and the test phase was indicated (Tab. 5, Fig. 8B).

Tab. 5: Model output for the response variable number of quivers.

Explanatory variables	Estimates (95% CI)	SE	z value	p value	
(Intercept)	-1.13	0.45	-2.52	0.01	*
V condition	-0.24	0.53	-0.45	0.66	
AV condition	0.67	0.45	1.50	0.13	
Test phase	2.97	0.51	5.85	<0.001	***
Post-test phase	1.19	0.54	2.19	0.03	*
Male ID	-0.21	0.15	-1.41	0.15	
V condition : test phase	0.98	0.57	1.72	0.09	.
AV condition : test phase	0.41	0.50	0.82	0.41	
V condition : post-test phase	-0.17	0.64	-0.27	0.79	
AV condition : post-test phase	-1.65	0.61	-2.72	0.006	**

Significance codes: < 0.1; * < 0.05; ** < 0.01; *** < 0.001. Reference categories are “A” for “condition” and “pre-test” for “playback phase”. N(observations) = 216, N(subjects) = 12

Subsequent post hoc investigations contrasting condition across playback phases indicated that significantly fewer quivers occurred during auditory than during visual test phases (post-hoc: E = -0.74, SE = 0.25, p = 0.009) as well as during audiovisual test phases (post-hoc: E = -0.33, SE = 0.24, p < 0.0001). Additionally, slightly more quivers occurred during the post-test phase of A than AV conditions (post-hoc: E = 0.98, SE = 0.41, p = 0.045) (Fig. 9A). Comparisons between playback phases across conditions showed an increase in quivering from

the pre-test to the test phase and a decrease from the test to the post-test phase for all conditions. Consequently, significantly fewer quivers occurred in the pre-test than the test phase for A conditions (post-hoc: E = -2.97, SE = 0.51, $p < 0.0001$), for V conditions (post-hoc: E = -3.95, SE = 0.54, $p < 0.0001$) and for AV conditions (post-hoc: E = -3.38, SE = 0.45, $p < 0.0001$), whereas more quivers occurred in the test than the post-test phases of A conditions (post-hoc:

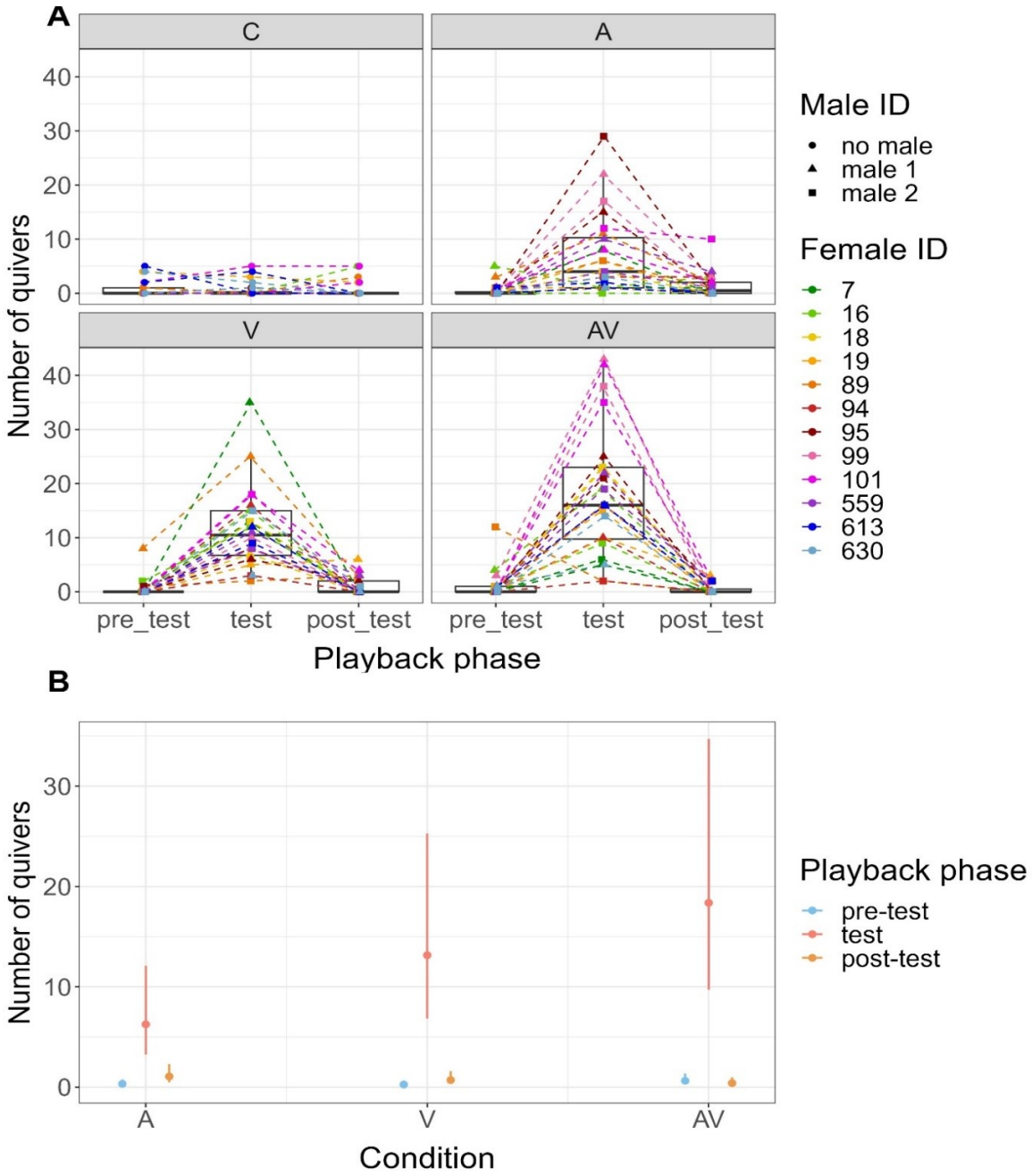


Fig. 8: Number of quivers. A) Boxplots of the number of quivers across conditions per playback phase using the data obtained through video scoring. Shapes represent male ID as well as absence of any male stimulus, while female ID is marked by color. Letters indicate condition: C = control, A = auditory, V = visual, AV = audiovisual. **B)** Plots of model predictions for the number of quivers per condition using the model results. Colors indicate playback phases.

E = 1.78, SE = 0.62, p = 0.002), V conditions (post-hoc: E = 2.93, SE = 0.53, p < 0.0001) and also AV conditions (post-hoc: E = 3.84, SE = 0.56, p < 0.0001). Additionally, a trend was found indicating slightly fewer quivers occurred during the pre-test than the post-test in the A condition (post-hoc: E = -1.19, SE = 0.54, p = 0.07) (Fig. 9B).

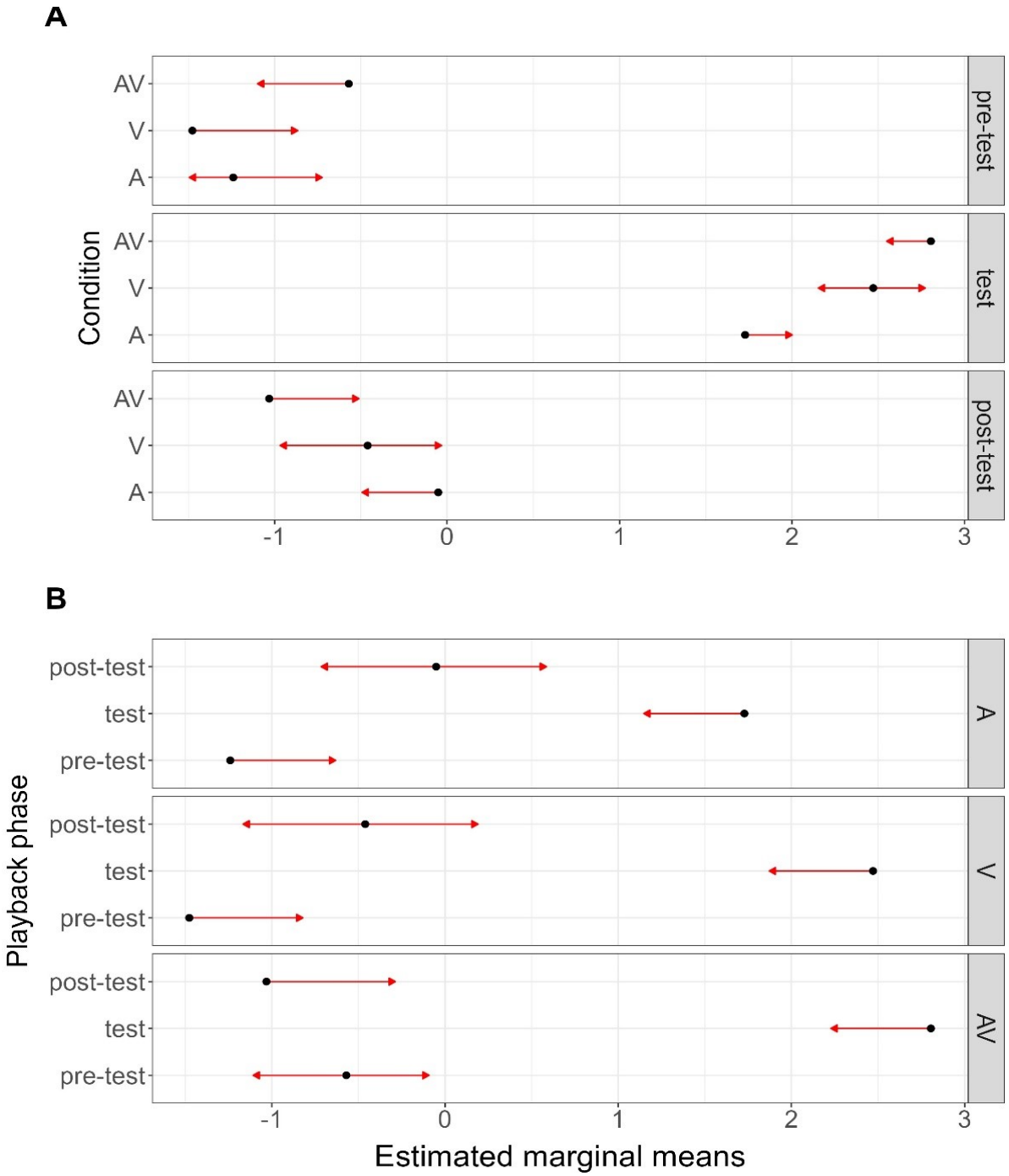


Fig. 9: Contrasts between condition and playback phase of the number of quivers resulting from post hoc testing. A) Contrasts across conditions grouped by playback phase. **B)** Contrasts across playback phases by condition. Lack of overlap between arrows of the same group indicates significant differences between the respective conditions or phases.

3.1.4 Composite sexual behavior

Overall sexual behavior was analyzed in the form of a composite measure including the durations of preening, quivers, circling, nest coo position, nest coos, sex crouch and rudimentary crouch. Durations were longest in the test phases of visual (mean = 29.83 s, sd = 25.79, N = 24) and audiovisual conditions (mean = 54.41 s, sd = 20.81, N = 24) and to a lesser extent in the auditory condition (mean = 7.70 s, sd = 7.53, N = 24) (Fig. 10A, Tab. A3). For detailed information on the durations of the behaviors making up the sexual behavior variable as well as the composite measure itself, see Table A3 in the Appendix.

The model of the sexual behavior response including the interaction between condition and playback phase was a significantly better fit than the one lacking the interaction (full vs. reduced: χ^2 = 38.65, df = 4, p < 0.001). The interaction between the test phase with the V condition and the AV condition, respectively, as well as between the post-test phase and the AV condition were significant, but main effects of condition, playback phase and stimulus male were not (Tab. 6, Fig. 10B).

Tab. 6: Model output for sexual behavior model.

Explanatory variables	Estimates (95% CI)	SE	z value	p value	
(Intercept)	-2.73	0.27	-10.27	< 0.001	***
V condition	-0.15	0.29	-0.50	0.62	
AV condition	-0.33	0.36	-0.93	0.35	
Test phase	0.38	0.28	-1.37	0.17	
Post-test phase	-0.11	0.28	-0.40	0.69	
Male ID	-0.12	0.15	-0.80	0.43	
V condition : test phase	1.38	0.38	3.61	0.0003	***
AV condition : test phase	2.51	0.43	5.84	< 0.001	***
V condition : post-test phase	0.31	0.39	0.78	0.43	
AV condition : post-test phase	0.88	0.43	2.06	0.04	*

Significance codes: < 0.1; * < 0.05; ** < 0.01; *** < 0.001. Reference categories are “A” for “condition” and “pre-test” for “playback phase”. N(observations) = 216, N(subjects) = 12

Post hoc contrasts across conditions revealed that females spent significantly less time exhibiting sexual behavior in the test phase of A conditions than of V (post-hoc: E = -1.24, SE = 0.27, p < 0.0001) and AV conditions (post-hoc: E = -2.18, SE = 0.32, p < 0.0001). Similarly, significantly less sexual behavior was observed in the test phase of V conditions than AV conditions (post-hoc: E = -0.97, SE = 0.29, p = 0.004) (Fig. 11A). Contrasts across playback phases

showed that in V conditions females exhibited significantly less sexual behavior in the pre-test than test phases (post-hoc: E = -1.77, SE = 0.28, p < 0.0001) and significantly more in the test phases than the post-test phases (post-hoc: E = 1.57, SE = 0.30, p < 0.0001).

