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Identity encoding and recognition in greylag goose departure calls

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1. Acknowledgements

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Ethics statement

This study complies with all current Austrian laws and regulations and was supported by Animal Experiment License Number 66.006/0026-WF/V/3b/2014 issued by the Austrian Federal Ministry for Science and Research (EU Standard, equivalent to the Animal Ethics Board). All data collected for this study were obtained using non-invasive methods. Birds were habituated to the presence of humans, as the flock has

been observed at the Konrad Lorenz Research Center for Behavior and Cognition

(KLF) since 1973.

2. Abstract

In animal communication, vocalizations can transmit information about the identity of the sender (identity signature), which conspecifics may use to differentiate between individuals based on acoustic information alone (individual vocal recognition). Greylag geese (*Anser anser*) are a waterfowl species with a rich and, thus far, understudied call repertoire. In this thesis, I investigated identity signatures and individual vocal recognition in departure calls of greylag geese. Departure calls are produced shortly before taking wing as part of a pre-flight ritual. To assess whether departure calls carry identity signatures, I recorded 562 departure calls produced by 10 different individuals. From each call, I extracted 23 acoustic parameters and used these to train a discriminant function classifier to differentiate between individuals, testing whether it would perform above chance. To assess whether greylag geese recognize departure callers based on acoustic information alone, I conducted playback experiments, broadcasting departure calls of partners and non-partners to the same individuals and recording their behavioural response. I found evidence for an identity signature in greylag goose departure calls, as the discriminant function classifier performed above chance on unseen data. Furthermore, focal individuals reacted with increased attentive behaviours in response to calls from their partner compared to a non-partner, thus supporting the potential for individual vocal recognition. This finding of an acoustic identity signature in an ancient avian lineage that lives in complex social groups raises questions about its functional relevance and suggests that acoustic individuality signals may be evolutionarily widespread in group-living species.

3. Zusammenfassung

Lautäußerungen können in tierischer Kommunikation Information über den Sender übermitteln (Identitätssignatur), die Artgenossen nutzen können, um Individuen allein mithilfe akustischer Information zu unterscheiden (individuelle Stimmerkennung). Graugänse (*Anser anser*) sind eine Wasservogelspezies mit vielfältigem, und, bisher, wenig erforschtem Rufrepertoire. In dieser Thesis untersuche ich Identitätssignaturen und individuelle Stimmerkennung in Abflugrufen (departure calls) von Graugänsen. Abflugrufe werden kurz vor dem Abflug als Teil eines dem Flug vorhergehenden Rituals abgegeben. Um festzustellen, ob Abflugrufe Identitätssignaturen enthalten, habe ich 562 Abflugrufe aufgenommen, die von 10 verschiedenen Individuen abgegeben worden sind. Ich habe aus jedem Ruf 23 akustische Parameter extrahiert und mit ihnen mithilfe einer Diskriminanzfunktionsanalyse ein Modell trainiert, Individuen zu unterschieden, um zu testen, ob Individuen anhand ihrer Rufe überzufällig gut erkennbar sind. Um festzustellen, ob Graugänse Abflugrufer allein anhand akustischer Information erkennen können, habe ich Playback-Experimente durchgeführt, im Rahmen derer ich denselben Individuen Abflugrufe von Partnern und Nicht-Partnern vorgespielt und ihre Verhaltensantwort gemessen habe. Ich habe Hinweise auf eine Identitätssignatur in Graugans-Abflugrufen gefunden, da das Diskriminanzfunktionsmodell ungesehene Daten überzufällig häufig richtig zuordnen konnte. Darüber hinaus haben Individuen auf Rufe ihrer Partner, verglichen mit denen von Nicht-Partnern, mit erhöhtem aufmerksamem Verhalten reagiert, was die Möglichkeit individueller Stimmerkennung nahelegt. Dieses Ergebnis einer akustischen Identitätssignatur in einer evolutionär basalen Vogelspezies, die in komplexen sozialen Gruppen lebt, wirft Fragen über dessen funktionale Relevanz auf und legt nahe, dass akustische Identitätssignale evolutionär in gruppenlebenden Spezies weitverbreitet sein könnten.

4. Introduction

In acoustic communication, the sender of a signal often encodes information about class-level or individual-level traits. For example, class-level information could include general characteristics of the sender, such as their sex (Bouchet et al., 2010; Shen et al., 2020; Taoka & Okumura, 1990), age (Jones et al., 1992; Reby & McComb, 2003; Stoeger et al., 2014), or body size (Bowling et al., 2017; Zhao et al., 2018). Broadcasting class-level information may affect the outcome of mating or territory competition, by allowing two interactants to quickly gauge other individuals' sex, fighting potential that is based on body size (Hartshorne, 1978), or immunocompetence that is signaled by plumage coloration (Saks et al., 2003).

At the individual level, some signals encode specific information about individual identity. For example, some vocalizations can be said to carry an acoustic, or vocal, identity signature (Carlson et al., 2020; Jensen et al., 2024; Martin et al., 2022) that may be independent of other classes, such as sex (Colombelli-Négrel & Evans, 2017). The functional significance of identity signatures can be varied, such as keeping contact with key individuals important to the sender over distance and when not in sight of each other (Guggenberger et al., 2022; Lehmann et al., 2022; Mouterde et al., 2014), or discriminating residents of neighboring territories, who may not pose a threat, from novel rivals (Hardouin et al., 2006; Myrberg & Riggio, 1985).

The encoding of such identity information may be particularly helpful in group-living species, as acoustic signals can be received by many individuals almost instantaneously and without significant loss of information across visual obstacles. This could allow the rapid deployment of resources for the defense of important individuals, such as offspring (Wittig et al., 2007). Furthermore, understanding the mechanisms that underpin leader and follower dynamics and subgroup movement

decisions in group-living animals is a growing field of research (Herbert-Read, 2016), whereby individuality signatures may also play an important role. To better understand the potential myriad biological functions of vocalization signatures, we need to better understand how widespread they are across taxonomic groups.

Among vocalization types, researchers typically distinguish between calls and songs, though the distinction is rather arbitrary (Catchpole & Slater, 2003; Colombelli-Négrel et al., 2021; Rose et al., 2022). Calls tend to be shorter and composed of a simple syllable type that can be repeated several times, whereas a song tends to be longer and composed of complex syllable types, though there are exceptions, e.g., songs composed of one simple syllable type repeated few to many times (Podos, 2001). In general, calls tend to be more stereotyped despite potential individual variation and tend to represent a class of information, and hence can be used to categorically communicate about, for example, an external threat (Hollén & Radford, 2009; Zuberbühler, 2009) or a motivation to move (Bousquet et al., 2011).

One of the best-known examples of calls referring semantically to different classes of external threats are the alarm calls of vervet monkeys (*Cercopithecus aethiops*). The monkeys produce at least three alarm calls differing in acoustic structure that each (experimentally) refer to eagle, snake, or leopard, respectively. Using broadcast of the call types, each call type elicited different responses in the monkeys: when exposed to an 'eagle call', they ran down from the trees; when exposed to a 'snake call', they stood up and looked around; and when exposed to a 'leopard call', they ran up into the trees (Seyfarth et al., 1980). Similarly, in great tits (*Parus major*), nestlings responded differentially to parents' 'crow' versus 'snake' alarm calls (Suzuki, 2011). This exemplifies the value of investigating different call types within a species to unveil complex differentiation in vocal communication patterns. Accordingly, across taxa, researchers are collecting information on species' call type repertoires and

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using experimental studies to infer the function of the various call types, including in anurans (Toledo et al., 2015), whales (Rekdahl et al., 2013; Selbmann et al., 2023), primates (Bezerra & Souto, 2008; Fischer & Hammerschmidt, 2002), and birds (Colombelli-Négrel et al., 2012; Ficken et al., 1978; Kleindorfer et al., 2024; Marler, 2004). Recording and experimentally testing call type function is especially useful when studying populations with individually marked animals, since both call characteristics and function can be investigated at an individual rather than group level.

While many calls encode identity information on top of their context-specific content (Carlson et al., 2020; Jensen et al., 2024; Lameira & Wich, 2008; Watanabe et al., 2010), the importance of encoding identity information may differ between call types within a species due to varying selection pressure on caller identifiability in different contexts. In particular, call types used in agonistic versus affiliative contexts may undergo such different selection pressures (Wyman et al., 2022). In general, affiliative calls studied to date encode more identity information than agonistic or alarm/under threat calls, as in rhesus monkeys (*Macaca mulatta*) (Rendall et al., 1998), southern white rhinoceroses (*Ceratotherium simum simum*) (Cinková & Policht, 2014; Linn et al., 2021), dwarf mongooses (*Helogale parvula*) (Rubow et al., 2018), south polar skuas (*Catharacta maccormicki*) (Charrier et al., 2001), apostlebirds (*Struthidea cinerea*) (Warrington et al., 2014), and Australian zebra finches (*Taeniopygia castanotis*) (Elie & Theunissen, 2018); but see also red-capped mangabeys (*Cercocebus torquatus*), where, next to affiliative contact calls, agonistic threat calls carry a strong identity signature, more so than alarm calls and intergroup loud calls (Bouchet et al., 2012). This gradient of identity signatures between call types may reflect different needs for identity encoding across different contexts. In affiliative contexts, such as keeping contact, it may generally be relevant to know whether the caller – and thus the individual who wants to establish or maintain contact – is a

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mate, kin, or enemy. By contrast, in alarm calls, the risk of not attending to the call, irrespective of caller identity, may relax selection pressures on also encoding individuality signatures (Schibler & Manser, 2007). However, there could be more and less reliable callers in the face of danger (Blumstein et al., 2004; Hare & Atkins, 2001), or even individuals who deceptively use alarm calls (Munn, 1986), underscoring a selection pathway also for alarm calls to include caller identity.

Even if identity information is encoded in a certain call type, this would not necessarily have to relate to its function. First, encoded identity information could be a byproduct of anatomical individual differences that are not relevant for receiver response – the information is either not detected or not important for the response. For example, alarm calls of meerkats (*Suricata Suricatta*) carry a strong identity signature, but receivers appear not to distinguish between callers (Schibler & Manser, 2007). Also, in grey seals (*Halichoerus grypus*), mothers did not distinguish between pup vocalizations despite their calls encoding identity information (McCulloch et al., 1999). Finally, juvenile Richardson's ground squirrels (*Urocittelus richardsonii*) did not distinguish between alarm calls from their mother versus less familiar conspecifics (Hare & Warkentin, 2012), despite these calls encoding enough individual-specific information to differentiate neighbours and non-neighbours (Hare, 1998).

Second, the capacity for individual vocal recognition may not be linearly associated with the strength of the identity signature encoded in the signal (Elie & Theunissen, 2018). That is, independent of encoded information, receivers of vocalization signatures may show systematic response patterns towards calls from certain classes of individuals, or always react similarly regardless of the caller, or not react at all. Therefore, to measure the occurrence and function of vocal identity signatures across call types, one needs to conduct experiments within specific call types to test whether group members distinguish between calls of this type with different vocal identity

signatures. As we begin to better understand the occurrence and taxonomic distribution of vocalization signatures, we are also gaining insights into their possible roles at different life stages (Goncharova et al., 2015; Wyman et al., 2022), social contexts (Carlson et al., 2020; Shapiro, 2010), and threatening contexts (Colombelli-Négrel & Evans, 2017; Kleindorfer et al., 2014; Masco, 2013).