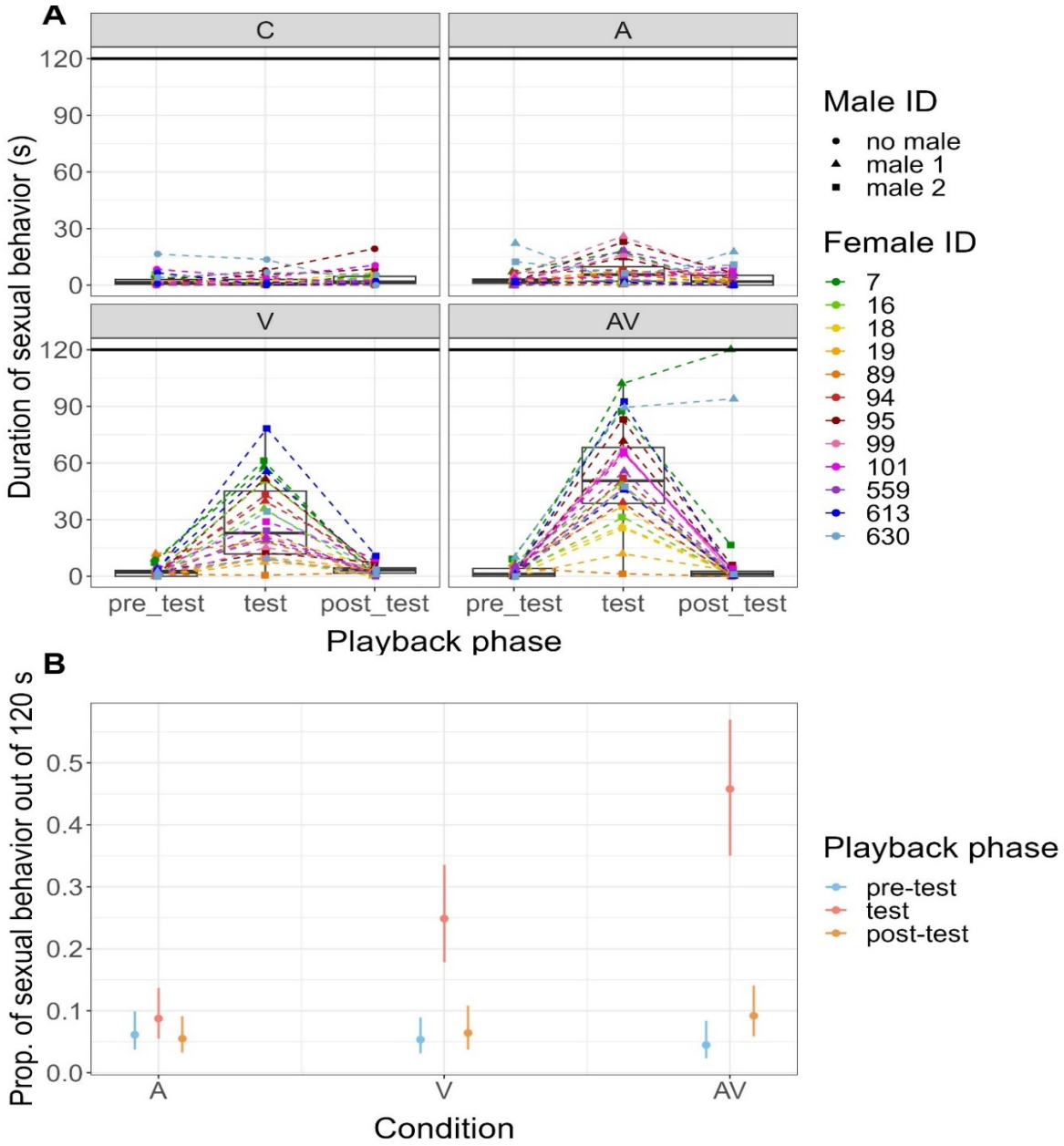


Fig. 10: Composite variable of sexual behavior. A) Boxplots of the duration of sexual behavior across conditions per playback phase using the data obtained through video scoring. Shapes represent male ID as well as absence of any male stimulus, while female ID is marked by color. Letters indicate condition: C = control, A = auditory, V = visual, AV = audiovisual. Bold horizontal lines indicate the total duration of each phase (120 s). **B)** Plots of model predictions for the proportion of sexual behavior out of 120 seconds representing the length of each playback phase (marked by bold line in plot **A**) per condition using the model results. Transforming data into proportions of total phase duration (120 s) was required for using a beta distribution in the model. Colors represent playback phases.

The same became apparent for the AV condition with significantly less time spent showing sexual behavior in pre-test than test phases (post-hoc: E = -2.89, SE = 0.35, $p < 0.0001$) and significantly more in test than post-test phases (post-hoc: E = 2.12, SE = 0.24, $p < 0.0001$), but additionally a slightly significant result for pre-test versus the post-test phases emerged (post-hoc: E = -0.77, SE = 0.32, $p = 0.04$) (Fig. 11B).

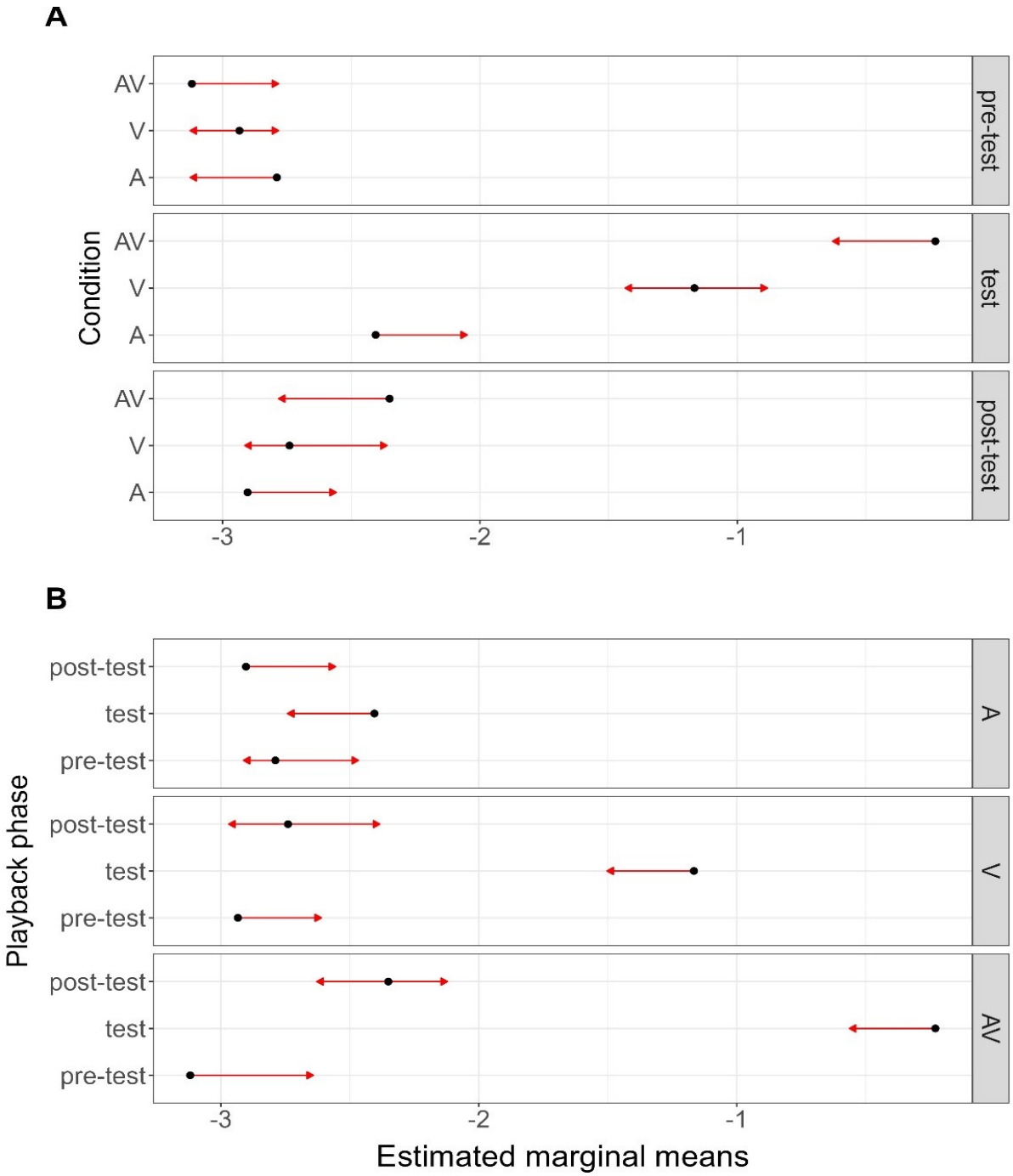


Fig. 11: Contrasts between condition and playback phase of the proportion of sexual behavior resulting from post hoc testing. A) Contrasts across conditions grouped by playback phase. **B)** Contrasts across playback phases by condition. Lack of overlap between arrows of the same group indicates significant differences between the respective conditions or phases.

3.2 Non-parametric tests

3.2.1 Perch coos

The number of perch coos was analyzed using a non-parametric Friedman test including the control condition and summing over playback phases as it was not possible to fit a GLMM within the scope of this Master's thesis (see Chapter 2.6.2). However, through visual inspection it became clear that experimental conditions had an effect on perch-cooing, with considerably more perch coos observed in the test (mean = 5.88, sd = 6.32, N = 24) and post-test phases of the auditory conditions (mean = 7.38, sd = 11.01, N = 24) than in any other phase of any condition (Fig. 12, Tab. A2).

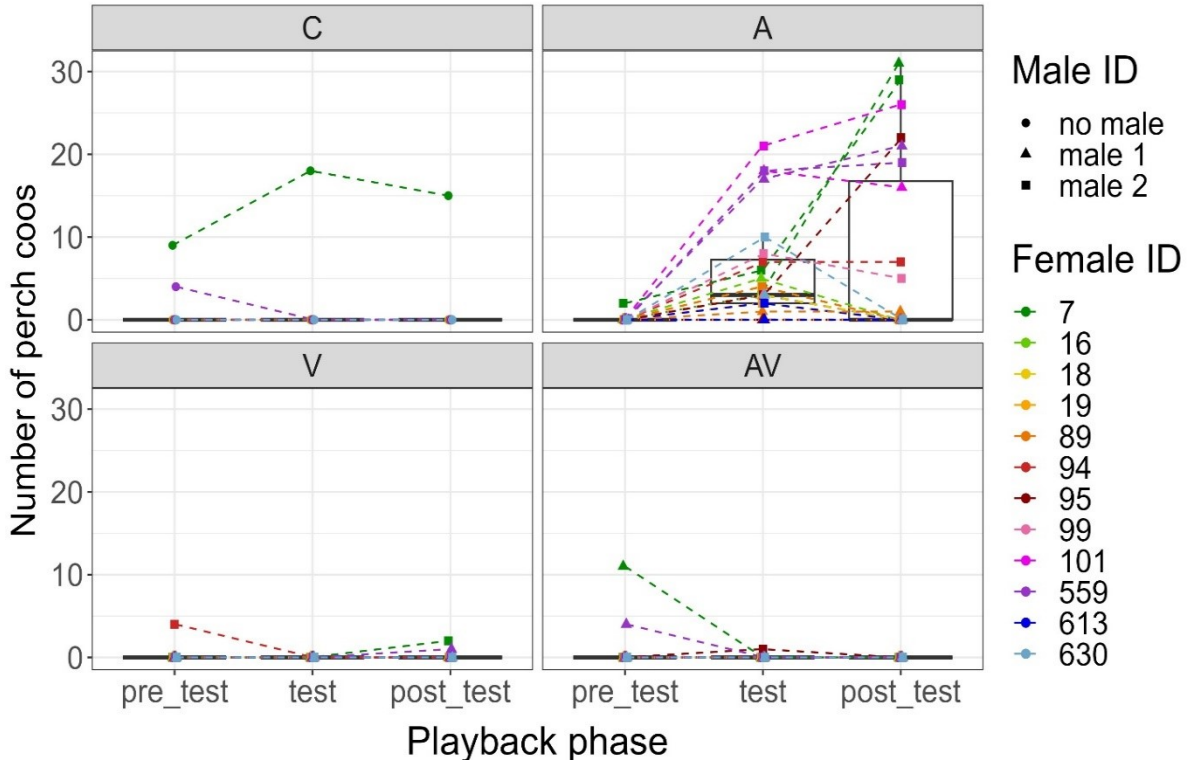


Fig. 12: Boxplots of the number of perch coos across condition and playback phase. Shapes represent male ID as well as absence of any male stimulus, and female ID is marked by color. Letters indicate condition: C = control, A = auditory, V = visual, AV = audiovisual.