Greylag geese (*Anser anser*) are group-living waterfowl (Anseriformes) that produce about 10 different call types (Kleindorfer, 2024; Lorenz et al., 1988). They live in large flocks with over 100 members on average (Rosin et al., 2012), but can occur in aggregations of thousands (Kleindorfer, 2024). They are monogamous and start to form a pair bond around age 1–3 years, living on average around 8 years with a maximum longevity of about 25 years (Scheiber et al., 2013). Greylag geese engage in various forms of social organization, including single unpaired, paired, trios with two males and one female, homosocial bonds, family clans, and matrilineal sub-clan units (Scheiber et al., 2005, 2009; Szipl et al., 2019; Weiß et al., 2010; Weiß & Kotrschal, 2004). They are a model system for testing ideas about the costs and benefits of group living (Scheiber et al., 2013). Despite the complexity of their social bonds and the number of call types, there has been little systematic inquiry into their call type repertoire or the function of the different call types. Two notable exceptions are an experimental study into the gosling distress call (Loth et al., 2018) and the adult distance call (Guggenberger et al., 2022). In the first study, goslings from different families did not differ in call characteristics and goose parents responded to the experimental broadcast of any gosling distress call, regardless of relatedness (Loth et al., 2018). In the second study, adult distance calls carried a vocalization signature and partners responded more strongly to the broadcast of their partner's distance call than to any other class of caller (Guggenberger et al., 2022). Two studies on the same flock of greylag geese found evidence for identity-dependent variation in the contact call (Körmer, 2022) and the departure call (Weinhäupl, 2022),

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but did not carry out experimental playback studies to test receiver discrimination of caller identity. To date, no studies have been published on the call structure or response to call playback for any of the species' other call types.

The aim of this study is to investigate individuality signatures in greylag goose departure calls, which are loud single calls produced just before taking flight. If these calls encode individuality information, then I expect them to systematically differ between individuals in their acoustic structure and to be assignable to caller identity above chance using discriminant function analysis. To test whether receivers recognize caller identity, I will experimentally broadcast departure calls and measure receiver responses when exposed to departure calls from either their partner or another flock mate. I predict a stronger response to experimental playback of a departure call if it is from the focal goose's partner versus another flock mate.

5. Methods

<u>Study system and site</u>

I recorded departure calls and performed experimental call playback in a flock of free-roaming, food-supplemented, individually color-banded greylag geese living in the Alm Valley (Upper Austria). The flock became established in the Alm Valley in 1973 when ethologist Konrad Lorenz translocated 148 greylag geese from Seewiesen, Germany, to the Alm valley; since then, their behaviour and life history have been monitored by staff and students of the Konrad Lorenz Research Center for Behavior and Cognition, a core facility of the University of Vienna (Scheiber et al., 2013). The geese have been food supplemented with grains and pressed grass pellets twice daily since 1973. The two buckets (ca. 5 L) of pellets are placed in five 1.5 m × 0.4 m food troughs located on the meadow in front of the Auingerhof (47°48'49.7412" N, 13°56'51.72" E), the original research center. Due to being food supplemented daily and having access to lakes that do not freeze during winter, the geese do not migrate (Scheiber et al., 2013).

This study population is habituated to humans. At the start of data collection in October 2023, the flock consisted of 90 individuals (mean ± SD age in years: 6.9 ± 5.1, range 0-20; female:male 37:53; partnered:unpartnered 55:35), of which three went missing over the course of this study. Of these 90 geese, 11 were hand-raised by humans as part of a long-term research program (Hemetsberger et al., 2010).

The geese are fed at 0800 and 1600–1900 (winter or summer hours, respectively) at the Auingerhof, after which time they tend to move in several smaller subgroups to the adjacent Cumberland Gamepark (47°48'37.6704" N, 13°56'53.9196" E), the two locations where most of the data were collected (Scheiber et al., 2013). In the afternoon, the geese that visited the Auingerhof leave in smaller subgroups to nearby sleeping areas at Lake Alm (47° 45' 12.1356" N, 13° 57' 24.9948" E), Oberganslbach

(47° 47' 36.762" N, 13° 56' 57.2316" E), or the Cumberland Gamepark
(47°48'37.6704" N, 13°56'53.9196").

The departure call

The greylag goose departure call (Fig. 1) is a high-amplitude single-element
vocalization that is generally produced just before flight departure. Departure calls
have a relatively fixed temporal position in the sequence of behavioral events leading
to group flight departure to feeding areas and sleeping sites. Beginning up to half an
hour before taking flight, individuals start to walk and position themselves in the
direction of takeoff with the outcome that their body orientation is parallel to that of
others (Schmitt, 1990), with heads and necks facing the direction of takeoff. While this
orienting behaviour occurs, more and more individuals start to shake their necks and
recruitment call – a repetitive staccato call produced in long bouts of the same
syllable (Lorenz et al., 1988). Therefore, leading up to flight departure, there is a loud
background of vocalizations that increases in intensity until individuals take flight.
Most of the time, when a departure call is produced, the caller departs shortly
thereafter (within seconds to minutes). Departure calls pierce the uniform staccato
background recruitment calls as loud and distinct vocalizations. Not all individuals
emit departure calls in the minutes prior to flight departure and, for those that do, calls
can be produced in slow bouts.

Call recordings

I recorded all calls between October 11, 2023, and December 9, 2023. Departure
calls were recorded during subgroup flight departures in the mornings at the
Auingerhof, and in the afternoons at the trail intersection at the Gamepark. I recorded
vocalizations using a Sennheiser MKE 600 directional microphone (Sennheiser
electronic SE & Co. KG, Germany) with a Zoom F3 field recorder (Zoom Corporation,

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Japan). The sampling rate for all recordings was 48 kHz and sampling depth was 32-bit float. I recorded goose calls opportunistically – if a goose produced a departure call, I approached it up to approximately 1.5 m if possible. I noted the goose's identity by voicing its leg-band colors on the audio track. From all recordings, I extracted shorter sub-recordings (= tracks) in Audacity® version 3.4.0 (Audacity Team, 2023) and reduced the sampling depth to 16-bit for further analyses. I manually annotated single call elements from these tracks using Raven Lite version 2.0.5 (K. Lisa Yang Center for Conservation Bioacoustics, 2023) selection tables with the help of the waveform and the spectrogram display, which was calculated via a fast Fourier transform with window type Hann and a window length of 512, overlap of 50%, 50% brightness and contrast, a power threshold floor of 7.5 dB, and ceiling of 82.5 dB. Before further analysis, I manually discarded elements that were overlapping with other vocalizations or had poor signal-to-noise ratio. This was based on the spectrogram display in Raven with the same settings as above. The distribution of departure callers was heavily skewed so that most geese never produced any during data collection and, among those that did, only few produced departure calls often. I discarded call elements of individuals with fewer than 10 total call elements, due to too little training data, or when all recorded call elements were from the same track, due to temporal autocorrelation concerns. This led to the removal of 53 calls from 13 individuals in total. I analysed the remaining 562 departure call elements from 10 individuals (details in Table 1) for acoustic structure analysis.

Partner playbacks

Playback track construction

I constructed the 2-min playback tracks using Audacity with 1 min of silence as baseline and 1 min of playback, which was structured in 10 s intervals. During each 10 s interval, departure calls were broadcast in a 5 s call pulse followed by 5 s of

silence. Each 5 s call pulse consisted of five departure call elements from the same individual and track, each separated by 1 s of silence. Their order was randomized and kept constant in every 10 s interval of a playback track. In total, departure calls of 14 different individuals were used. To ensure the amplitude was associated with the natural call type amplitude, I normalized each departure call element to 0 dB. Peak replay amplitude was on average 86 dBa (SD ± 1.39). Stimulus construction is summarized in Fig. 2.

Playback procedure

Each focal goose received two playback stimuli presented across separate trials in a randomized order: (1) departure calls from their partner, and (2) departure calls from another familiar flock mate. Between both trials, there were at least six hours and at most four days. I was blind to the category of playback. After broadcasting a call to a focal individual, I did not target the focal individual again for at least three trials. I performed playback trials at times when the flock had low chance of flight departure, such as when most of the flock was resting, and when there was no or only very mild precipitation. I controlled the playbacks on a smartphone connected via Bluetooth to an Ultimate Ears HYPERBOOM loudspeaker (model S00175; Ultimate Ears, United States of America), both turned up to full volume. For three weeks prior to the first trial, geese were habituated to the presence of the loudspeaker using two flowerpots (filled with stones and wrapped in black tape) that mimicked the appearance of the loudspeaker. Before each playback trial, I placed the loudspeaker next to the focal individual on the ground (distance ~5 m). I started the trial with the baseline silence when the focal individual was resting, feeding, or being vigilant. During the playback, I recorded the focal individual constantly via either a handheld FDR-AX53 Sony (Sony Group Corporation, Japan) or HC-V770 Panasonic (Panasonic Corporation, Japan) camcorder and additionally commented on the observed response behaviour.

I conducted partner playback trials across two separate periods: November 6– December 6, 2023, and February 5–9, 2024. I discarded four trials without video footage and another two associated trials where one of the stimuli was broadcast to the wrong individual. After this, I was left with 54 playback trials using 14 focal individuals. I coded focal goose behaviour using the software Solomon Coder (Péter, 2019). I coded the following behavioural variables (defined in Table 2): steps towards the loudspeaker, steps away from the loudspeaker, gazes, neck rolls, vigilance duration, stare duration, time within 2 m, minimum distance, departure calls, recruitment calls, contact calls, takeoff, and down-up head movement. Across all playbacks, focal geese never responded with departure calls or takeoffs, so I did not analyse these variables further. Similarly, I observed recruitment calls in only one trial, and neck shakes in only four, and so did not analyse these variables further. Finally, time within 2 m and minimum distance to approach the speaker were not analyzed further, because there was no variance in these variables: the geese generally remained either within or further than 2 m and did not approach; the main response variables were in relation to attention, such as vigilance and gaze at the speaker. As a safeguard, I calculated two linear mixed effects models using the function *lme* from the package 'nlme' (Pinheiro et al., 2022), one for time within 2 m and one for minimum distance as response variables, with partner status, experimental condition, and their interaction as predictors, in which no effects reached significance (all p > 0.05). I coded and analysed the remaining variables: number of steps to the loudspeaker, number of steps away from the loudspeaker, number of gazes, the duration (s) of stares (gaze longer than ~1 s), the duration (s) of vigilance postures, number of contact calls, and number of abrupt down-up head movements.

Data analysis

I conducted all statistical analyses and created all plots using R version 4.1.3 in RStudio version 2023.06.1 (Posit team, 2023; R Core Team, 2022). The following R

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packages were used on multiple occasions or for general operations: 'readxl'
(Wickham & Bryan, 2023), 'dplyr' (Wickham et al., 2023), 'soundgen' (Anikin, 2018),
'tuneR' (Ligges et al., 2023), 'seewave' (Sueur et al., 2008), 'warbleR' (Araya-Salas &
Smith-Vidaurre, 2016), 'stringr' (Wickham, 2023), and 'ggplot' (Wickham, 2009).
Further R packages used in specific analyses are cited below. The significance
threshold was α = 0.05 in all analyses.

Call structure analysis

I set a bottom frequency of 100 Hz for all analyses to exclude high-energy low-
frequency noise. Due to an oversight in call extraction from the initial recordings, I
clipped some of the call elements with a sampling rate of 48 kHz, but others with a
sampling rate of 44.1 kHz. Therefore, I downsampled all call elements that were
recorded at 48 kHz to 44.1 kHz after applying a low-pass filter using the function
resample from the package 'soundgen' (Anikin, 2018) with lowPass = TRUE.
Furthermore, I excluded call elements on tracks with a manually-identified upper-
frequency noise threshold of ≥ 500 Hz. Additionally, I excluded tracks with a signal-to-
noise ratio of less than 5 using the function *sig2noise* from the package 'warbleR' with
a threshold of 0.0015 s.

Since identity signatures can depend on a multivariate combination of several
structural properties across the frequency and time domain (Hambálková et al., 2021;
Levréro et al., 2009), I extracted the following 23 spectrographic parameters: duration
(s) using the function *auto_detec* from the package 'warbleR' with a threshold of 20%
of peak amplitude, and the following parameters using *spectro_analysis* from the
same package: mean frequency (kHz), standard deviation of frequency (kHz), median
frequency (kHz), frequency at first and third quartile (both kHz), interquartile
frequency range (kHz), median time (s), time at first and third quartile (both s),
interquartile time range (s), skewness, kurtosis, spectral entropy, time entropy, total
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entropy, spectral flatness, mean dominant frequency (kHz), maximum dominant frequency (kHz), range of dominant frequency, modulation index, slope of dominant frequency over time, and mean peak frequency (kHz). Variable definitions are reported in Table 3.

Next, I scaled the resulting data matrix of all call elements for normalization. Then, I ran principal component analysis (PCA) and then used all six acoustic principal components with eigenvalues > 1 as predictors in the call individuality analysis via linear discriminant function analysis (DFA). Multivariate normality and variance homoscedasticity assumptions were violated, which may influence the accuracy of my results. Thus, in addition to linear DFA, I also ran a quadratic DFA, which is robust to violations of these assumptions, to ensure those violations did not impact my results in a meaningful way.

I ran the DFAs as follows: To obtain classification accuracy, I split the data into a training and a test set with a ratio of 0.8:0.2 using *sample_split* from the package 'caTools' (Tuszynski, 2021). I scaled the training set for normalization, then scaled the testing set with the same scaling parameters that were used for the training set to prevent information leakage between both sets (Wiemken & Kelley, 2020). A linear discriminant function model was trained on the training set to discriminate between individuals, using the functions *lda* (linear DFA) and *qda* (quadratic DFA) from the package 'MASS', which incorporate Bayesian priors (Venables & Ripley, 2002). I then used this model to predict individuals in the test set. Finally, I divided the sum of all correct predictions by the total number of calls in the test set to obtain the classification accuracy. To compare this against chance, I followed the same steps with scrambled goose identity information to obtain chance accuracy. I calculated 100 iterations of DFA and report the means. To test whether call elements differ systematically in their acoustic structure between individuals, I performed χ^2-tests

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between the real and random classifications. Finally, I report Beecher's information statistic, which is a measure of the degree of individuality encoded that takes into account the number of individuals to classify between in a given sample (Beecher, 1989; Linhart et al., 2019). I calculated it using the function *calcHS* from the package 'IDmeasurer' (Linhart et al., 2019).

For individuality analyses, it is likely that call elements in the same call bout or even on the same track are more similar compared to each other than to those on other tracks, due to similar background noise conditions and recording distance (Alcocer et al., 2022). This temporal autocorrelation could lead to measuring the discriminability between track-specific factors instead of between individuals. To address this, I had already excluded geese who were recorded on only one track. As an additional control, I repeated the linear DFA steps detailed above, except that the split between training and test sets was now across tracks instead of randomly across all calls. Here, I selected a random track per individual per linear DFA iteration to be in the test set, while all others were in the training set. Therefore, priors were set to be equal for all individuals here.

Partner playback analysis

To account for multicollinearity between the analysed variables ('stepsTo', 'stepsAway', 'gazes', 'vigilance', 'contact calls', 'stare', 'down-up head'), I conducted a PCA and retained four response principal components with eigenvalues > 1. To test whether subjects differed in their response to partner versus non-partner calls, I conducted four linear mixed effects models (LMM) using the function *lme* from the package 'nlme' (Pinheiro et al., 2022) with each of these principal components as the response variable and partner (partner, non-partner) as a fixed effect. First, I compared partner and non-partner responses across the baseline period. Since there was no difference for all four principal components (all $p > 0.05$, see Table S2), I then

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compared partner and non-partner responses during the experimental broadcast. I included 'GooseID' as random factor to account for systematic differences between individual's reactions over multiple trials.

Exploratory additional analysis

I exploratorily investigated repeatability of subgroup departure order and group size, as well as potential explanatory factors (sex, age, personality). This was topically not related to the thesis. The preliminary findings are detailed in the supplementary material.

6. Results

<u>Acoustic structure discriminability between individuals</u>

Departure call elements showed evidence for classification above chance based on identity of the caller. The first six principal components of the PCA had eigenvalues > 1, cumulatively explaining 85.53% variance in the data, and so were used in both linear and quadratic DFA analyses. I report means of 100 DFA iterations per dataset in Table 4. Both DFA models could classify individuals with similar accuracy and above chance based on departure call element spectrographic measurements. Beecher's information statistic was highest for the first principal component. Loadings of components with eigenvalues > 1 are reported in Table 5.

When controlling for temporal autocorrelation by splitting train and test set across tracks, accuracy still was significantly above chance, albeit lower than in the random split. I report these results in Table S1.

<u>Partner playbacks</u>

The first four principal components of the PCA had eigenvalues > 1, cumulatively explaining 79.40% of variance in the data. The first principal component significantly differed between partners and non-partners while controlling for 'GooseID' as random factor (t = 3.79, p = 0.001; see Fig. 3). The variables 'vigilance' and 'stare' loaded most strongly on this component, with 'gazes', 'contact calls', and 'down-up head movement' also contributing (see Table 7). Focal greylag geese had a stronger response to departure call playback from their partner versus a non-partner (see Table 6 for means of all variables per partner condition). The other three principal components did not differ between partners and non-partners (see Table S2).

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Circumstantial additional finding of note: Non-linear phenomena in calls

While most departure call elements consist purely of chaotic non-linear phenomena, 22% contained harmonic structure elements with varying degrees of clarity on top of the chaos. These calls with harmonic elements were audibly distinct and even appeared in other call types not reported on here, but anecdotally most often in departure calls. They appeared in bouts before or after "normal" chaotic ones or in succession without obvious pattern. Examples of spectrograms are shown in Fig. 4. Results of an exploratory individuality analysis when splitting between chaotic elements, and elements that included harmonic elements on top of the chaos, using the same methodology as in the individuality analysis detailed above, are reported in Table 8. While DFA classification accuracy and Beecher's information statistic in (partially) harmonic calls indicated stronger vocal identity signatures than in chaotic calls, findings are not yet conclusive due to low sample size and the graded harmonicity between calls.

7. Discussion

In this thesis, I investigated vocal signatures and their recognition in greylag goose departure calls. First, I trained a discriminant function classifier to differentiate between call elements of different individuals based on spectrographic measurements. Testing the classifier on previously unseen data, I showed that it performed significantly above chance, demonstrating the presence of vocal identity signatures. Second, I experimentally broadcast departure calls to focal individuals, using calls from either their partner or another familiar flock mate. Subjects reacted more strongly towards partner calls than non-partner calls (with more attentive behaviour, such as vigilance or down-up head movements), providing evidence for individual or at least class-level (partner versus non-partner) vocal recognition.

The presence of acoustic identity signatures and individual vocal recognition in the departure calls of greylag geese aligns with similar findings across taxa (Carlson et al., 2020). This includes acoustic identity signatures found in other studies in geese, such as loud calls in barnacle geese, *Branta leucopsis* (Hausberger et al., 1994) and non-vocal hisses in Bilgoraj geese (Policht et al., 2020), but also in previous investigations of greylag goose vocalizations specifically (Guggenberger et al., 2022; Körmer, 2022; Weinhäupl, 2022) with the possible exception of gosling distress calls (Loth et al., 2018). Hence, further study of the development of vocal identity signatures could elucidate when and how such differences develop and whether they differ between call types.

Importantly, the presence of stable individual differences in acoustic structure does not require that conspecifics use this information (McCulloch et al., 1999; Schibler & Manser, 2007). Hence, it is necessary to combine descriptive analytic approaches, such as analyzing time and frequency parameters of vocalizations, with experimental

call broadcasts and receiver response observations. Only then is it possible to test for individual vocal recognition, as I have done in this study.

Future studies could additionally investigate if greylag geese also respond with differing types of behaviour when socially relevant non-partner individuals engage in departure calling, such as kin or dominant individuals. Another open question is the importance of visual information in identity recognition compared to acoustic information (Kleindorfer et al., 2023; Trillmich, 1976): Is the likely recognition of identity signatures in departure calls functionally relevant in most flight departure contexts, or is visual recognition (Kleindorfer et al., 2023) more important? However, because I used an experimental design with exclusively acoustic stimuli, the present finding supports the presence of functionally meaningful identity signatures in adult goose departure calls independently of the role of visual recognition. In a larger context, these findings help to deepen our understanding of selection pathways that may shape affiliative calls compared to more intensely studied other call types, such as alarm calls (Diggins, 2021).

The function of departure calls is unknown. Recently, leader-follower dynamics in bird flock movement have been reported, with current investigations centering on homing pigeons (Chen et al., 2015; Pettit et al., 2015). Similarly, departure calls in greylag geese may be rallying cries by a leader to initiate group takeoff, and as such could signal strong and acute individual departure motivation to followers (Cobb et al., 2022). Of course, in this context, it may be especially important for social allies, such as the partner, to be aware that flight departure is imminent, so they can ready themselves and reduce the risk of being left behind. Moreover, in greylag goose departure events, individuals often take flight in small subgroups instead of as part of the whole flock (see supplementary material). The order of individual subgroup departure events, as well as group size, are repeatable for individuals within these

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subgroups and independent of partnership status, which may indicate that subgroups across departure events are often composed of the same individuals (see supplementary material). In this case, individual vocal recognition of departure calls by a motivational group leader could support joining the correct subgroup in subgroup flight departures, while many individuals, of which only a few belong to a given subgroup, concurrently produce recruitment calls. However, a previous Master study found that departure calls of a given individual's partner do not increase their likelihood of taking flight (Weinhäupl, 2022).

Moreover, the ritualized pre-departure behaviour, such as building levels of recruitment calling, could be involved in a quorum decision process – in this case, the more individuals that display behaviour that is consistent with flight departure motivation, the likelier (sub)group takeoff may become. Such quorum decision processes governed by vocalizations have been shown before in mammals such as meerkats, *Suricata suricatta* (Bousquet et al., 2011) and African wild dogs, *Lycaon pictus* (Walker et al., 2017), and in birds such as jackdaws, *Corvus monedula* (Dibnah et al., 2022), whooper swans, *Cygnus cygnus*, and Bewick's swans, *Cygnus columbianus bewickii* (Black, 1988). In goose departures, consensus decision-making by allomimetic behaviour has been proposed, given that the number of geese oriented in the presumed movement direction predicts the number of total movers (Ramseyer et al., 2009), and that individuals continuously adjust their orientation before takeoff so as to be parallel to conspecifics (Schmitt, 1990).

Neck shaking before departure may be an "intention signal" to fly (Raveling, 1969). However, to my knowledge, quorum decisions mediated through vocalization levels have not yet been tested in any goose species. If it were the case that adjusting movements, neck shakes, and recruitment call levels all factor in a quorum decision process, departure calls, which suddenly increase the cacophonic amplitude, could

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ensure the quorum threshold is reached, which, by its suddenness, may help trigger mass-takeoff and thereby coordinate flight departure. This is also supported by the fact that if two individuals' departure calls overlap, a flight departure event is more likely to occur, independent of partnership (Weinhäupl, 2022).

In my study, the reactions of partners to departure calls varied from no noticeable reaction, to one or two glances to the loudspeaker or sudden startle after the first calls, up to intense and prolonged visual searching behaviour (vigilance, frequent turns of the head). However, no focal individual departed during the experimental broadcast. Thus, some of this variation in responses may have been an artifact of the experimental design, because the geese were not in an orienting position before takeoff. Perhaps the reactions across focal geese would be different if they had received the broadcast when positioned towards takeoff, and in the presence of recruitment calling and other geese ready to fly.

While my results strongly support the presence of vocal identity signatures in greylag goose departure calls, there are limitations to consider in interpreting their strength and generalizability. For example, the temporal autocorrelation inherently present between calls on the same track in the acoustic structure analysis makes it hard to precisely estimate the strength of the signature. Additionally, the widespread occurrence of nonlinear phenomena and in other cases varying clarity of harmonics may lead to an underperformance in DFA, due to the confounding influence of "harmonicity", which may vary between calls independently of caller identity. In the same vein, identity signatures encoded in harmonic calls may be stronger than in chaotic ones, as in zebra finches' distance versus 'wsst' calls (Elie & Theunissen, 2018). Finally, since the departure calls I recorded, analysed, and broadcast to partners and non-partners were almost exclusively produced by males, the

generalizability of my findings would yet need to be established in a more sex-balanced sample.