This difference in number of perch coos across conditions proved to be significant (Friedman test: $\chi^2 = 31.8$, df = 3, $p < 0.001$), so subsequent pairwise comparisons using paired Wilcoxon signed-rank tests with Bonferroni adjustments were applied for investigating the pairwise differences between conditions. A significant effect was found for all comparisons that included the A condition (C vs. A: p = 0.015, A vs. V: p = 0.015, A vs. AV: p = 0.015), but for none of the remaining comparisons (C vs. V: p = 1, C vs. AV: p = 1, V vs. AV: p = 1) (Fig 13).

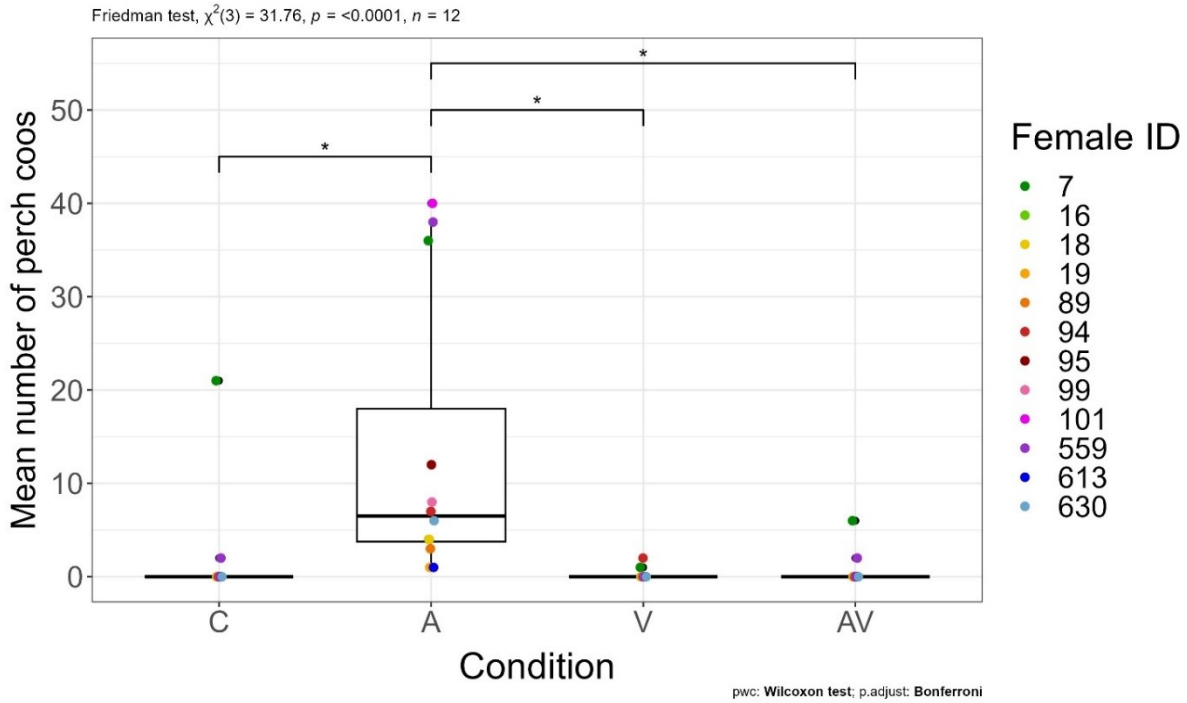


Fig. 13: Boxplots of the mean number of perch coos averaged per condition. For statistical analysis using the Friedman test, playback phases were summed and subsequently averaged over repeated presentations per condition, thus N(observations) was 48. Significant comparisons are marked by brackets and asterisks indicating the level of significance after Bonferroni adjustment (* < 0.05). Female ID is represented by colors of points.

3.2.2 Circling

Circle walking was also analyzed using a Friedman test after all attempts to fit a GLMM failed (see Chapter 2.6.2). Overall, most circling events occurred in the test phase of the audiovisual condition (mean = 4.00, sd = 3.81, N = 24), followed by the test phase of the visual condition (mean = 1.00, sd = 1.98, N = 24) (Fig. 14), which was also reflected in the test results (Friedman test: $\chi^2 = 21.8$, df = 3, $p < 0.001$). Subsequent pairwise comparisons using a paired Wilcoxon signed-rank test indicated a significant difference in circling between the C and the AV condition ($p = 0.03$) as well as between the A and AV condition ($p = 0.04$), while the remaining comparisons did not reach significance (C vs. A: $p = 1$, C vs. V: $p = 0.59$, A vs. V: $p = 1$, V vs. AV: $p = 0.17$), although in the latter case a significant result was found before Bonferroni correction (V vs. AV before adj: $p = 0.03$) (Fig. 15).

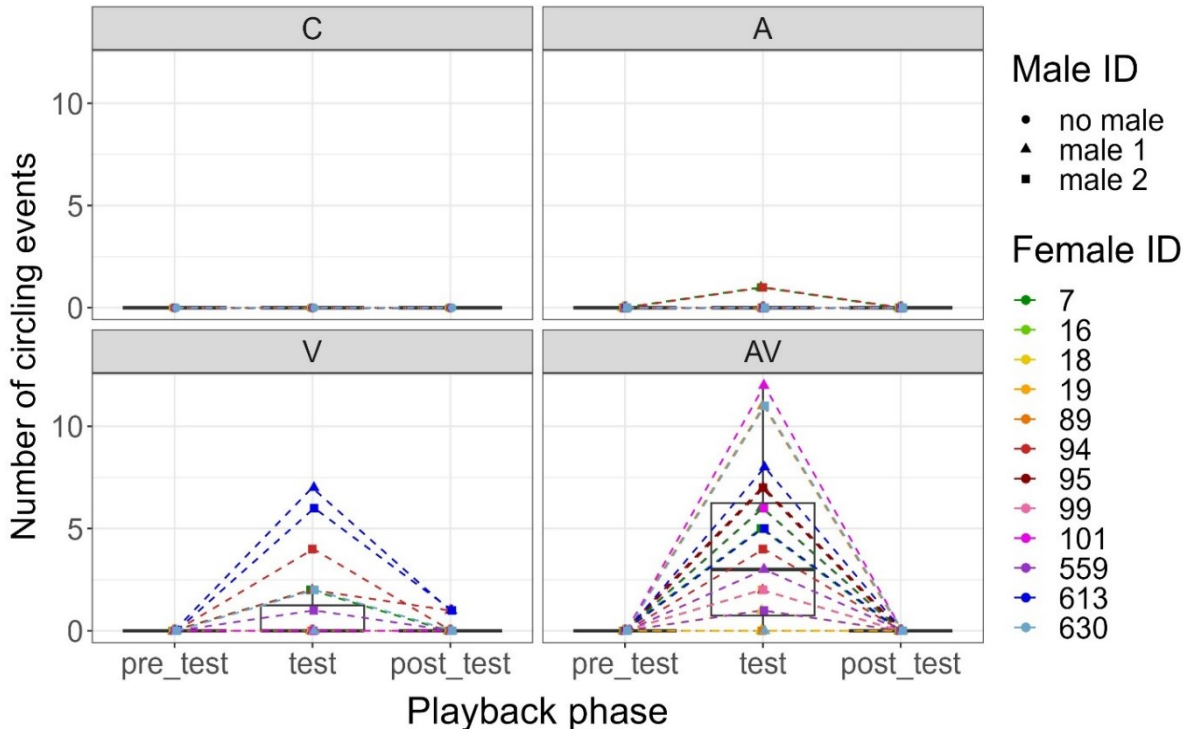


Fig. 14: Boxplots of the number of circling events across conditions and playback phase. Shapes represent male ID as well as absence of any male stimulus, while female ID is marked by color. Letters indicate condition: C = control, A = auditory, V = visual, AV = audiovisual.

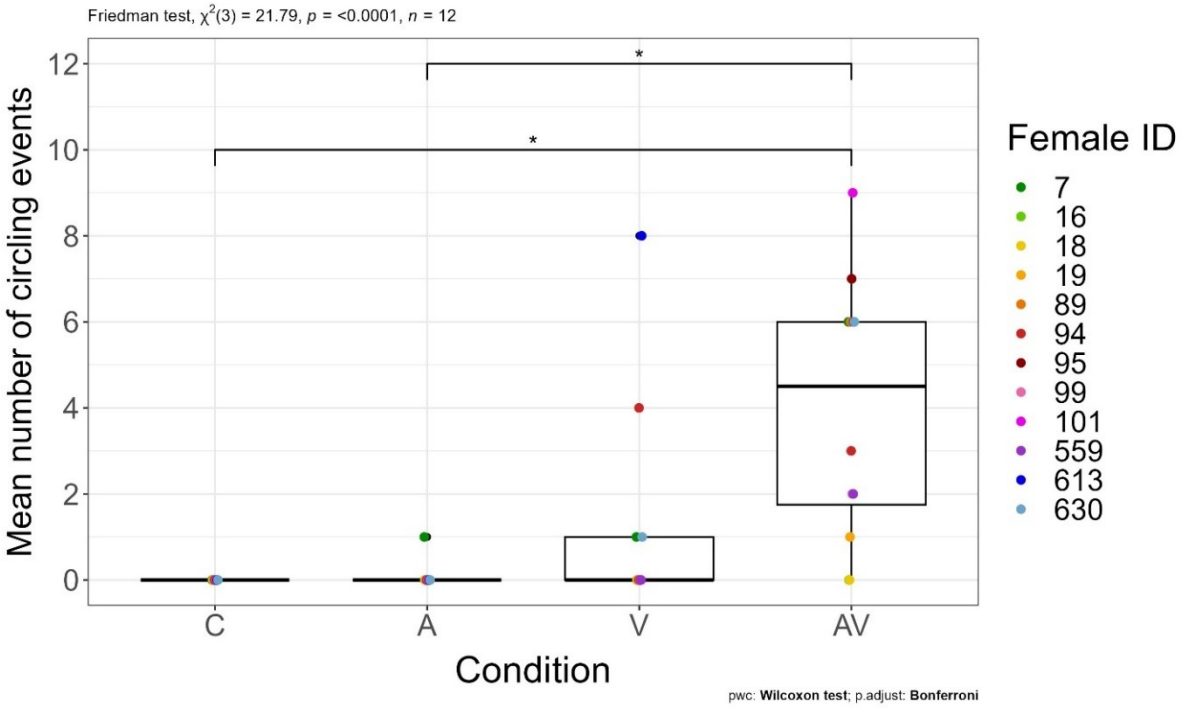


Fig. 15: Boxplots of the mean number of circling events per condition. For statistical analysis using the Friedman test, playback phases were summed and subsequently averaged over repeated presentations per condition, thus N(observations) was 48. Significant comparisons are marked by brackets and asteriks indicating the level of significance after Bonferroni adjustment (* < 0.05). Female ID is represented by colors of points.

3.3 Inter-individual differences

Over the whole experiment, all 12 females exhibited steps (min. = 497, max = 2423, total = 14762), perch coos (min. = 2, max. = 126, total = 389), preening (summed wing and other, min. = 19, max. = 325, total = 2488) and quivers (min. = 38, max. = 168, total = 1051), but to varying degrees (Fig. 16). Only 11 birds displayed circling (min. = 0, max. = 28, total = 126), 3 assumed the nest coo position (min. = 0, max. = 7, total = 13) with two of them also nest-cooing (min. = 0, max. = 31, total = 34) and only 3 showed rudimentary crouching (min. = 0, max. = 7, total = 16). Only one instance of sex crouching was scored in all of the recorded material. An overview of degrees with which behaviors were shown by each female is given in figure 16, which additionally depicts females grouped by age (younger = 14 – 11 months, older = 4 – 6 years) and origin (France or Austria). Altogether, females of different age groups and origin showed similar patterns of behaviors, although behaviors like crouching and nest-coo position were almost exclusively shown by older females, and the degree to which these behaviors were exhibited varied between birds (Fig. 16). Detailed information on the displayed behaviors for each female are summarized in Table A4 of the Appendix.

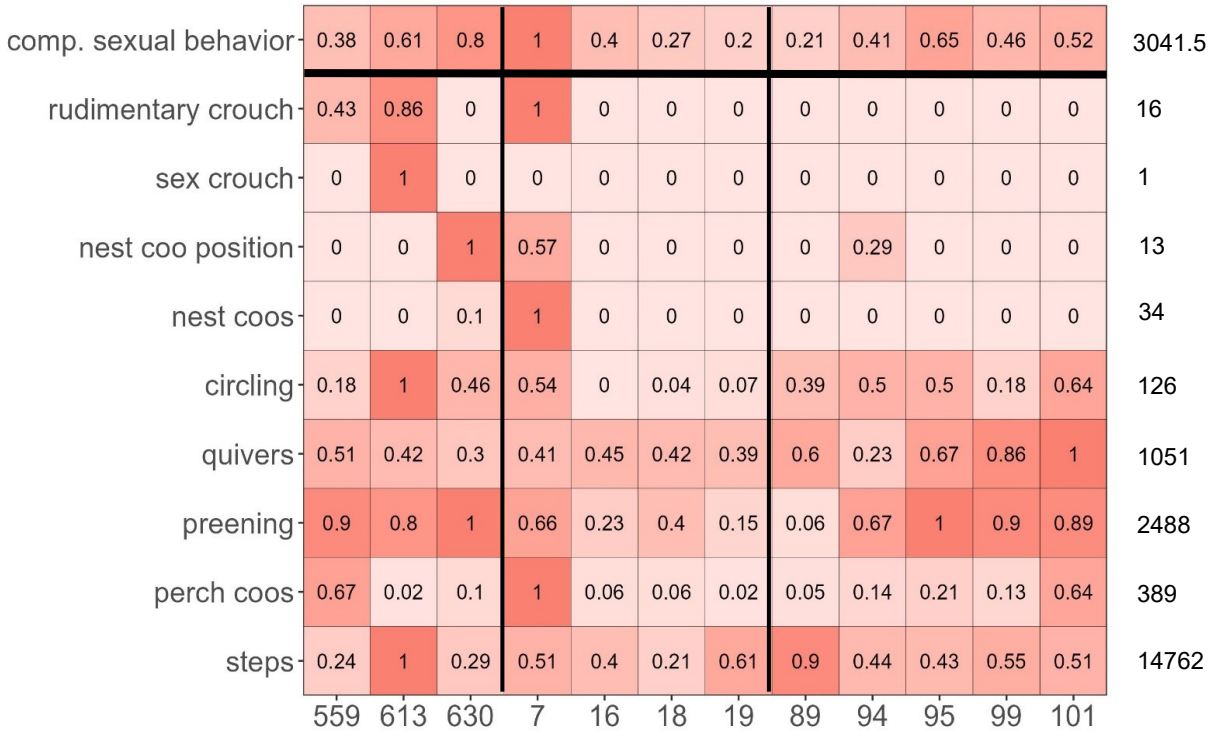


Fig. 16: Heatmap of scaled behavioral measures per subject. Behaviors are shown in rows with their names indicated on the left-hand side and females in columns with their ID numbers shown underneath the heatmap. Behavioral counts of steps, perch coos, preening, quivers, circling, nest coos, nest coo positions, sex crouches and rudimentary crouches as well as the sexual behavior duration (in seconds) were summed over playback phases and conditions and then scaled by dividing values for each female by the maximum number/duration of the respective behavior over all females. Numbers on the right-hand side represent total counts/duration for each behavior. Sections divided by vertical lines indicate groups of age/origin: birds 559, 613 and 630 = older/French, birds 7, 16, 18 and 19 = older/Austrian, birds 89, 94, 95, 99 and 101 = younger/Austrian.

3.4 GoPro recordings

Over the whole experimental period, birds were kept in indoor isolation cages and their behavior was recorded for half an hour every day after testing of all the birds was completed on experimental days or at around the same time on rest days. Subsequent behavioral scoring in Loopy focused on vocalizations, especially on cooing behavior. All presented results are purely descriptive due to a time constraint prohibiting the execution of any statistical tests.

Every female cooed in isolation, but to different degrees (Fig. 17). Of all females, number 7 cooed the most (total = 858) over the whole isolation period, followed by number 99 (total = 537), whereas female 19 exhibited the fewest coos (total = 10), followed by female 16 (total = 22) and 18 (total = 30). The remaining birds vocalized at intermediate levels (95: total = 90, 94: total = 99, 101: total = 102, 89: total = 108, 559/630: total = 109, 613: total = 150), with coos distributed more or less evenly between experiment and rest days for most of the birds. Vocalization behaviors seemingly did not follow any patterns based on condition or the number of days in isolation, with some females consistently cooing during early days (e.g. female 7) and others cooing more towards the end of the experimental period (e.g. female 99). Interestingly, consistently high numbers of coos exhibited by female 7 rapidly declined on rest day 5 and experiment day 6, which coincided with the day before as well as the exact day she laid her first egg.

Additionally, I visually compared the total number of coos exhibited between experiment and rest days (Fig. 18) and based on the experimental condition birds were presented with on experiment days (Fig. 19). Overall, no striking pattern emerged between day types, although slightly more coos were observed on rest days (mean = 14.20, sd = 25.04, total = 1193) than on experiment days (mean = 10.74, sd = 21.98, total = 1031). Females tended to coo less on experiment days on which they were exposed to the V condition (mean = 7.75, sd = 12.63, total = 186) than on the directly following rest days (mean = 17.62, sd = 34.33, total = 423). Slightly fewer coos were found on experiment days (mean = 10.08, sd = 17.57, total = 242) than rest days for A conditions as well (mean = 15.71, sd = 28.82, total = 377), while no such patterns were found for C conditions (experiment days: mean = 11.88, sd = 24.48, total = 285; rest days: mean = 10.32, sd = 14.60, total = 196) or AV conditions (experiment days: mean = 13.25, sd = 30.17, total = 318; rest days: mean = 11.59, sd = 8.90, total = 197), although less variability was indicated for rest days (Fig. 19).

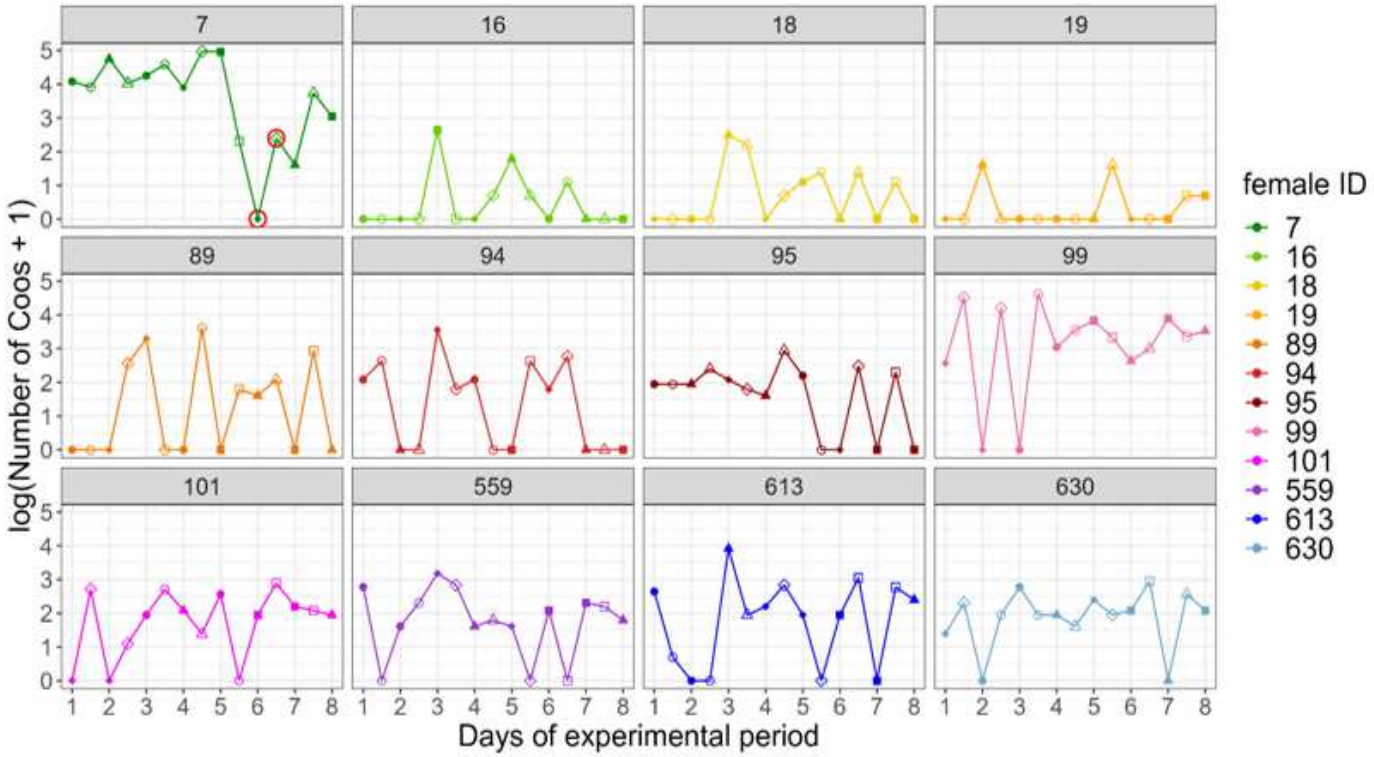


Fig. 17: Number of coos per female observed in the isolation cages over days of the experimental period. A logarithmic scale is used for better visualization. Color indicates female ID, shape indicates the condition shown to the respective female for each experiment day (**triangle** = control, **circle** = auditory, **diamond** = visual, **square** = audiovisual), **filled** shapes indicate experiment days, while **open** shapes indicate rest days. Red circles in the plot of female number 7 show days on which eggs were found in her cage.

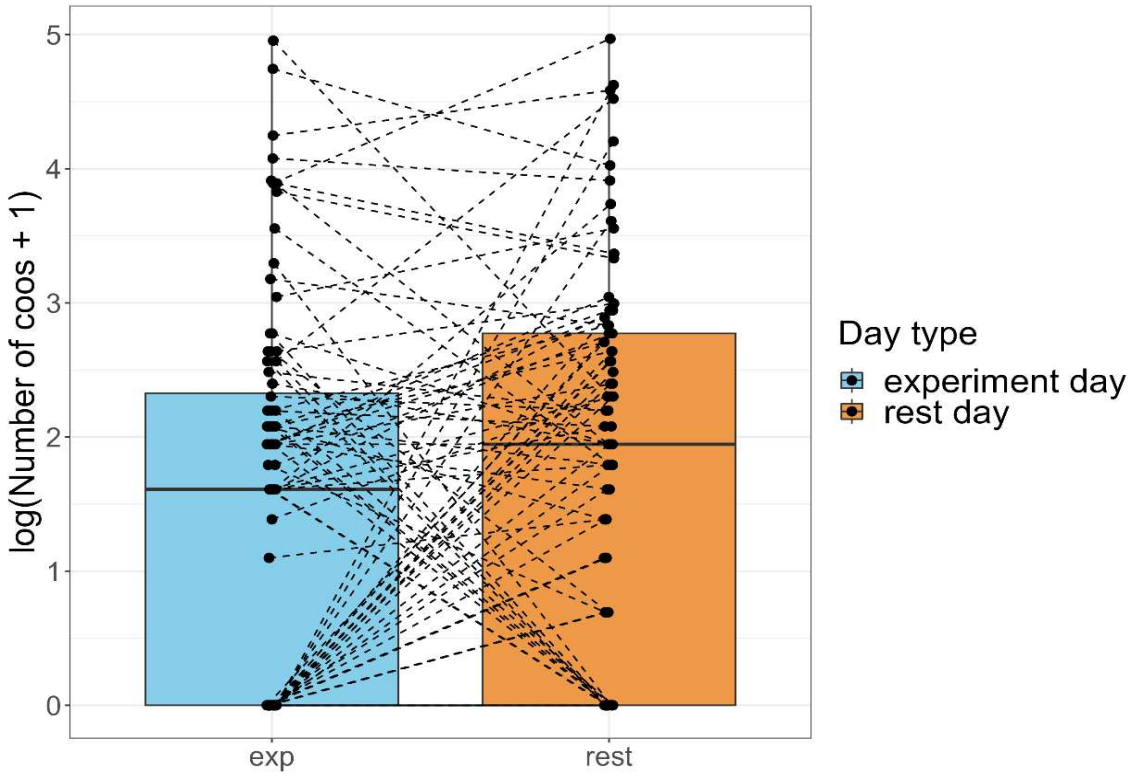


Fig. 18: Boxplots of the number of coos compared between experiment and rest days. A logarithmic scale is used for improved visualization as there was high variability among females. Dashed lines connect experiment days with the following rest day for each female. Experiment day 8 is not depicted in this plot as birds were released into the outdoor aviaries on the last experiment day, hence there was no rest day to compare it to.