Altogether, I could demonstrate both the presence of a vocal identity signature in greylag goose departure calls and experimental evidence supporting individual vocal recognition. One function of departure call identity signatures could be to maintain contact with important individuals prior to movement in the air, across hundreds to thousands of meters. Coordination during the often complex sequences of behaviour leading up to flight departures, in which up to dozens of individuals begin moving around and loudly producing recruitment calls, might benefit from an individual and loud vocal signal. Departure calls, which are louder and less repetitive than recruitment calls, and which are individually distinct, could saliently pierce this background noise and allow partners or perhaps other social allies to infer position information without sight contact and coordinate flight departure, perhaps in allied subgroups. Future investigations into the ontogeny of departure calls could investigate the development of vocal identity signatures, which could also lead to a better understanding of the features of the departure call that other individuals recognize. Furthermore, there could be multiple functions of departure calls, for example, in the context of leader-follower dynamics, or in the coordination of subgroup movement. Finally, it may be fruitful to investigate the structure and function of the newly described, sporadically occurring call elements with varying degrees of harmonicity, compared to the usually chaotic departure calls.

8. References

Alcocer, I., Lima, H., Sugai, L. S. M., & Llusia, D. (2022). Acoustic indices as proxies for biodiversity: A meta-analysis. *Biological Reviews*, *97*(6), 2209–2236. https://doi.org/10.1111/brv.12890

Anikin, A. (2018). Soundgen: An open-source tool for synthesizing nonverbal vocalizations. *Behavior Research Methods*, *51*. https://doi.org/10.3758/s13428-018-1095-7

Araya-Salas, M., & Smith-Vidaurre, G. (2016). warbleR: An R package to streamline analysis of animal acoustic signals. *Methods in Ecology and Evolution*, *8*. https://doi.org/10.1111/2041-210X.12624

Audacity Team. (2023). *Audacity®* (3.4.0) [Computer software]. https://www.audacityteam.org/download/windows/

Beecher, M. D. (1989). Signalling systems for individual recognition: An information theory approach. *Animal Behaviour*, *38*(2), 248–261. https://doi.org/10.1016/S0003-3472(89)80087-9

Bezerra, B. M., & Souto, A. (2008). Structure and usage of the vocal repertoire of *Callithrix jacchus*. *International Journal of Primatology*, *29*(3), 671–701. https://doi.org/10.1007/s10764-008-9250-0

Black, J. M. (1988). Preflight signalling in swans: A mechanism for group cohesion and flock formation. *Ethology*, *79*(2), 143–157. https://doi.org/10.1111/j.1439-0310.1988.tb00707.x

Blumstein, D. T., Verneyre, L., & Daniel, J. C. (2004). Reliability and the adaptive utility of discrimination among alarm callers. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1550), 1851–1857. https://doi.org/10.1098/rspb.2004.2808

Bouchet, H., Blois-Heulin, C., Pellier, A.-S., Zuberbühler, K., & Lemasson, A. (2012). Acoustic variability and individual distinctiveness in the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*). *Journal of Comparative Psychology*, *126*(1), 45–56. https://doi.org/10.1037/a0025018

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Bouchet, H., Pellier, A.-S., Blois-Heulin, C., & Lemasson, A. (2010). Sex differences in the

vocal repertoire of adult red-capped mangabeys (*Cercocebus torquatus*): A multi-level

acoustic analysis. *American Journal of Primatology*, *72*(4), 360–375.

https://doi.org/10.1002/ajp.20791

Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2011). Moving calls: A vocal

mechanism underlying quorum decisions in cohesive groups. *Proceedings of the

Royal Society B: Biological Sciences*, *278*(1711), 1482–1488.

https://doi.org/10.1098/rspb.2010.1739

Bowling, D. L., Garcia, M., Dunn, J. C., Ruprecht, R., Stewart, A., Frommolt, K.-H., & Fitch,

W. T. (2017). Body size and vocalization in primates and carnivores. *Scientific

Reports*, *7*(1), 41070. https://doi.org/10.1038/srep41070

Carlson, N. V., Kelly, E. M., & Couzin, I. (2020). Individual vocal recognition across taxa: A

review of the literature and a look into the future. *Philosophical Transactions of the

Royal Society B: Biological Sciences*, *375*(1802), 20190479.

https://doi.org/10.1098/rstb.2019.0479

Catchpole, C. K., & Slater, P. J. B. (2003). *Bird Song: Biological Themes and Variations*.

Cambridge University Press.

Charrier, I., Jouventin, P., Mathevon, N., & Aubin, T. (2001). Individual identity coding

depends on call type in the South Polar skua *Catharacta maccormicki*. *Polar Biology*,

24(5), 378–382. https://doi.org/10.1007/s003000100231

Chen, Z., Zhang, H.-T., Chen, X., Chen, D., & Zhou, T. (2015). Two-level leader-follower

organization in pigeon flocks. *EPL (Europhysics Letters)*, *112*(2), 20008.

https://doi.org/10.1209/0295-5075/112/20008

Cinková, I., & Policht, R. (2014). Contact calls of the Northern and Southern White

Rhinoceros allow for individual and species identification. *PLOS ONE*, *9*(6), e98475.

https://doi.org/10.1371/journal.pone.0098475

Cobb, B., Morris-Drake, A., Kennedy, P., Layton, M., Kern, J. M., & Radford, A. N. (2022).

Factors affecting follower responses to movement calls in cooperatively breeding

dwarf mongooses. *Animal Behaviour*, *192*, 159–169.

https://doi.org/10.1016/j.anbehav.2022.07.009

Colombelli-Négrel, D., & Evans, C. (2017). Superb fairy-wrens respond more to alarm calls from mate and kin compared to unrelated individuals. *Behavioral Ecology*, *28*(4), 1101–1112. https://doi.org/10.1093/beheco/arx071

Colombelli-Négrel, D., Hauber, M. E., Evans, C., Katsis, A. C., Brouwer, L., Adreani, N. M., & Kleindorfer, S. (2021). Prenatal auditory learning in avian vocal learners and non-learners. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1836), 20200247. https://doi.org/10.1098/rstb.2020.0247

Colombelli-Négrel, D., Hauber, M. E., Robertson, J., Sulloway, F. J., Hoi, H., Griggio, M., & Kleindorfer, S. (2012). Embryonic learning of vocal passwords in Superb Fairy-Wrens reveals intruder Cuckoo nestlings. *Current Biology*, *22*(22), 2155–2160. https://doi.org/10.1016/j.cub.2012.09.025

Dibnah, A. J., Herbert-Read, J. E., Boogert, N. J., McIvor, G. E., Jolles, J. W., & Thornton, A. (2022). Vocally mediated consensus decisions govern mass departures from jackdaw roosts. *Current Biology*, *32*(10), R455–R456. https://doi.org/10.1016/j.cub.2022.04.032

Diggins, C. A. (2021). Behaviors associated with vocal communication of squirrels. *Ecosphere*, *12*(6), e03572. https://doi.org/10.1002/ecs2.3572

Elie, J. E., & Theunissen, F. E. (2018). Zebra finches identify individuals using vocal signatures unique to each call type. *Nature Communications*, *9*(1), 4026. https://doi.org/10.1038/s41467-018-06394-9

Ficken, M. S., Ficken, R. W., & Witkin, S. R. (1978). Vocal repertoire of the Black-Capped Chickadee. *The Auk*, *95*(1), 34–48. https://doi.org/10.2307/4085493

Fischer, J., & Hammerschmidt, K. (2002). An overview of the Barbary Macaque, *Macaca sylvanus*, vocal repertoire. *Folia Primatologica*, *73*(1), 32–45. https://doi.org/10.1159/000060417

Goncharova, M. V., Klenova, A. V., & Bragina, E. V. (2015). Development of cues to individuality and sex in calls of three crane species: When is it good to be recognizable? *Journal of Ethology*, *33*(3), 165–175. https://doi.org/10.1007/s10164-015-0428-6

Guggenberger, M., Adreani, N. M., Foerster, K., & Kleindorfer, S. (2022). Vocal recognition of distance calls in a group-living basal bird: The greylag goose, *Anser anser*. *Animal Behaviour*, *186*, 107–119. https://doi.org/10.1016/j.anbehav.2022.01.004

Hambálková, L., Policht, R., Horák, J., & Hart, V. (2021). Acoustic individuality in the hissing calls of the male black grouse (*Lyrurus tetrix*). *PeerJ*, *9*, e11837. https://doi.org/10.7717/peerj.11837

Hardouin, L. A., Tabel, P., & Bretagnolle, V. (2006). Neighbour–stranger discrimination in the little owl, *Athene noctua*. *Animal Behaviour*, *72*(1), 105–112. https://doi.org/10.1016/j.anbehav.2005.09.020

Hare. (1998). Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. *Animal Behaviour*, *55*(2), 451–460. https://doi.org/10.1006/anbe.1997.0613

Hare, J., & Atkins, B. (2001). The squirrel that cried wolf: Reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral Ecology and Sociobiology*, *51*, 108–112. https://doi.org/10.1007/s002650100414

Hare, & Warkentin, K. J. (2012). The song remains the same: Juvenile Richardson's ground squirrels do not respond differentially to mother's or colony member's alarm calls. *Current Zoology*, *58*(5), 773–780. https://doi.org/10.1093/czoolo/58.5.773

Hartshorne, I. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, *274*.

Hausberger, M., Richard, J. P., Black, J. M., & Quris, R. (1994). A quantitative analysis of individuality in Barnacle Goose loud calls. *Bioacoustics*, *5*(4), 247–260. https://doi.org/10.1080/09524622.1994.9753255

Hemetsberger, J., Scheiber, I., Weiß, B., Frigerio, D., & Kotrschal, K. (2010). Influence of socially involved hand-raising on life history and stress responses in greylag geese. *Interaction Studies*, *11*. https://doi.org/10.1075/is.11.3.03hem

Herbert-Read, J. E. (2016). Understanding how animal groups achieve coordinated movement. *Journal of Experimental Biology*, *219*(19), 2971–2983. https://doi.org/10.1242/jeb.129411

Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, *78*(4), 791–800. https://doi.org/10.1016/j.anbehav.2009.07.021

Inglis, I. R., & Lazarus, J. (1981). Vigilance and flock size in Brent Geese: The Edge Effect. *Zeitschrift Für Tierpsychologie*, *57*(3–4), 193–200. https://doi.org/10.1111/j.1439-0310.1981.tb01921.x

Jensen, T. R., Anikin, A., Osvath, M., & Reber, S. A. (2024). Knowing a fellow by their bellow: Acoustic individuality in the bellows of the American alligator. *Animal Behaviour*, *207*, 157–167. https://doi.org/10.1016/j.anbehav.2023.11.009

Jones, G., Gordon, T., & Nightingale, J. (1992). Sex and age differences in the echolocation calls of the lesser horseshoe bat, *Rhinolophus hipposideros*. *Mammalia*, *56*(2). https://doi.org/10.1515/mamm-1992-0202

K. Lisa Yang Center for Conservation Bioacoustics. (2023). *Raven Lite: Interactive sound analysis software* (2.0.5) [Computer software]. The Cornell Lab of Ornithology. https://ravensoundsoftware.com/

Kleindorfer, S. (2024). *Die erstaunliche Welt der Graugänse: Wie sie leben, kommunizieren und füreinander sorgen*. Christian Brandstätter Verlag.