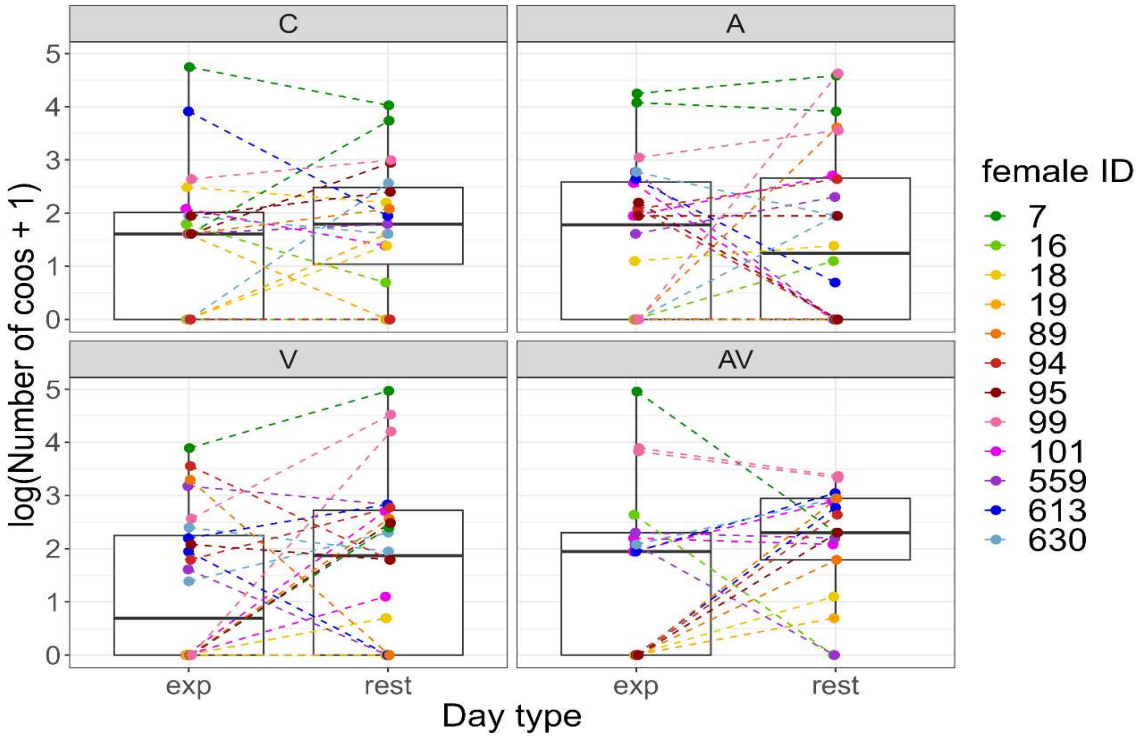


Fig. 19: Boxplots of the number of coos across conditions compared between experiment and rest days. A logarithmic scale is used for improved visualization. Colors indicate female identity. C = control, A = auditory, V = visual, AV = audiovisual.

4. Discussion

The main purpose of the present study was to shed light on the meaning conveyed via the components of the audiovisual bow-coo display in the courtship of ring doves (*Streptopelia risoria*). Using a similar approach as Partan and colleagues (2005), who investigated multimodal signaling in pigeons (*Columba livia*), a cue occlusion experiment was carried out, exposing twelve female ring doves to audiovisual playback of the male courtship display in a within-individual design. Two main questions were addressed. First, I wanted to discern whether the auditory and visual component of the bow-coo display contained the same or different information and which of the categories proposed by Partan and Marler (1999, 2005) it can be assigned to. The hypothesis that the components were nonredundant with the visual component modulating the meaning of the auditory component could not be entirely confirmed due to small degrees of sexual behavior also occurring in the auditory condition. Second, based on the previous observation of substantial inter-individual differences in female tail quivering (Mitoyen et al. 2021, Bourgmeyer 2022), I asked whether behavioral responses depended on differences caused by female identity or on the experimental conditions. Females did show similar behavioral patterns depending on condition, but the degree to which they showed certain behaviors in the same situations differed between individuals. Thus, evidence in favor of the second prediction that female differences would not exceed effects of condition emerged, although only descriptively. Statistical analyses of inter-individual differences were outside the scope of this master's thesis, but could reveal interesting patterns in future analyses.

4.1 Behavioral responses between conditions

4.1.1 Activity level

To assess the general activity level exhibited by the birds, the number of steps taken by each individual was scored and subsequently compared between conditions, excluding the control condition, and playback phases. Against my prediction and previous results obtained in the pilot study (Hacek 2022), significant effects of the conditions were found with fewer steps occurring in the test phase of visual than both auditory and audiovisual conditions (see Fig. 4A and 5A). This may either indicate the auditory component of the bow-coo display to contain some kind of information that results in enhanced female activity or other factors to have affected female responses in the visual and the auditory condition independently. For example, during video scoring I noticed behaviors in the auditory condition that may be interpreted as searching behaviors. Females tended to frantically walk up and down in front of the displaying screen intermitted by short pauses of stretching the neck or lowering the head down as if trying

to catch a glimpse of the male behind the plants used as visual occlusion stimulus, leading to high numbers of steps. This would also be in line with the increased numbers of perch coos found in auditory conditions, potentially representing the attempt to make the male approach her, but see below for thorough discussion of perch-cooing. Similarly, the low activity level in the test phase of visual conditions may be a result of fear in response to the vacuum cleaner noise serving as auditory occlusion stimulus. This possibility is underlined by the fact that the only three instances in which birds started flying in the experimental setup all occurred in test phases of visual conditions and that some birds, although responding to the playback, appeared hesitant during visual conditions, indicating at least a certain level of discomfort. We attempted to avoid such an effect by using noise samples even quieter than male cooing and by thoroughly habituating the females to the noise in advance. In previous experiments, using the same auditory occlusion stimulus, no such fear responses occurred (Biegler 2021, Hacek 2022), giving us no reason to assume females might react negatively to it. It may be that the period between the end of the habituation and the start of the experiment was too long as we had to postpone the start by a few days after one of the females had laid eggs (see Methods section). However, it seems unlikely that the effects of habituation would degrade within only a week, although we do not know for how long memory is retained in this species. Alternatively, it may also be that other unidentified factors increased a general nervousness in the females.

In addition to the differences found between conditions, significant effects were also found between playback phases (see Fig. 5B). The number of steps showed a significant increase from the pre-test to the test phase in the auditory condition as well as from the test to the post-test phase in visual conditions, whereas no differences emerged between playback phases in the audiovisual condition. This further contradicts previous results demonstrating an increase in the number of steps when females were confronted with a live male (Mitoyen et al. 2021) or with playback of a courting male rather than no male stimulus (Hacek 2022). Given these previous results, it would have been expected to see higher activity levels in test phases of all conditions rather than a decrease in the visual and no change in the audiovisual condition. If the auditory component of the bow-coo display contains some kind of information leading to higher activity levels in the females, a more severe increase in the test phase of the AV condition may have been expected. A possible explanation for the lack of such an increase could be the fact that females preened a lot in the AV condition, which they usually do while stationary. The same could be claimed for the V condition, although a slight, non-significant decrease in the number of steps in the test phase cannot be explained by this, especially given that there was no increase in preening from the pre-test to the test phase (see Fig. 7B). Again, this points

towards another factor influencing activity levels in V conditions, likely represented by the vacuum cleaner noise. Further analyses on the obtained data could be used to test this hypothesis. For example, I also scored startling events (see Tab. A1) and an increase in startles during test phases of V conditions may reveal itself.

Taken together, activity levels may be influenced by some characteristic inherent to the auditory component of the bow-coo display, in which case the current results would suggest a modulation effect for the number of steps, where the auditory component modulates the response to the visual component by increasing activity levels in females. However, it is quite conceivable that other factors influenced female behavior in the unimodal conditions, such as the lack of a visual stimulus of a male leading to searching behavior or the loud vacuum cleaner noise restricting females in exhibiting their full behavioral repertoire.

4.1.2 Preening

Self-preening has been previously suggested to indicate sexual interest in ring doves and represents an immediate response to male courtship in females (Craig 1909, Goodwin 1956, Cheng 1973). Previous work conducted in the Dove Lab revealed diverging results with one study finding no differences in preening behavior depending on whether females were confronted with a live male or not (Mitoyen et al. 2021), whereas others found significantly lower preening rates when females only heard but did not see playback of a courting male (Biegler, 2021) and significantly more preening occurrences when playback of male courtship was presented (Mitoyen et al. 2022). The present results are in line with the latter findings as well as with my initial prediction in that significantly fewer preening events occurred in the auditory condition than in both the visual and audiovisual condition. In addition to that, significantly more preening was observed in test than control phases of audiovisual conditions (see Fig. 7A and B).

At the beginning of the courtship cycle in the ring dove, females tend to respond to the male bow-coo display with self-preening and on occasion the male may join her in doing so (Cheng 1973). Thus, preening may exhibit an interactive component and in fact, this simultaneous self-preening by male and female has previously been dubbed a “mutual display” (Cheng 1973). Provided this is in fact the case, females may require visual input from the male in order to evaluate his behavior and accurately respond to it. In the present study, females were never exposed to recordings of males engaging in self-preening, but from the female’s point of view the possibility that he might start preening exists and to be able to assess whether he does or does not join her in preening may suffice as motivation for her to self-preen. This becomes

even more likely taking into account that it usually seems to be the female that initiates this mutual self-preening (Cheng 1973). Additionally, the female may require some reassurance that the male's courtship is directed towards her rather than another female. This possibility is enforced by the findings of Friedman (1977), who demonstrated that follicular growth was enhanced in females that had observed a male courting in her direction instead of a different direction. Males furthermore actively courted these females as they were the only individuals the males were able to see, making the experience for those females even more interactive and underlining the importance of two-way communication in courtship (Friedman 1977). Additionally, females may have exhibited less preening in the auditory condition simply because they predominantly engaged in different behaviors such as perch-cooing or searching, preventing them from self-preening. As a result, the difference in the number of preening events may have further grown.

In fact, preening even significantly decreased from pre-test to test phases in the A condition, indicating that females actively allocated their time to behaviors other than preening. However, in the visual condition no difference was found between playback phases, which could once again be explained by their hesitant demeanor during test phases in V conditions, likely caused by the loud vacuum cleaner noise. On the other hand, females still showed quite considerable amounts of self-preening in the visual condition as showcased by the lack of a significant difference compared to the test phase of the AV condition. Instead, a slightly significant difference between V and AV conditions was found in the post-test phase, which could be indicative of a more long-lasting effect of the AV than the V playback stimulus on female preening behavior. More nuanced analyses of preening behavior may be necessary to reveal significant differences also between playback phases in the V condition and to shed light onto potential explanations for the higher numbers of preening events in the AV condition after the test phase had already ended.

It has been suggested that self-preening observed during courtship represents a form of displacement preening (Cheng 1973). Displacement behaviors, in general, are commonly described as behaviors that seem out of context in the situations they occur in, apparently not fulfilling any direct function instrumental to the present situation, and were first described in birds in the 1940s (Tinbergen 1940). Such behaviors are usually characterized by incomplete executions of the respective behavior such as lowering the head as if pecking at non-existent food without actually coming into contact with the ground (Tinbergen 1940). Similarly, displacement preening may be characterized by incomplete movements of the beak along the feathers,

sometimes even without touching them. In a few instances I have indeed come across such incomplete preening movements, but they occurred only very rarely. Alternatively, other characteristics of the behavior may differentiate preening between sexual and non-sexual contexts such as the body area preened or the duration of individual preening events. In a study on domestic fowl, preening morphologies did indeed differ between situations where a food reward was out of reach to the individuals versus when it was not, in that separate preening movements were shorter and concentrated to easily accessible areas (Duncan & Wood-Gush 1972). In the doves, it has been indicated that mainly the wings are preened during courtship, specifically the scapulars (Cheng 1973) or the inside of the wing (Craig 1909). The present study analyzed preening irrespective of the body area preened, but thorough analyses including sub-areas for the wing could bring forward interesting patterns. Similarly, as preening events seemed to be quite short in most instances during male playback, it may be interesting to analyze differences in the length of preening events in and outside the courtship context to investigate the hypothesis that displacement preening is indeed represented by shorter preening events. This is also conceivable as preening rates but not preening durations showed significant results in a previous playback study of the Dove Lab (Biegler 2021).