Kleindorfer, S., Brouwer, L., Hauber, M. E., Teunissen, N., Peters, A., Louter, M., Webster, M. S., Katsis, A. C., Sulloway, F. J., Common, L. K., Austin, V. I., & Colombelli-Négrel, D. (2024). Nestling begging calls resemble maternal vocal signatures when mothers call slowly to embryos. *The American Naturalist*, *203*(2), 267–283. https://doi.org/10.1086/728105

Kleindorfer, S., Evans, C., & Colombelli-Négrel, D. (2014). Females that experience threat are better teachers. *Biology Letters*, *10*, 20140046. https://doi.org/10.1098/rsbl.2014.0046

Kleindorfer, S., Heger, B., Tohl, D., Frigerio, D., Hemetsberger, J., Fusani, L., Fitch, W. T., & Colombelli-Négrel, D. (2023). Cues to individuality in Greylag Goose faces: Algorithmic discrimination and behavioral field tests. *Journal of Ornithology*. https://doi.org/10.1007/s10336-023-02113-4

Körmer, E.-M. (2022). The call structure of contact calls in greylag geese (*Anser anser*) [unpublished master thesis].

Lameira, A. R., & Wich, S. A. (2008). Orangutan long call degradation and individuality over distance: A playback approach. *International Journal of Primatology*, *29*(3), 615–625. https://doi.org/10.1007/s10764-008-9253-x

Lehmann, K. D. S., Jensen, F. H., Gersick, A. S., Strandburg-Peshkin, A., & Holekamp, K. E. (2022). Long-distance vocalizations of spotted hyenas contain individual, but not group, signatures. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1979), 20220548. https://doi.org/10.1098/rspb.2022.0548

Levréro, F., Durand, L., Vignal, C., Blanc, A., & Mathevon, N. (2009). Begging calls support offspring individual identity and recognition by zebra finch parents. *Comptes Rendus. Biologies*, *332*(6), 579–589. https://doi.org/10.1016/j.crvi.2009.02.006

Ligges, U., Krey, S., Mersmann, O., & Schnackenberg, S. (2023). *tuneR: Analysis of music and speech* [Computer software]. https://CRAN.R-project.org/package=tuneR

Linhart, P., Osiejuk, T., Budka, M., Spinka, M., Policht, R., Syrová, M., & Blumstein, D. (2019). Measuring individual identity information in animal signals: Overview and performance of available identity metrics. *Methods in Ecology and Evolution*, *10*. https://doi.org/10.1111/2041-210X.13238

Linn, S. N., Schmidt, S., & Scheumann, M. (2021). Individual distinctiveness across call types of the southern white rhinoceros (*Ceratotherium simum simum*). *Journal of Mammalogy*, *102*(2), 440–456. https://doi.org/10.1093/jmammal/gyab007

Lorenz, K., Martys, M., & Tipler, A. (1988). *Hier bin ich—Wo bist du? Ethologie der Graugans*. Piper.

Loth, A., Frigerio, D., Kotrschal, K., & Szipl, G. (2018). Differential responses to gosling distress calls in parental and non-parental Greylag Geese. *Journal of Ornithology*, *159*(2), 401–412. https://doi.org/10.1007/s10336-017-1521-0

Marler, P. (2004). Bird calls: Their potential for behavioral neurobiology. *Annals of the New York Academy of Sciences*, *1016*(1), 31–44. https://doi.org/10.1196/annals.1298.034

Martin, M., Gridley, T., Elwen, S., & Charrier, I. (2022). Early onset of postnatal individual vocal recognition in a highly colonial mammal species. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1988), 20221769. https://doi.org/10.1098/rspb.2022.1769

Masco, C. (2013). Neighbor-stranger discrimination on the basis of a threat vocalization in the great Black-Backed Gull. *The Wilson Journal of Ornithology*, *125*(2), 342–347. https://doi.org/10.1676/12-095.1

McCulloch, S., Pomeroy, P. P., & Slater, P. J. B. (1999). Individually distinctive pup vocalizations fail to prevent allo-suckling in grey seals. *Canadian Journal of Zoology*, *77*, 716–723.

Mouterde, S. C., Theunissen, F. E., Elie, J. E., Vignal, C., & Mathevon, N. (2014). Acoustic communication and sound degradation: How do the individual signatures of male and female Zebra Finch calls transmit over distance? *PLOS ONE*, *9*(7), e102842. https://doi.org/10.1371/journal.pone.0102842

Munn, C. A. (1986). Birds that 'cry wolf'. *Nature*, *319*(6049), 143–145. https://doi.org/10.1038/319143a0

Myrberg, A. A., & Riggio, R. J. (1985). Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*). *Animal Behaviour*, *33*(2), 411–416. https://doi.org/10.1016/S0003-3472(85)80065-8

Péter, A. (2019). *Solomon Coder* (beta 19.08.02) [Computer software].

Pettit, B., Ákos, Z., Vicsek, T., & Biro, D. (2015). Speed determines leadership and leadership

    determines learning during Pigeon flocking. *Current Biology*, *25*(23), 3132–3137.

    https://doi.org/10.1016/j.cub.2015.10.044

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2022). *nlme: Linear and*

    Nonlinear Mixed Effects Models (3.1-155) [Computer software]. https://CRAN.R-

    project.org/package=nlme

Podos, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's

    finches. *Nature*, *409*(6817), 185–188. https://doi.org/10.1038/35051570

Policht, R., Kowalczyk, A., Łukaszewicz, E., & Hart, V. (2020). Hissing of geese: Caller

    identity encoded in a non-vocal acoustic signal. *PeerJ*, *8*, e10197.

    https://doi.org/10.7717/peerj.10197

Posit team. (2023). *RStudio: Integrated Development Environment for R* (2023.06.1)

    [Computer software]. Posit Software, PBC. http://www.posit.co/

R Core Team. (2022). *R: A language and environment for statistical computing* (4.1.3)

    [Computer software]. R Foundation for Statistical Computing. https://www.R-

    project.org/

Ramseyer, A., Boissy, A., Dumont, B., & Thierry, B. (2009). Decision making in group

    departures of sheep is a continuous process. *Animal Behaviour*, *78*(1), 71–78.

    https://doi.org/10.1016/j.anbehav.2009.03.017

Raveling, D. G. (1969). Preflight and flight behavior of Canada Geese. *The Auk*, *86*(4), 671–

    681. https://doi.org/10.2307/4083454

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: Acoustic cues to

    age and weight in the roars of red deer stags. *Animal Behaviour*, *65*(3), 519–530.

    https://doi.org/10.1006/anbe.2003.2078

Rekdahl, M. L., Dunlop, R. A., Noad, M. J., & Goldizen, A. W. (2013). Temporal stability and

    change in the social call repertoire of migrating humpback whales. *The Journal of the*

    Acoustical Society of America, *133*(3), 1785–1795. https://doi.org/10.1121/1.4789941

Rendall, D., Owren, M., & Rodman, P. (1998). The role of vocal tract filtering in identity

cueing in rhesus monkey (*Macaca Mulatta*) vocalizations. *The Journal of the*

Acoustical Society of America, *103*, 602–614. https://doi.org/10.1121/1.421104

Rose, E. M., Prior, N. H., & Ball, G. F. (2022). The singing question: Re-conceptualizing

birdsong. *Biological Reviews*, *97*(1), 326–342. https://doi.org/10.1111/brv.12800

Rosin, Z., Skórka, P., Wylegała, P., Krąkowski, B., Tobółka, M., Myczko, L., & Sparks, T.

(2012). Landscape structure, human disturbance and crop management affect

foraging ground selection by migrating geese. *Journal of Ornithology*, *153*, 747–759.

https://doi.org/10.1007/s10336-011-0791-1

Rubow, J., Cherry, M. I., & Sharpe, L. L. (2018). A comparison of individual distinctiveness in

three vocalizations of the dwarf mongoose (*Helogale parvula*). *Ethology*, *124*(1), 45–

53. https://doi.org/10.1111/eth.12698

Saks, L., Ots, I., & Hõrak, P. (2003). Carotenoid-based plumage coloration of male

greenfinches reflects health and immunocompetence. *Oecologia*, *134*(3), 301–307.

https://doi.org/10.1007/s00442-002-1125-z

Scheiber, I. B. R., Kotrschal, K., & Weiß, B. M. (2009). Benefits of family reunions: Social

support in secondary greylag goose families. *Hormones and Behavior*, *55*(1), 133.

https://doi.org/10.1016/j.yhbeh.2008.09.006

Scheiber, I. B. R., Weiß, B. M., Frigerio, D., & Kotrschal, K. (2005). Active and passive social

support in families of greylag geese (*Anser anser*). *Behaviour*, *142*(11–12), 1535–

1557. https://doi.org/10.1163/156853905774831873

Scheiber, I. B. R., Weiß, B. M., Hemetsberger, J., & Kotrschal, K. (Eds.). (2013). *The Social*

Life of Greylag Geese: Patterns, Mechanisms and Evolutionary Function in an Avian

Model System. Cambridge University Press.

https://doi.org/10.1017/CBO9781139049955

Schibler, F., & Manser, M. B. (2007). The irrelevance of individual discrimination in meerkat

alarm calls. *Animal Behaviour*, *74*(5), 1259–1268.

https://doi.org/10.1016/j.anbehav.2007.02.026

Schmitt, A. (1990). Adjusting movements in greylag geese during pre-roosting and mass fleeing. *Bird Behavior*, *9*(1–2), 41-48(8).

Selbmann, A., Deecke, V. B., Filatova, O. A., Fedutin, I. D., Miller, P. J. O., Simon, M., Bowles, A. E., Lyrholm, T., Lacey, C., Magnúsdóttir, E. E., Maunder, W., Wensveen, P. J., Svavarsson, J., & Samarra, F. I. P. (2023). Call type repertoire of killer whales (*Orcinus orca*) in Iceland and its variation across regions. *Marine Mammal Science*, *39*(4), 1136–1160. https://doi.org/10.1111/mms.13039

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803.

Shapiro, A. D. (2010). Chapter 11.4: Recognition of individuals within the social group: Signature vocalizations. In S. M. Brudzynski (Ed.), *Handbook of Behavioral Neuroscience* (Vol. 19, pp. 495–503). Elsevier. https://doi.org/10.1016/B978-0-12-374593-4.00045-0

Shen, D., Fang, K., Fan, Y., Shen, J., Yang, J., Cui, J., Tang, Y., & Fang, G. (2020). Sex differences in vocalization are reflected by event-related potential components in the music frog. *Animal Cognition*, *23*(3), 477–490. https://doi.org/10.1007/s10071-020-01350-x

Stoeger, A. S., Zeppelzauer, M., & Baotic, A. (2014). Age-group estimation in free-ranging African elephants based on acoustic cues of low-frequency rumbles. *Bioacoustics*. https://www.tandfonline.com/doi/full/10.1080/09524622.2014.888375

Stoffel, M., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *8*. https://doi.org/10.1111/2041-210X.12797

Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, *18*, 213–226. https://doi.org/10.1080/09524622.2008.9753600

Suzuki, T. N. (2011). Parental alarm calls warn nestlings about different predatory threats. *Current Biology*, *21*(1), R15–R16. https://doi.org/10.1016/j.cub.2010.11.027

Szipl, G., Depenau, M., Kotrschal, K., Hemetsberger, J., & Frigerio, D. (2019). Costs and benefits of social connectivity in juvenile Greylag geese. *Scientific Reports*, *9*(1), 12839. https://doi.org/10.1038/s41598-019-49293-9

Taoka, M., & Okumura, H. (1990). Sexual differences in flight calls and the cue for vocal sex recognition of Swinhoe's Storm-Petrels. *The Condor*, *92*(3), 571. https://doi.org/10.2307/1368674

Toledo, L. F., Martins, I. A., Bruschi, D. P., Passos, M. A., Alexandre, C., & Haddad, C. F. B. (2015). The anuran calling repertoire in the light of social context. *Acta Ethologica*, *18*(2), 87–99. https://doi.org/10.1007/s10211-014-0194-4

Trillmich, F. (1976). Learning experiments on individual recognition in Budgerigars (*Melopsittactus undulatus*). *Zeitschrift Für Tierpsychologie*, *41*, 372–395.