One hypothetical function that displacement behaviors may fulfill is to facilitate the transition from one behavioral state to another. For example, more displacement behaviors occurred before honey bees (*Apis mellifera*) transitioned from waggle dancing to leaving the hive (Root-Bernstein 2010) and in lemurs (*Lemur catta*) more self-grooming was observed before a behavioral transition than afterwards (Buckley & Semple 2012). It is conceivable that displacement preening serves a similar function in dove courtship to facilitate the transition from one behavioral state in the courtship sequence to the next, which often is assuming the sex crouch position and subsequent copulation. Alternatively, preening may even play a role in olfactory communication. For example, roosters have been shown to prefer females with an intact uropygial gland (“preening gland”) only when their olfactory sense was not impaired (Hirao et al. 2009). However, the function of this gland is still very much debated in most bird species (reviewed in Moreno-Rueda 2017). In conclusion, many interesting factors may influence preening behavior in the sexual context, but are still under-researched.

With respect to the purpose of the present study, results indicate a multimodal enhancement effect of preening occurrence, although the decrease in number during the test phase of the auditory condition may also be interpreted as a modulation effect. Here, too, more detailed analyses of preening may help in obtaining a more complete picture of the processes at play.

4.1.3 Quivers

Quivers are rapid vibratory movements of the wing or tail in birds and have been described for a number of bird species in both males and females (reviewed in Andrew 1961). In the context of courtship, quivers have been proposed to be a solicitation display performed by females for example in zebra finches (Witte 2006) and domestic canaries (Amy et al. 2015). A first description of tail quivering in female ring doves was made very recently in the Dove Lab, when it was demonstrated that females quivered their tail significantly more when confronted with a live male than no male and when the male performed courtship than when he did not (Mitoyen et al. 2021). In subsequent playback studies, the role of tail quivering in ring dove courtship was further strengthened (Mitoyen et al. 2022), although significant results did not always emerge (Bourgmeyer 2022). Based on these previous findings, I predicted more quivers to occur in the audiovisual condition followed by the visual condition and fewest in the auditory condition. Statistical analyses were conducted using only quivers that did not coincide with coos to create a conservative measure avoiding biases due to the possibility that quivers may be caused by the movements of the body during vocalizing. Indeed, significant differences between the auditory condition and both the visual and audiovisual condition emerged, but the difference between the visual and audiovisual condition was not significant (see Fig. 9A). Interestingly, slightly more quivers were observed in the post-test phase of the auditory than the audiovisual condition, indicating a stronger carry-over effect in the A condition. Additionally, significantly more quivers occurred in the test phases of all conditions than in the control phases (see Fig. 9B), further confirming not only the efficacy of the playback method but also the role of quivering in female ring doves in indicating sexual interest to a potential mate. Furthermore, a slight trend emerged between the pre- and the post-test phase of the A condition with more quivers exhibited after the test phase had ended than beforehand.

These results, furthermore, suggest no negative effect of the vacuum cleaner noise in the V condition on quivering behavior, which could be explained in two, not necessarily mutually exclusive, ways. First, quivering may be a behavior that expresses immediate release of strong emotions that can only be partly controlled by the females and second, these emotions may not only be of sexual nature, but generally indicate excitement or arousal. For example, even the vacuum cleaner noise itself may have enhanced quiver responses if they are also exhibited by birds in response to being startled. Similarly, increased quiver responses in the post-test phase of A conditions may point towards frustration that the male never became visible. Alternatively, the subtle nature of quivering may have allowed startled females in the V condition to express their sexual arousal without having to overcome their fear. In any case, quivering

seems to be one of the, if not the most immediate response to courtship at least for some individuals. Additionally, quivering seems to be a behavior that differs quite substantially between females, as has already been indicated in previous findings (Mitoyen et al. 2021, Bourgmeyer 2022), with some producing very conspicuous, large-amplitude vibrations that make the whole body appear to be trembling, whereas others produce incredibly subtle and inconspicuous quivers that are easily overlooked, making it questionable if quivers are indeed a signal used for deliberate communication or an unconscious expression of inner processes.

Unfortunately, to my knowledge, systematic studies revolving around quivering are rare and very little is known about it in ring doves at this point, making further research essential in determining the potential functions of this behavior. For instance, the present study did not differentiate between wing and tail quivers and although no significant differences emerged previously (Bourgmeyer 2022), differentiating between the two quiver types may still reveal interesting patterns. Similarly, differences in quivering intensity, for example measured as the duration of single quiver events, may be worth investigating. To me, subtle as well as large quivers seemed to be produced voluntarily by the birds, but quantitative research is needed to test this assumption and much could be learned by investigating whether receiving birds use quivers as communicative cues. Nevertheless, the fact that considerably more quivering is exhibited by females when presented with male playback provides strong evidence of this behavior playing some role in courtship and the present study indicates that the visual component is essential in enhancing this behavior. Therefore, also for quivering a multimodal enhancement effect is likely, as quivers occurred in all conditions. However, some quivering also occurred during pre-test phases and control conditions, suggesting them to not be a solely sexual behavior.

4.1.4 Composite sexual behavior

In order to quantify sexual responses accounting for the fact that females may express sexual interest differently, durations of behaviors considered to indicate sexual interest were fused into one composite measure of sexual behavior. This measure included the durations of preening, quivering, circling, nest coo position, nest-cooing, sex crouch and rudimentary crouch. A similar approach was used in the pilot study, but only circling and nest coo position were included in a sexual behavior variable (Hacek 2022). Significantly less sexual behavior was found in the auditory condition in both the pilot and the present study, whereas visual and audiovisual conditions differed in the current study (12 females) but not in the pilot (6 females). Longer durations of sexual behavior were found in the AV than the V condition (see Fig. 11A).

Playback phases did not differ from each other in the A condition, whereas significantly less sexual behavior was found in both control phases compared to the test phase in conditions containing a visual courtship stimulus (see Fig. 11B). Additionally, slightly more sexual behavior was observed in the post-test than the pre-test phase of the AV condition, once again indicating a longer lasting effect of the AV condition.

The behaviors that affected the sexual behavior variable the most considering their mean durations were preening and quivering (see Tab. A3 in the Appendix), providing an explanation for slight divergences with the pilot study and highlighting the importance of these immediate responses. The third most exhibited behavior was circling, which usually occurs in early courtship phases as well (Craig 1909, Goodwin 1956, Cheng 1973) albeit not being as immediate as preening and quivering. The remaining behaviors were all shown quite rarely and except for crouching behaviors, all behaviors also occurred in the auditory condition. Thus, it seems both unimodal components are sufficient in eliciting sexual responses. However, it still needs to be kept in mind that preening and potentially also quivering are not strictly sexual behaviors as indicated by their occurrence in pre-test phases and control conditions. In addition to that, the fact that no significant increase in sexual behavior occurred from the pre-test to the test phase of the auditory condition speaks for the auditory component to not have a primarily sexual meaning for the females on its own.

In general, the visual component seems to be more effective in eliciting sexual responses, not only in the form of behavioral but also physiological responses. In an experiment presenting different females with a courting male, varying the visual input, higher follicular growth was found in females that had both heard and seen the male than those that had only heard him (Friedman 1977). Similarly, combinations of the male coo with his shadow increased the likelihood of females to lay eggs in comparison with females that had not received any visual input (Lambe & Erickson 1973). On the other hand, auditory stimuli are also capable of eliciting physiological responses in females, as was shown by enhanced follicular development in visually isolated females that had been presented with recordings of conspecific vocalizations than those that had not (Lehrman & Friedman 1969).

A possible explanation for the strong effect of the visual component of the bow-coo display on female sexual behavior may be that it is simply more salient than the auditory component on its own. For instance, in the visual condition the female has access to several cues apart from the bowing movement itself such as the male's general appearance as well as po-

tential visual cues that he is cooing. When ring doves vocalize, their throat exhibits an expansion and although no evidence exists that females interpret throat inflations as cue for amplitude of the cooing in the way that Anurans have been proposed to (Starnberger et al. 2014), it nonetheless seems to act as an amplifier and increases the range of transmission (Fletcher et al. 2004, Riede et al. 2004). Thus, the expansion of the throat sac during vocalizing may provide cues for the females that the male is cooing albeit the loudness of his coos may not be directly inferable. Additionally, the visual component may provide a less ambiguous stimulus than the auditory component given that the different ring dove cooing vocalizations sound almost identical in different situations (at least to the human ear). Therefore, the male's intentions may be clearer to the female when she can see him, leading to higher sexual responses. In relation to that, as mentioned before, information on whether the male is actually courting her and not a different female may be essential, too, as was indicated by Friedman (1977).

Overall, auditory playback was enough to elicit sexual responses in the females, mostly in the form of preening and quivering and to a lower degree also circling, but considerably more sexual behavior was observed in conditions containing a visual courtship stimulus (see Fig. 10A). A significant increase from the visual to the audiovisual condition, furthermore, indicates an enhancement effect. Thus, regarding sexual behavior, the components of the bow-coo display seem to be redundant. However, the lack of a significant difference between playback phases in the auditory condition may also point towards a modulation effect and nonredundant information to be contained in the two components. More fine-grained analyses of preening and quivering may help in shedding some light onto these contradictory findings.

4.1.5 Perch coos

For analysis of perch-cooing, number of coos were summed over playback phases and compared between conditions using the control condition as baseline. Perch-cooing appears to fulfill the function of contact calling in ring doves as they are often uttered in response to other vocalizing birds or in the dark (Craig 1909, Davies 1974). In pigeons, females have been demonstrated to vocalize more in test phases of the auditory condition presenting only the auditory component of the bow-coo display (Partan et al. 2005). Similar patterns were found in ring doves in previous playback experiments of the Dove Lab (Biegler 2021, Hacek 2022) and were replicated in the present study, confirming my initial prediction. Perch coos occurred in all conditions, including the control condition, but in far greater numbers in the auditory condition (see Fig 12 in the Methods section). Although no statistical analyses regarding differences between playback phases were conducted, I want to direct attention towards the fact that perch

coos in the visual condition only occurred in pre- and post-test phases, but never in the test phase (see Tab. A2 in the Appendix). Thus, perch coos were exclusively shown either when no conspecific stimulus was shown (control phases and control condition) or when an auditory courtship stimulus was included (A and AV conditions). In addition to that, a number of birds showed an increase in perch-cooing from the test to the post-test phase in the A condition (see Fig. 12).

Taken together, these results strongly suggest that perch coos indeed serve the purpose of contact calling as indicated by some individuals cooing when the presence of a conspecific is expected but not yet confirmed or when cues to the presence of a conspecific disappear (i.e. perch-cooing in control phases and control conditions). It is conceivable that females expected to hear or see a conspecific during the playback test phase if they had already experienced it at least once before, which was the case for most of the test trials except for day 1 of the experiment. In addition to that, when the presence of a conspecific is confirmed through the auditory channel but no visual information is accessible, contact calling seems to be enhanced. A possible explanation for this may be that females are calling for the conspecific and to make their own presence known so that the other bird may approach.

Females may require the visual component for assessing the whole display and deciding whether to reciprocate his advances or to guarantee the male is directing his courtship towards her. However, this would presume that females can not only distinguish between male and female coos but also between male coo types. In fact, the bowing movement has previously been suggested to communicate the sender's sex (Fusani et al. 1997) and may thus be required for the female to respond accordingly. If females really cannot distinguish between sexes, her perch-cooing may simply be the response to the presumed contact calls of another conspecific. In the collared dove (*S. decaocto*), however, female perch coos have been shown to differ in some acoustic characteristics from male perch coos (e.g. in fundamental frequency, spectrotemporal properties and overtones) (Ballintijn & ten Cate 1997) and male perch and bow-coos have been indicated to slightly differ in their frequency profiles and modulation (Ballintijn & ten Cate 1999). Thus, differences between male bow-coos and female perch coos may allow conspecifics to distinguish between sexes.

he is courting at all. This would imply no sexual information to be contained within the auditory component of the bow-coo and the components to be considered nonredundant, likely with the visual component providing the context in which to interpret the display and, hence, modulating the meaning of the auditory component. Experiments presenting females with the

perch or bow-coos of a certain male and then switching to the respective other coo type of the same male to see if her response changes may shed some light onto this open question.

On the other hand, we do not know whether the bowing movement impacts acoustic properties of the coo and, if so, whether females pick up on such cues. Additionally, some females also showed distinctive sexual behavior in the auditory conditions, indicating that females did interpret the vocalizations in a sexual context. In some cases, this may have been due to previous exposure to the visual condition, which may have served as some sort of primer for interpreting the general context of the experiment and setting females' expectations. Nonetheless, the fact that females only perch-cooed in test phases of conditions that included an auditory courtship stimulus, but not in the test phases of visual conditions, points towards a modulation effect for perch coos. This is additionally enforced by the finding that the auditory condition was significantly more effective in eliciting perch coos than the audiovisual condition, when the effect of the visual component seems to overshadow that of the auditory component.