Tuszynski, J. (2021). *caTools: Tools: Moving window atatistics, GIF, Base64, ROC AUC, etc. R package version 1.18.2* [Computer software]. https://CRAN.R-project.org/package=caTools

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. Springer. https://doi.org/10.1007/978-0-387-21706-2

Walker, R. H., King, A. J., McNutt, J. W., & Jordan, N. R. (2017). Sneeze to leave: African wild dogs (*Lycaon pictus*) use variable quorum thresholds facilitated by sneezes in collective decisions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1862), 20170347. https://doi.org/10.1098/rspb.2017.0347

Warrington, M. H., McDonald, P. G., Rollins, L. A., & Griffith, S. C. (2014). All signals are not equal: Acoustic signalling of individuality, sex and breeding status in a cooperative breeder. *Animal Behaviour*, *93*, 249–260. https://doi.org/10.1016/j.anbehav.2014.05.007

Watanabe, Izawa, & Kondo. (2010). Perceptual mechanism for vocal individual recognition in jungle crows (*Corvus macrorhynchos*): Contact call signature and discrimination. *Behaviour*, *147*(8), 1051–1072. https://doi.org/10.1163/000579510X505427

Weinhäupl, V. (2022). Departure calls in Greylag Geese (*Anser anser*) [unpublished master thesis].

Weiß, B. M., Kehmeier, S., & Schloegl, C. (2010). Transitive inference in free-living greylag geese, *Anser anser*. *Animal Behaviour*, *79*(6), 1277–1283. https://doi.org/10.1016/j.anbehav.2010.02.029

Weiß, B. M., & Kotrschal, K. (2004). Effects of passive social support in juvenile Greylag Geese (*Anser anser*): A study from fledging to adulthood. *Ethology*, *110*(6), 429–444. https://doi.org/10.1111/j.1439-0310.2004.00979.x

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. Springer. https://doi.org/10.1007/978-0-387-98141-3

Wickham, H. (2023). *Stringr: Simple, consistent wrappers for common string operations. R package version 1.5.1.* [Computer software]. https://CRAN.R-project.org/package=stringr

Wickham, H., & Bryan, J. (2023). *Readxl: Read Excel files. R package version 1.4.2* [Computer software]. ttps://CRAN.R-project.org/package=readxl

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *Dplyr: A grammar of data manipulation. R package version 1.1.2* [Computer software]. https://CRAN.R-project.org/package=dplyr

Wiemken, T. L., & Kelley, R. R. (2020). Machine learning in epidemiology and health outcomes research. *Annual Review of Public Health*, *41*(1), 21–36. https://doi.org/10.1146/annurev-publhealth-040119-094437

Wittig, R. M., Crockford, C., Seyfarth, R. M., & Cheney, D. L. (2007). Vocal alliances in Chacma baboons (*Papio hamadryas ursinus*). *Behavioral Ecology and Sociobiology*, *61*(6), 899–909. https://doi.org/10.1007/s00265-006-0319-5

Wyman, M. T., Walkenhorst, B., & Manser, M. B. (2022). Selection levels on vocal

    individuality: Strategic use or byproduct. *Current Opinion in Behavioral Sciences*, *46*,

    101140. https://doi.org/10.1016/j.cobeha.2022.101140

Zhao, X., Jiang, T., Gu, H., Liu, H., Sun, C., Liu, Y., & Feng, J. (2018). Are aggressive

    vocalizations the honest signals of body size and quality in female Asian particoloured

    bats? *Behavioral Ecology and Sociobiology*, *72*(6), 96.

    https://doi.org/10.1007/s00265-018-2510-x

Zuberbühler, K. (2009). Chapter 8 survivor signals: The biology and psychology of animal

    alarm calling. In *Advances in the Study of Behavior* (Vol. 40, pp. 277–322). Elsevier.

    https://doi.org/10.1016/S0065-3454(09)40008-1

9. Appendix

	Number elements	By females	By males	Number individuals	Number female callers	Number male callers
Departure calls	562	34	528	10	1	9

Table 1: Summary of sample sizes in the individuality analysis.

Variable	Operationalization
Steps towards (count)	Steps towards loudspeaker
Steps away (count)	Steps away from loudspeaker
Gazes (count)	Looking at loudspeaker for a short amount of time or moving the head in discrete ranges with loudspeaker in view
Neck rolls (count)	Neck rolls displayed in departure contexts (Schmitt, 1990)
Vigilance (s)	Attentive with upright neck, often extended, and horizontal beak (Inglis & Lazarus, 1981)
Within 2 m (s)	Estimated 2 m perimeter around loudspeaker
Minimum distance (m)	Estimated minimum distance to loudspeaker
Departure calls (count)	High-amplitude single calls, almost always accompanied by departure behaviour displays (orientation towards takeoff, neck rolls…)
Recruitment calls (count)	High amplitude calls in bouts, often accompanied by departure behaviour displays
Contact calls (count)	Soft calls, almost always in bouts without any other characteristic behaviour
Takeoff (yes/no)	Taking flight
Stare (s)	Continually looking in the approximate direction of the loudspeaker for prolonged episodes of time
Down-up head (count)	Raising the head rapidly a bit or a lot, often accompanied by abrupt body movement

Table 2: Coded variables and their operationalizations in partner playbacks.

Spectrographic variable	Definition
Duration (s)	Call element length, measured automatically by marking the 20% threshold of peak amplitude of a signal at the start and the end and calculating the time in between
Mean frequency (kHz)	Weighted average of the frequency spectrum
SD of frequency (kHz)	Weighted standard deviation of the frequency spectrum
Median frequency (kHz)	Frequency where the frequency spectrum is divided in two equal-energy frequency intervals
1st quartile frequency (kHz)	Frequency where the frequency spectrum is divided in frequency intervals with 25:75 energy
3rd quartile frequency (kHz)	Frequency where the frequency spectrum is divided in frequency intervals with 75:25 energy
Interquartile frequency range (kHz)	The frequency range between 1st and 3rd quartile frequency
Median time (s)	Time where the time envelope is divided in two equal-energy intervals
1st quartile time (s)	Time where the time envelope is divided in intervals with 25:75 energy
3rd quartile time (s)	Time where the time envelope is divided in intervals with 75:25 energy
Interquartile time range (s)	The time range between 1st and 3rd quartile time
Skewness	Asymmetry of the frequency spectrum
Kurtosis	Peakedness of the frequency spectrum
Spectral entropy (0-1)	Energy distribution of the frequency spectrum (0 = pure, 1 = noisy)
Time entropy (0-1)	Energy distribution of the time envelope (0 = all amplitude at timepoint x, 1 = amplitude is equal over time)
Total entropy (0-1)	Spectral entropy * time entropy
Spectral flatness (0-1)	Ratio between geometric and arithmetic mean (0 = pure, 1 = noisy)
Mean dominant frequency (kHz)	Average of the dominant frequency
Maximum dominant frequency (kHz)	Maximum of the dominant frequency
Range of dominant frequency	Range of the dominant frequency
Modulation index	The cumulative absolute difference between adjacent measurements of the dominant frequency, divided by the range of dominant frequency (1 = not modulated)
Slope of dominant frequency over time	Slope of the change in dominant frequency over time
Mean peak frequency (kHz)	Frequency with the highest energy from the mean frequency spectrum

Table 3: Automatically measured spectrographic variables in the acoustic structure analysis. All definitions are taken from the official documentation of the *spectro_analysis* function of the package warbleR (Araya-Salas & Smith-Vidaurre, 2016) except for 'duration' (self-written) and 'spectral flatness', which is from the documentation of the *sfm* function of the package seewave (Sueur et al., 2008).

DFA	Sample size	Number individuals	Correct classification	Random classification	X^2-test	Beecher's information statistic (Hs)
linear	562	10	51.24%	17.11%	$X^2 = 28.04$ $p < 0.001$	1.23
quadratic	562	10	51.00%	14.35%	$X^2 = 32.86$ $p < 0.001$	1.23

Table 4: Summary of results of identity classification using several acoustic parameters of calls in linear and quadratic discriminant function analysis (DFA). The six principal components with eigenvalues > 1 were used as predictors.

Acoustic variable	PC1_Acoustic	PC2_Acoustic	PC3_Acoustic	PC4_Acoustic	PC5_Acoustic	PC6_Acoustic
Duration	0.092	0.393	0.083	0.038	-0.066	-0.331
Mean frequency	-0.323	-0.026	0.125	0.11	-0.071	0.005
SD of frequency	-0.232	-0.056	0.36	0.191	0.072	-0.095
Median frequency	-0.308	-0.021	0.027	0.056	-0.105	0.035
1st quartile frequency	-0.271	0.031	-0.095	0.081	-0.373	0.089
3rd quartile frequency	-0.316	-0.018	0.143	0.076	0.031	-0.008
Interquartile frequency range	-0.256	-0.045	0.259	0.051	0.288	-0.069
Median time	0.103	0.379	0.083	0.228	0.038	0.233
1st quartile time	0.078	0.304	0.076	0.193	0.178	0.568
3rd quartile time	0.104	0.409	0.091	0.219	-0.075	-0.063
Interquartile time range	0.081	0.319	0.064	0.147	-0.244	-0.534
Skewness	0.156	-0.255	0.12	0.469	-0.008	-0.007
Kurtosis	0.137	-0.241	0.131	0.484	0.01	0.005
Spectral entropy	-0.258	0.184	0.141	-0.169	0.222	0.005
Time entropy	-0.064	-0.339	-0.069	0.012	-0.219	-0.133
Total entropy	-0.289	0.061	0.118	-0.169	0.145	-0.045
Spectral flatness	-0.257	0.011	0.309	0.137	0.001	-0.059
Mean dominant frequency	-0.269	0.062	-0.273	0.108	-0.212	0.135
Maximum dominant frequency	-0.221	0.092	-0.392	0.143	0.179	0.016
Range of dominant frequency	-0.191	0.116	-0.406	0.144	0.227	-0.011
Modulation index	-0.067	0.162	0.123	-0.344	-0.232	0.027
Slope of dominant frequency over time	0.085	-0.025	0.352	-0.182	-0.361	0.382
Mean peak frequency	-0.184	0.071	-0.168	0.196	-0.47	0.116

Table 5: Loadings per variable for all six principal components (PCs) with eigenvalue > 1 for my individuality analysis of greylag goose departure calls.

Variable	Non-partner	Partner
stepsTo	1.778	1.741
stepsAway	9.481	9.037
gazes	0.704	1.667
vigilance	7.541	19.963
contact	0.407	0.852
stare	6.311	13.911
headUp	0.593	1.296

Table 6: Mean values of all analysed response variables in the departure call broadcasts to greylag geese during the treatment (replay) phase. All variables except vigilance and stare, which were durations (s), were coded as events, meaning, for example, that focal individuals made on average 1.778 steps towards the loudspeaker during the treatment phase, while they were vigilant for 7.541 s.

	PC1_Response	PC2_Response	PC3_Response	PC4_Response
stepsTo	0.1025	0.221	0.3533	-0.7798
stepsAway	-0.066	0.2587	-0.6811	-0.4898
gazes	0.3397	-0.5536	-0.1985	-0.2025
vigilance	0.5977	0.304	0.0043	0.0199
contact	0.3067	0.1865	-0.5406	0.2596
stare	0.5927	0.1866	0.2766	0.117
headUp	0.259	-0.6447	-0.0561	-0.1716

Table 7: Loadings per variable for all four principal components (PCs) with eigenvalue > 1 for my analysis of greylag goose behavioural responses to departure call playback.

Dataset	Sample size	Number individuals	Correct classification	Random classification	X^2-test	Beecher's information statistic (Hs)
Chaotic departure calls	420	8	57.27%	19.64%	$X^2 = 23.56$, $p < 0.001$	1.24
Harmonic departure calls	117	5	71.04%	27.04%	$X^2 = 7.62$, $p = 0.006$	1.39

Table 8: Summary of results of identity classification between chaotic departure calls and departure calls with harmonic elements using several acoustic parameters of calls in discriminant function analysis (DFA). Principal components with eigenvalues > 1 were used as predictors (5 in chaotic, 6 in harmonic departure calls).
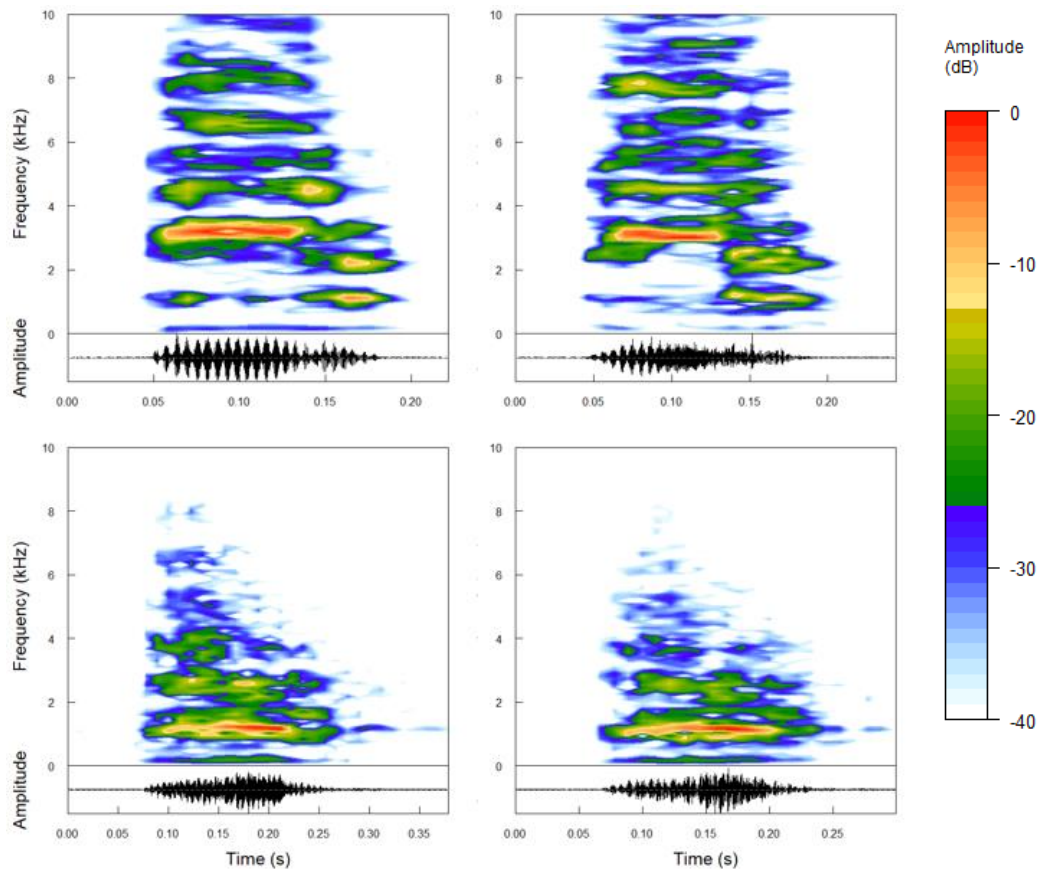
Figure 1: Example oscillograms and spectrograms of departure call elements of two male geese. Upper calls are from the individual Bruce Springsteen, lower calls are from Babaco. All spectrograms depict a frequency range of 0 to 10 kHz and were created with a window length of 512 samples after filtering out the 0–100 Hz range. Note the different time (x) axis scales.
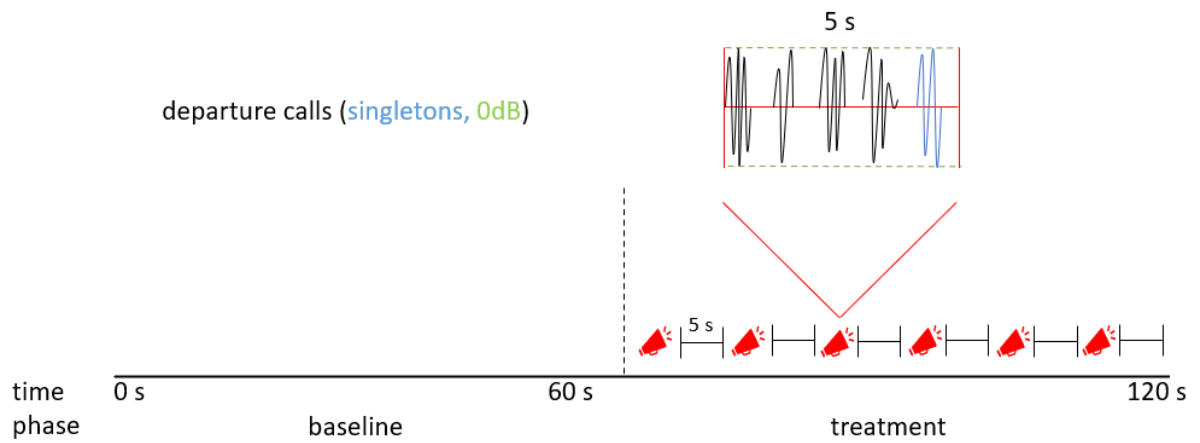
51

Figure 2: Structure of playback stimuli for partner playback trials. The 1 min of silence (baseline) was followed by 1 min of departure call playback (treatment). The playback period comprised alternating "action intervals" (red) and 5 s silent intervals. Action intervals consisted of 5 alternating singleton call elements (blue) with 1 s silent intervals. Call elements were normalized to 0 dB (green dashed lines).
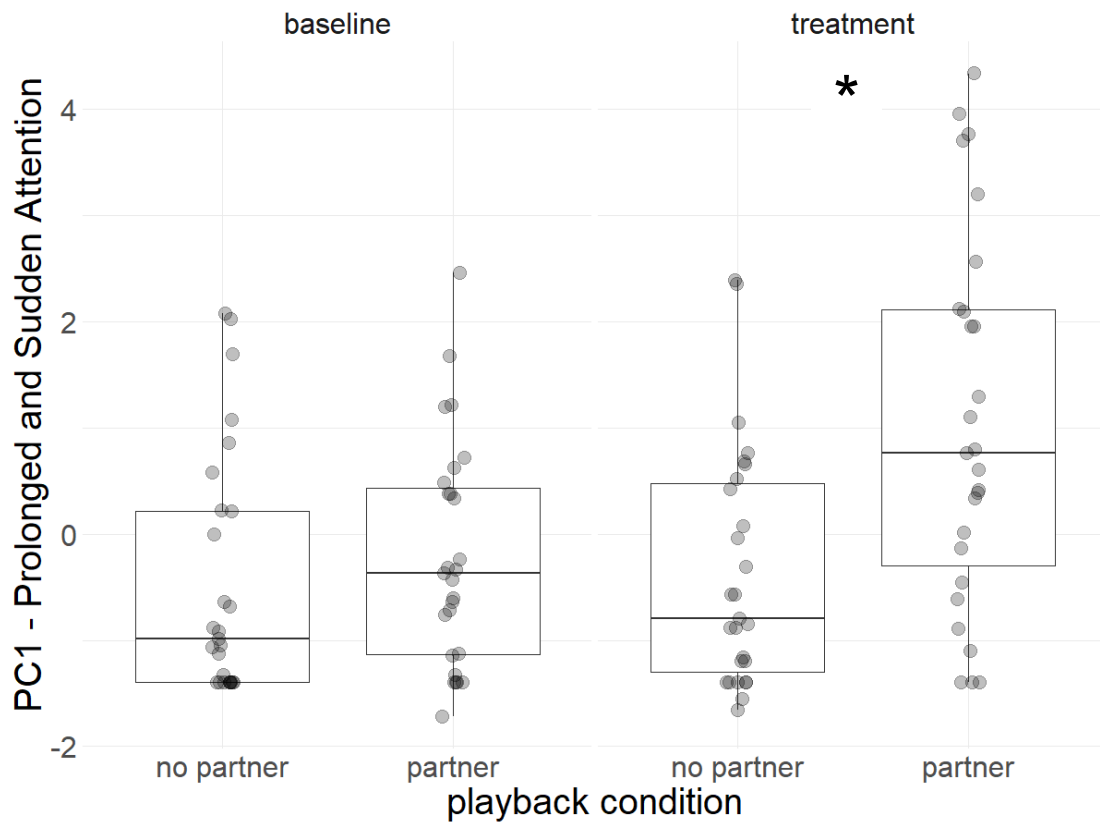
Figure 3: Behavioural response of greylag geese to experimental playback of partner versus non-partner departure calls. Higher scores on the first principal component (PC1_Response) indicate more attentive behaviours such as being vigilant or gazing to the speaker. The behavioural response to partner departure call playbacks was significantly stronger than to non-partner departure call playbacks. Boxplots indicate the range between first and third quartile as well as the median. Dots indicate single datapoints, jittered for better visibility. The asterisk (*) denotes a significant difference between partner and non-partner responses on PC1_Response during the treatment (replay) phase.
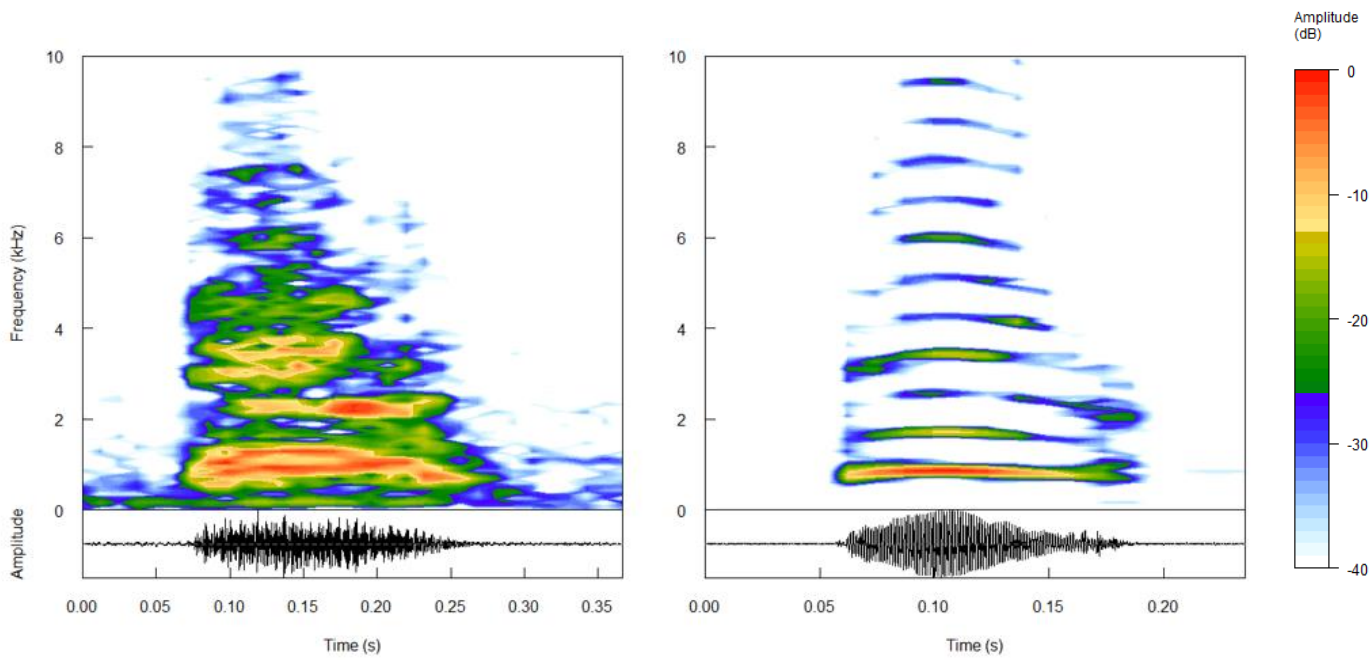
Figure 4: Example oscillograms and spectrograms of chaotic (left) versus more harmonic (right) departure call elements. Both calls are from the same individual, Bernard. The spectrograms depict a frequency range of 0 to 10 kHz and were created with window length of 512 samples after filtering out the 0–100 Hz range. Note the different time (x) axis scales.