4.1.6 Circling

Circling is a behavior usually associated with relatively early courtship phases in ring doves and was long assumed to be a primarily male behavior. Quite recently, circling was also observed in female ring doves in playback experiments (Biegler, 2021, Mitoyen et al. 2022, Hacek 2022). In line with previous results, the present study found circling to predominantly occur in test phases of conditions containing a visual courtship stimulus, whereas only very few circling events occurred in the auditory condition and none in the control condition (see Fig. 14). Similar to preening and sexual behavior in general, it appears as though visual input increases females' motivation to show circling behavior. Circling usually occurs when the male starts chasing around the female during courtship, indicating that the male may be instrumental in initiating the behavior and that circling may be highly interactive. Pigeons also exhibit a form of circle walking and it has been shown that both males and females engage more in circle walking when they are confronted with a live conspecific that can respond accordingly to their cues rather than when exposed to a recording (Ware et al. 2017). The authors of the study concluded that social interactivity plays an essential role in the courtship of pigeons and the same may be conceivable for ring doves. Interestingly, in the study conducted by Partan and colleagues (2005), more circle walking was found in the auditory than in the visual condition, although no significance was reported, indicating that visual responses to female circle walking are not of utmost importance in pigeons.

Based on the fact that the visual and auditory condition did not differ significantly from each other in the number of circling events and that the differences between the visual and audio-visual condition were significant only before Bonferroni correction, it is conceivable that the auditory component enhances responses to the visual component. A previously suggested enhancement effect for circling thus seems likely in ring doves (Biegler 2021).

4.2 Behavioral responses between females

In previous experiments of the Dove Lab, considerable inter-individual differences in female behavioral responses to male courtship became apparent (Mitoyen et al. 2021, Bourgmeyer 2022), leading to the question of whether effects found in experiments using a between-individual approach were actually the result of such inter-individual differences (Biegler 2021). To address this question, a pilot study using a within-individual approach was conducted (Hacek 2022) and subsequently extended to the present study. As predicted, females exhibited the same behaviors to different degrees (see Fig. 16), but significant mixed model results for an interaction between condition and playback phase (fixed effects) emerged despite the inclusion of female identity as random effect, indicating that inter-individual differences were not stronger than the effects caused by playback condition and test phase. Additionally, simpler non-parametric testing accounting for repeated measures yielded significant results of playback condition as well, although no comparison between playback phases or of an interaction between condition and phase was possible. Thus, taken together, dominance of inter-individual differences over effects caused by condition appear unlikely. Nonetheless, further statistical analyses into individual differences in the future may reveal different results.

For example, future analyses may reveal an effect of age as it appeared that behaviors usually associated with later courtship phases such as nest coo position or rudimentary crouching were mostly demonstrated by older females (see Fig. 16). Female satin bowerbirds have been shown to switch from mainly using bower decorations in mate choice to paying more attention to the intensity of the courtship display with age (Coleman et al. 2004). The authors suggested that older females may be less startled by the male display due to previous experience, which could also be a reason for female ring doves to behave differently depending on age, especially given that older females in the present study had participated in previous studies presenting male courtship. Male ring doves perform the same display in male-male aggression, suggesting a capacity of the bow-coo display to scare other doves. In fact, females have been shown to prefer courtship made up of many shorter bouts of bow-cooing over single long

ones (Mitoyen et al. 2021), which was hypothesized to be a result of long bow-coo bouts appearing more aggressive to the females. This may additionally be part of the reason for displacement preening exhibited by females during courtship. Preening may help the females to handle or express their fear and the male may in turn start self-preening to further reduce the female's fear. Thus, male self-preening may be an example for the threat reduction hypothesis of coy displays (McGillavry et al. 2023).

On the other hand, despite the isolation phase before the start of the experiment, females may have been in different physiological states. This is showcased by one female laying eggs during the first days of isolation leading to the postponement of the experiment start. The respective female was one of the lowest responders during the experiment (see Fig. 16). Contrarily, a second female that laid eggs during the experimental period was one of the strongest responders and one of the only females to show nest coo positions, nest-cooing and rudimentary crouching, possibly representing a rise in progesterone concentration (Cheng & Silver 1975). Females were visually but not acoustically isolated during the period of the experiment and conspecific vocalizations have been shown to elicit follicular development even without visual input (Lehrman & Friedman 1969). We did not record female cooing behavior before the start of the experiment and females probably vocalized a lot in the absence of human observers, inducing physiological responses in each other. Additionally, female physiology has been shown to be strongly influenced by an individual's own nest-cooing (Cheng 1986) and very vocal individuals may therefore have experienced more pronounced physiological development. However, this does not explain why it was mostly older females that exhibited behaviors indicative of such a progressed hormonal states and it remains to be seen whether these apparent age differences are in fact statistically significant.

Overall, some evidence in favor of my initial hypothesis that female differences exist but are not stronger than effects caused by experimental conditions emerged, as accounting for identity in the models still led to significant effects of playback condition and phase.

4.3 Vocalization behavior outside the experiment

In addition to the main questions, I also conducted explorative investigations on female cooing behavior in the isolation cages based on recordings obtained every experiment and rest day. Vocalizations were generalized as definite identification of coo types was not feasible due to the posture of individual females not being clearly visible. Females cooed to varying degrees with some birds vocalizing more at the beginning, others at the end and in some cooing fluctuated over the whole experimental period (see Fig. 17). This suggests the amount of cooing did

not overall increase over days and that the playback did not have substantial effects on the females' reproductive state indicating, at least to some extent, that the approach of interspersing experiment days with rest days fulfilled its purpose of keeping females at a reproductive baseline. Another explanation for this may be the restrictions we defined for the presentation order of playback conditions with AV conditions only shown to individuals that had previously been exposed to both the A and V condition of the respective stimulus male. This resulted in most AV conditions being presented during the last two to three experiment days and if combined signal components elicit higher physiological responses than the unimodal components alone, which has not yet been confirmed (Biegler 2021), changes in the females' hormonal states may simply not have been substantial enough to also cause behavioral changes. However, females appeared to differ from each other in cooing activity with some birds cooing more (e.g. bird 7) than others (e.g. bird 19) and very vocal birds seemed to also be more responsive during the experiment (see Fig. 16). This hints at some interactive effects of the playback and the exhibited behavior outside the experiment. However, no difference in the number of coos became apparent between experiment and rest days (see Fig. 18) and only marginal patterns emerged when additionally taking experimental conditions into account (see Fig. 19). Thus, the presentation of male courtship alone seems to not have substantially enhanced female behavior after experimental trials.

Females seemed to have vocalized slightly less on experiment days presenting V conditions than on the following rest days, which could be representative of cooing being predominantly elicited by conspecifics' vocalizations or by the urge to fill the silence in the complete absence of any conspecific cues. However, it seems more likely that some females primarily responded to the cooing of other females in neighboring cages, as ring doves often appear to do (Craig 1909). Those initiators may themselves have been motivated to coo by the respective condition they had seen that day, which differed between females on each experiment day. This would not have emanated from the present investigative figures and may be the reason for the lack of emerging patterns. Vocalizations uttered by females in isolation, furthermore, are likely to have impacted their physiology as well and potentially even to a larger degree than the playback. Female coos, especially a female's own nest coos, have been shown to be even more effective in enhancing such changes than male coos (Cheng 1986) and indeed, one of the most vocal females, number 7, laid two eggs on the eleventh and twelfth day of the experimental period followed by a sharp decrease in cooing (see Fig. 17). Thus, it is quite conceivable that cooing activity in the isolation cages was influenced by more complex interactions of a mixture of factors including their own as well as other females' cooing and the playback. In any

case, this is just speculation based on descriptive analyses and interpretations should be made with caution.

4.4 Summary

The main question addressed in the present thesis was whether the components of the bow-coo display in ring doves contained redundant or nonredundant information and which of the categories proposed by Partan and Marler (1999, 2005) it can be assigned to. I hypothesized that the bow-coo display represents an example for a nonredundant composite signal with the visual component providing the context in which to respond to the display, thereby modulating the meaning of the auditory component. This hypothesis was based on previous results of a pilot study (Hacek 2022) as well as the fact that at least to the human ear all coo types are essentially indistinguishable and accompanied by usually distinct body postures (Davies 1974). All statistically analyzed behaviors occurred in all conditions at least to some degree with stepwise increases from the auditory to the audiovisual condition for sexual behaviors, whereas steps and perch coos occurred most in the auditory condition. In general, the visual component has been shown in previous experiments to be more effective in eliciting sexual responses, not only in the form of behavioral but also physiological responses (Lambe & Erickson 1973, Friedman 1977), although the auditory component is also capable of inducing a similar effect albeit to a lower degree (Lehrman & Friedman 1969, Friedman 1977).

Due to the fact that most sexual behaviors, except for crouching behaviors, were shown also in the auditory condition but significantly more in visual and audiovisual conditions, a multimodal enhancement effect is suggested, indicating the two components of the bow-coo display to be redundant. On the other hand, the finding that significantly more perch coos were observed in the auditory than any other condition and the lack of perch coos in test phases of the visual condition suggest a modulation effect for perch-cooing and consequently the components to be nonredundant. These results are slightly contradictory to each other and only partly confirm my initial hypothesis. The most frequently occurring sexual behaviors in the auditory condition were preening and quivering, which are both behaviors that are or may not be purely indicative of sexual interest and more in-depth analyses of these behaviors may reveal interesting patterns. However, also circling and nest coo positions occurred in the auditory condition. The latter was shown by only one female in one unimodal auditory trial and may have been the result of a progressed hormonal state (Cheng & Silver 1975). Circling, on the contrary, has been observed in unimodal auditory conditions in previous playback studies of the Dove

Lab as well (Biegler 2021, Hacek 2022), pointing towards the auditory component being sufficient to elicit circling as a sexual response.

In conclusion, more evidence in favor of redundancy of the bimodal bow-coo display in ring doves emerged and the combination of visual and auditory components seems to enhance female responses. The same was suggested by previous playback results in the Dove Lab (Biegler 2021) as well as for pigeons, although in the latter case the auditory component was more effective in inducing sexual responses in the females (Partan et al. 2005), contrary to what seems to be the case in ring doves. Redundancy of signal components is hypothesized to predominantly serve as an insurance against noise or variable environments to cope with the risk of losing information when one signal component is obstructed (Johnstone 1996, Partan & Marler 2005, Hebets & Papaj 2005). The ring dove is a domesticated relative of the African collared dove (*S. roseogrisea*), that is known to occasionally aggregate in large groups at drinking or roosting sites (Gibbs et al. 2001). At such crowded sites it may become noisy with coos of several individuals interfering with each other, which may require redundant signal components to avoid loss of information.

Another, but not necessarily mutually exclusive, explanation for the use of redundant signal components in ring doves is that females may use information contained in the degree to which both components are coordinated with each other for assessing male quality ("multitasking", Hebets & Papaj 2005). Evidence for this was found in a recent playback experiment demonstrating that female ring doves preferred recordings of the unaltered bow-coo display rather than artificially shifted or jittered signal components (Mitoyen et al. 2022). In addition to that, the synchronization of the two bow-coo components has been indicated to differ between males (Fusani et al. 1997, Mitoyen et al. 2021). Thus, it is possible that the bow-coo display serves to inform about male quality through the degree of synchronization between the components.

The second question I wanted to address was regarding inter-individual differences affecting female responses to the playback as differences between females were found in previous experiments of the Dove Lab (Mitoyen et al. 2021, Bourgmeyer 2022). I predicted females to show similar behavioral patterns in the same experimental conditions but to different degrees. This was indeed suggested by the results with a slight pattern indicating differences based on age, but are more likely caused by varying physiological states (see Fig. 16). Mixed effects models used for analyzing behavioral differences between conditions and playback phases were employed for most scored behaviors and incorporated female identity as random effect.

Significant results of fixed effects nonetheless emerged (see Results section), indicating that inter-individual differences were not strong enough to override the effects of the playback. More in-depth investigations of the random effects, however, were beyond the scope of this Master's thesis. Altogether, the present results provide evidence in favor of my initial prediction and future statistical analyses will likely confirm this pattern.

In addition to that, recordings of female vocalizing behavior in the isolation cages further suggest differences in physiological states of the females from the start of the experiment, which were likely enhanced by several factors such as self-stimulation through vocalizing (Cheng 1986). No patterns emerged in exploratory comparisons between experiment and rest days as well as between conditions presented on respective experiment days, hinting at more complex interactions of experimental condition, vocalization of other females and individuals' own cooing. However, there is no evidence to suggest the playback altered female reproductive states to a degree detrimental to the results obtained in the experiment.