10. Supplementary Material

<u>Exploratory investigation of subgroup departures</u>

Exploratorily and additionally to the thesis topic, I investigated subgroup departure orders and group sizes based on anecdotal observations. In the following, I present a short summary of the methods and results.

Methods

1. Data collection

I recorded all goose identities and subgroup sizes I could observe in 27 departure events from and to the Cumberland Gamepark during the day between November 11, 2023, and November 29, 2023. The first measurement I noted was reverse rank of subgroup departure for that individual: a score of 1 meant the individual was part of the last observed subgroup to leave during that departure event, while higher values indicated earlier departures (mean maximum reverse rank ± SD: 11.85 ± 5.59). This approach was chosen since I did not always observe the start of the departures, but always observed the end. In some cases, several older geese (e.g., Julian or Joshua) showed no imminent signs of departure after the rest of the flock had left, and these were assigned a reverse rank of 0. The second measurement I noted was the size of the subgroup in which each individual departed, including the individual itself. The aim was to investigate whether there is repeatability in subgroup departure order or group size, and to explore factors that could be related to that.

2. Sample size

For reversed ranks, I observed 84 different geese at least once for a total of 471 observations, and for group size 84 geese for 462 observations. Mean group size of observed groups was 5.6, median 3. Groups of up to 7 geese were observed often, but above that there was a steep drop (Fig. S1).

3. Analysis

For both reverse ranks and group size, I calculated linear mixed effect models with stepwise backward elimination from a full additive model at the start with predictors pairing status, sex, age (in years), and location (KLF/Gamepark), with 'GooseID' included as a random factor. Then, with only significant predictors remaining, I calculated repeatability in this model using the function *rpt* from the package 'rptR' with an assumed Gaussian data distribution and 1000 bootstraps (Stoffel & Schielzeth, 2017).

For the second part, I excluded individuals with only one observation and then calculated the mean reverse rank and group size per individual as basis for correlations/regressions with personality ranks (influencer, follower, boldness, exploration), as well as sex, age, and partner status, and then I used stepwise backward elimination from a full additive model to see which predictors explain reverse rank and group size best while including personality ranks.

Results

1. Repeatability in subgroup departure order

'ReversedRank' data were square-root-transformed to ensure better model fit, according to a Q–Q plot. After eliminating non-significant factors, only location (location:KLF $t = 4.57$, $p < 0.001$) and age ($t = -4.65$, $p < 0.001$) remained as predictors of reverse rank. The location effect indicates that reverse ranks were slightly higher at the KLF. The age effect indicates that older geese departed in later subgroups. There was significant repeatability in subgroup departure order using reversed ranks while controlling for location and age: R = 0.27, 95% confidence interval [0.16; 0.37], $p < 0.001$.

'GroupSize' data were log-transformed for better model fit, according to a Q–Q plot. For group size, location was significant (location:KLF: t = -2.09, p = 0.038), indicating that average observed subgroup sizes were smaller at the KLF (explaining the higher reverse ranks above); age was significant (t = -2.83, p = 0.006), indicating that older geese subgroup sizes are smaller, maybe due to young ones often joining other pairs; and partnered geese departed in larger subgroups (t = 3.14, p = 0.002). This latter result is intuitive, given that partnered birds typically fly with their partner at a minimum. There was significant repeatability in subgroup departure size while controlling for location, age, and partner status: R = 0.17, 95% confidence interval [0.08, 0.27], p < 0.001

2. Associations with personality, age, and partner status

As a note, in the average reverse departure rank I could not control for location. This may confound results a bit, since geese may have systematically different preferences regarding departures from/to a given location.

For reverse rank analysis, I used mean reverse ranks. Starting from a full additive model (age + partnerStatus + InfluencerRank + BoldnessRank + ExplorationRank + FollowerRank) with stepwise backward elimination of least significant predictors, only age remained (t = -3.75, p < 0.001, Pearson r = -0.40, Fig. S2). 'FollowerRank' approached significance before being excluded with p = 0.051 in the direction of followers departing in later subgroups. When looking at the associations in isolation without controlling for confounding variables, influencers flew in later subgroups (t = 2.75, p = 0.007, Pearson r = 0.33), as well as more explorative individuals (t = 2.53, p = 0.014, Pearson r = 0.31), while the same tendency for boldness was slightly not significant. There was no effect of partner status.

Finally, older geese flew later (t = -3.65, p < 0.001, Pearson r = -0.40), and, as mentioned, when controlling for age, personality ranks lost their significance as predictors of reverse rank.

For group size analysis, I used mean group sizes per individual. Starting from a full additive model (age + partnerStatus + partnerStatus + InfluencerRank + BoldnessRank + ExplorationRank + FollowerRank) with stepwise backward elimination of least significant predictors, only age remained as a significant predictor (t = -2.16, p = 0.035, Pearson r = -0.24, Fig. S3), indicating again in this averaged data that younger geese flew in bigger groups while no personality measure was related to group size.

When looking at associations in isolation, in contrast to reverse ranks, only age was correlated to group size, while influencer and follower rank were not. This highlights one limitation of my dataset, namely that it does not contain information beyond size and relative order of subgroups and the individuals making them up. Less influential geese like unpartnered singles often join pairs, for example, and would then get assigned the same group size value for this event. In other words, influencers and followers for a given subgroup departure always were assigned the same group size.

I did not test interactions for both reverse ranks and group size. I did not explicitly investigate how often partners fly with each other. Any such observations would likely overestimate rates of shared departure – that is, once an observer identifies a partnered goose, its partner would be easier to locate if it flies together with its partner rather than separately. Nonetheless, based on anecdotal observations, it seems highly probable that partners almost always depart together, although I observed at least two cases where members of a breeding pair departed in separate subgroups.

Dataset	Sample size	Number individuals	Correct classification	Random classification	X^2-test
Departure calls	562	10	40.12%	10%	$X^2 = 16.71$ $p < 0.001$

Table S1: Summary of results of identity classification using several acoustic parameters of calls in discriminant function analysis when splitting by tracks. While classification accuracy is lower than when splitting all calls randomly, it is still significantly above chance.

PC	Phase	Value	Standard error	DF	t-value	p-value
PC1 Response	baseline	0.248	0.280	39	0.885	0.382
PC2 Response	baseline	0.349	0.206	39	1.695	0.098
PC3 Response	baseline	-0.027	0.289	39	-0.094	0.926
PC4 Response	baseline	-0.278	0.265	39	-1.047	0.301
PC1 Response	treatment	1.397	0.369	39	3.788	**<0.001**
PC2 Response	treatment	-0.430	0.375	39	-1.147	0.258
PC3 Response	treatment	-0.175	0.266	39	-0.659	0.514
PC4 Response	treatment	-0.074	0.287	39	-0.260	0.797

Table S2: Outputs of the linear mixed models used to test differences in baseline and treatment phases between partner and non-partner responses. In these models, principal components with eigenvalues > 1 were the response variables. Significant differences ($\alpha < 0.05$) are **bold**.
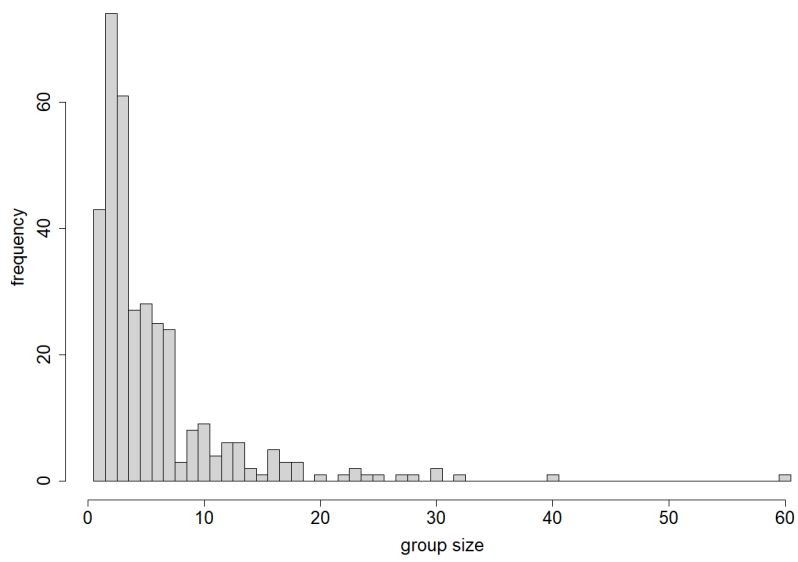
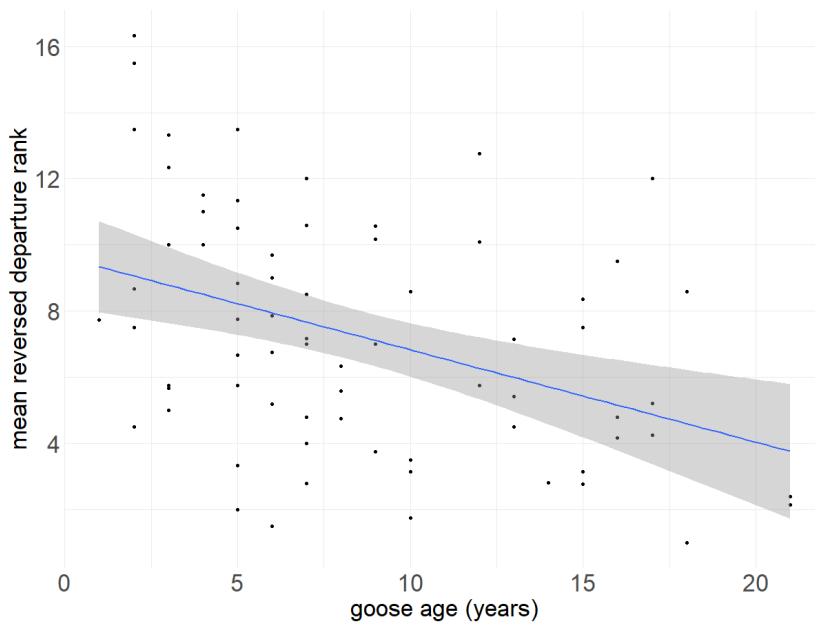Figure S1: Frequency of observed group sizes in subgroup departure events.

Figure S2: The linear relation of goose age (years) and mean reversed departure rank. A lower mean reversed rank indicates departing in a later subgroup. Younger geese departed in earlier subgroups and vice versa.
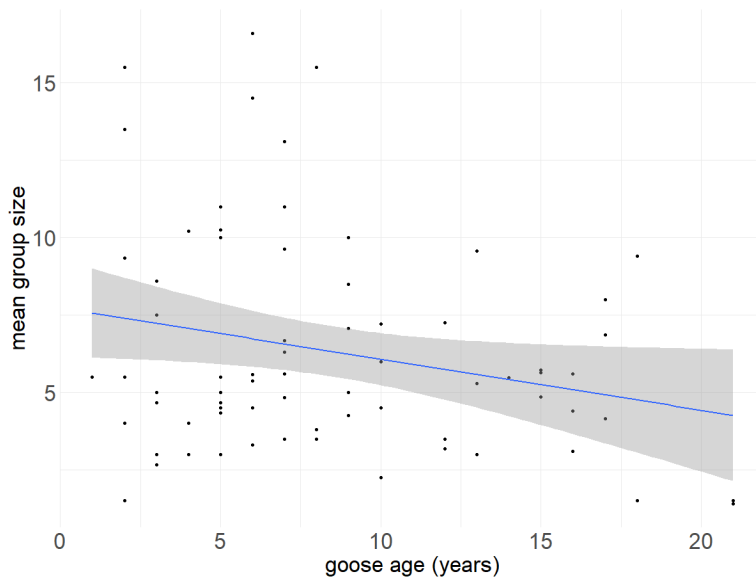
Figure S3: The linear relation of goose age (years) and mean group size. Younger geese flew in larger subgroups and vice versa.