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Appendix

Tab. A1: Ethogram of behaviors scored in video coding, but excluded from statistical analyses. Adapted from Biegler, 2021.

Category	Behavior	Definition
Duration Movement	fly	The dove moves a hasty manner as if fleeing using her wings in; both feet must leave the ground.
	hover-flight	The dove fully extends and flaps her wings; one or both feet may leave the ground at least temporarily. The wings have to be flapped at least twice consecutively.
	spider dove	The dove grips the net with one or both feet and stays suspended in the same place, hanging from the net and not touching the floor. One or both wings may be extended. She may flap her wings. At least one foot must stay in contact with the net.
Event Movement	startle	The dove flinches, twitches, jumps or flaps her wings suddenly as if startled.
	jump	The dove pushes herself off the ground with one or both feet without ex-tending or flapping her wings. Both feet must be out of floor contact simultaneously. Not scored when associated with “startle” behavior. Often occurs while circling.
	up-down tail	The dove moves her tail downwards and lifts it up again immediately so that the tail may touch the ground. Not scored when associated with restoring balance. Distinct from accidentally brushing the tail on the floor while walking.
	mouth open	The dove opens her mouth widely as if yawning.
	wing flip	The dove jerks her shoulders repeatedly at a frequency of approxi-mately 2 flips per second, similar to a shrugging motion. Usually both wings are flipped simultaneously, but single-winged wing flips may also occur. Wing flips are almost exclusively performed during nest-coo position.
Body Position	sit	The dove lowers her body to the floor so that her stomach and/or part of her chest are in floor contact. One or both wings may be tucked under her feet and her eyes may be closed fully or half-way.
Duration Vocalization	ambiguous coo	The dove produces a cooing sound while assuming an intermediate body position that cannot clearly be classified as a perching or nest coo position, i.e. the tail is not clearly held higher or lower than the head.
Event Vocalization	laugh	The dove produces a sound similar to a human laugh.
	other vocalization	The dove produces other short and deliberate sounds that cannot be classifies as any of the described vocalizations.

Tab. A2*:* **Means and standard deviations of scored count behaviors per condition and playback phase.** Each condition consisted of three phases and was shown to each female twice, the number of observations used for calculating means and standard deviations are N = 24 for each table cell. The total scored number of each behavior is given below. Condition abbreviations: C = control, A = auditory, V = visual, AV = audiovisual

condition \ behavior		steps	perch coos	preening	quivering	circling	nest coos	nest coo position	sex crouch	rudimentary crouch
C	pre-test	46.17 +/- 28.13	0.54 +/- 1.98	6.17 +/- 7.73	0.79 +/- 1.50	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
	test	37.75 +/- 34.82	0.75 +/- 3.67	5.29 +/- 7.56	0.67 +/- 1.40	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
	post-test	31.92 +/- 27.37	0.63 +/- 3.06	6.96 +/- 10.30	0.71 +/- 1.55	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
A	pre-test	45.83 +/- 29.15	0.08 +/- 0.41	7.25 +/- 9.13	0.50 +/- 1.18	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
	test	88.75 +/- 66.24	5.88 +/- 6.32	1.21 +/- 2.36	6.96 +/- 7.53	0.13 +/- 0.34	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
	post-test	61.62 +/- 64.43	7.38 +/- 11.01	4.13 +/- 6.65	1.38 +/- 2.22	0.00 +/- 0.00	0.08 +/- 0.41	0.13 +/- 0.61	0.00 +/- 0.00	0.00 +/- 0.00
V	pre-test	45.67 +/- 33.70	0.17 +/- 0.82	5.29 +/- 5.71	0.50 +/- 1.67	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
	test	33.71 +/- 34.82	0.00 +/- 0.00	22.00 +/- 25.82	11.58 +/- 7.44	1.00 +/- 1.98	0.00 +/- 0.00	0.04 +/- 0.20	0.00 +/- 0.00	0.21 +/- 0.58
	post-test	57.50 +/- 33.62	0.13 +/- 0.45	6.04 +/- 6.25	1.00 +/- 1.67	0.13 +/- 0.34	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
AV	pre-test	47.96 +/- 34.81	0.63 +/- 2.36	4.17 +/- 4.47	1.00 +/- 2.55	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00
	test	60.21 +/- 45.11	0.04 +/- 0.20	32.96 +/- 30.07	18.17 +/- 11.90	4.00 +/- 3.81	0.04 +/- 0.20	0.13 +/- 0.34	0.04 +/- 0.20	0.46 +/- 0.98
	post-test	58.00 +/- 34.33	0.00 +/- 0.00	2.21 +/- 2.96	0.54 +/- 0.98	0.00 +/- 0.00	1.30 +/- 5.54	0.25 +/- 0.74	0.00 +/- 0.00	0.00 +/- 0.00
total		14762	389	1488	1051	126	34	13	1	16

Tab. A3: Means and standard deviations of scored behaviors in seconds. Each conditions consisted of three phases and was shown to each of the 12 females twice, thus the number of observations used for calculating the value in each cell is N = 24. Behaviors to the left of the thick black line were included in creating the sexual behavior variable. For calculating the sexual behavior variable, behaviors occurring at the same time were not added twice. The total scored duration of each behavior is given below. Condition abbreviations: C = control, A = auditory, V = visual, AV = audiovisual

condition \ behavior		preening	quivering	circling	nest coos	nest coo position	sex crouch	rudi-mentary crouch	sexual behavior
C	pre-test	2.31 +/- 3.14	0.43 +/- 0.86	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	2.74 +/- 3.73
	test	1.98 +/- 3.12	0.32 +/- 0.69	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	2.30 +/- 3.30
	post-test	2.86 +/- 4.29	0.54 +/- 1.36	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	4.65 +/- 4.42
A	pre-test	3.16 +/- 5.00	0.27 +/- 0.68	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	3.43 +/- 4.88
	test	0.78 +/- 1.47	6.55 +/- 7.49	0.40 +/- 1.31	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	7.70 +/- 7.53
	post-test	1.84 +/- 2.86	0.87 +/- 1.39	0.00 +/- 0.00	0.18 +/- 0.89	0.74 +/- 3.62	0.00 +/- 0.00	0.00 +/- 0.00	3.45 +/- 4.44
V	pre-test	2.21 +/- 2.52	0.31 +/- 1.12	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	2.52 +/- 3.06
	test	7.95 +/- 9.77	16.45 +/- 15.00	2.70 +/- 5.14	0.00 +/- 0.00	0.03 +/- 0.14	0.00 +/- 0.00	3.00 +/- 9.20	29.83 +/- 20.81
	post-test	2.32 +/- 2.52	0.78 +/- 1.33	0.48 +/- 1.43	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	3.58 +/- 2.93
AV	pre-test	2.04 +/- 2.75	0.52 +/- 1.12	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	0.00 +/- 0.00	2.56 +/- 2.96
	test	11.80 +/- 10.66	20.08 +/- 14.64	14.46 +/- 13.78	0.09 +/- 0.45	4.56 +/- 16.99	0.85 +/- 4.16	5.18 +/- 12.29	54.41 +/- 25.79
	post-test	0.75 +/- 0.94	0.45 +/- 0.99	0.00 +/- 0.00	2.91 +/- 12.64	9.34 +/- 30.40	0.00 +/- 0.00	0.00 +/- 0.00	10.81 +/- 30.08
total		959.93	1,141.67	432.78	76.45	351.90	20.40	196.25	3,041.50

Tab. A4: Means, standard deviations and total counts of scored behaviors per female. Numbers were summed over playback phases and each of four conditions was shown twice to each of the twelve females, thus calculations were conducted using an N = 8 for each female.

behavior \ female ID		7	16	18	19	89	94	95	99	101	559	613	630
steps	mean	154.0	122.0	62.1	186.0	272.0	132.0	131.0	167.0	156.0	71.8	303.0	88.6
	sd	71.6	32.8	18.6	16.9	99.6	53.7	115.0	76.8	39.3	42.1	174.0	29.6
	total	1230	976	497	1490	2174	1058	1050	1336	1245	574	2423	709
perch coos	mean	5.3	0.3	0.3	0.1	0.3	0.8	1.1	0.7	3.4	3.5	0.1	0.5
	sd	9.2	1.2	1.0	0.4	0.8	2.1	4.5	2.0	8.0	7.1	0.4	2.1
	total	126	8	7	2	6	18	26	16	81	84	2	13
preening	mean	8.9	3.2	5.4	2.0	0.8	9.0	13.5	12.2	12.1	12.2	10.8	13.5
	sd	14.6	5.2	5.4	3.9	2.7	16.2	18.5	25.7	12.4	23.4	17.6	14.3
	total	213	76	129	48	19	217	325	294	290	292	260	325
quivers	mean	2.9	3.2	3.0	2.7	4.2	1.6	4.7	6.0	7.0	3.5	3.0	2.1
	sd	7.6	5.3	6.9	3.8	6.2	3.8	8.6	12.1	11.1	6.2	5.0	4.1
	total	69	76	71	65	101	38	113	144	168	85	71	50
circling	mean	0.6	0.0	0.0	0.1	0.5	0.6	0.6	0.2	0.8	0.2	1.2	0.5
	sd	1.6	0.0	0.2	0.4	2.3	1.2	2.0	0.7	2.7	0.7	2.5	2.2
	total	15	1	1	2	11	14	14	5	18	5	28	13
nest coos	mean	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
	sd	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
	total	31	0	0	0	0	0	0	0	0	0	0	3
nest coo position	mean	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.3
	sd	0.6	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.8
	total	4	0	0	0	0	2	0	0	0	0	0	7
sex crouch	mean	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	sd	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
	total	0	0	0	0	0	0	0	0	0	0	1	0
rudimen-tary crouch	mean	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.0
	sd	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.7	0.0
	total	7	0	0	0	0	0	0	0	0	3	6	0
sexual behavior	mean	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.0
	sd	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.7	0.0
	total	7	0	0	0	0	0	0	0	0	3	6	0

Zusammenfassung

Kommunikation bei Tieren, insbesondere im Kontext des Balzverhaltens, beinhaltet oftmals den Zusammenschluss mehrerer Signalkomponenten verschiedener Sinnesmodalitäten zu einem multimodalen Signal, welche redundante oder nicht-redundante Informationen enthalten können. Um zu bestimmen, was davon auf das bimodale Balzverhalten männlicher Lachtauben zutrifft, wurden zwölf weibliche Lachtauben mit audiovisuellem Playback in einem „Cue Occlusion“ Experiment konfrontiert. Das Playback Design bestand aus drei je zwei Minuten langen Phasen, wobei zwei Kontrollphasen eine Test Phase flankierten, in welcher eine von vier Experimentkonditionen präsentiert wurde: (1) audiovisuelles Balzsignal, (2) visuelle Komponente des Balzsignals kombiniert mit Staubsaugergeräuschen, (3) auditive Komponente des Balzsignals kombiniert mit einer Aufnahme von Pflanzen und (4) Kontrollkondition bestehend aus neutralen Stimuli in beiden Modalitäten. Aufnahmen der Verhaltensreaktionen der Vögel wurden manuell ausgewertet und darauffolgende statistische Analysen verglichen Verhaltensweisen zwischen Experimentkonditionen und Playback Phasen. In Übereinstimmung mit bisherigen Ergebnissen trat das meiste sexuelle Verhalten in Test Phasen von audiovisuellen Konditionen auf, gefolgt von visuellen Konditionen. Am wenigsten sexuelles Verhalten wurde in auditiven Konditionen gezeigt, wohingegen „Perch Coos“, eine Art Kontaktruf, fast ausschließlich in der auditiven, aber niemals in Test Phasen der visuellen Kondition auftraten. Daher legen die Ergebnisse bezüglich der Kontaktrufe nahe, dass die Komponenten des multimodalen Signals nicht-redundante Informationen enthalten, während jene Ergebnisse bezüglich sexuellen Verhaltens auf das Gegenteil schließen lassen. Genauere Analysen könnten in der Zukunft mehr Aufschluss über diese widersprüchlichen Ergebnisse geben. Zusätzlich lieferte der intra-individuelle Experimentansatz Hinweise darauf, dass vorherig nahegelegte inter-individuelle Unterschiede in den Reaktionen der Individuen nicht größer waren als die Effekte der Experimentkonditionen. Außerdem weisen Aufnahmen des Vokalisationsverhaltens der Individuen außerhalb des Experiments nur auf untergeordnete Einflüsse des Playbacks auf das reproduktive Stadium der meisten Weibchen hin.