Vocal recognition of distance calls in a group-living basal bird: the greylag goose, Anser anser

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Vocal communication in group-living animals represents a major challenge when multiple individuals call simultaneously and generate a complex soundscape. Decoding relevant information from a vocal signal and its emitter can determine the survival of the receiver. In hierarchical social groups, information on sex, size and age can provide relevant context for vocal signals. Ultimately, individual vocal recognition is a keystone in vocal communication systems, especially in the context of sociality. Greylag geese (Aves: Anseriformes) are a basal, gregarious and highly social species, and adults produce a distance call when approaching or leaving the flock. In this study we (1) quantified the acoustic properties of distance calls to test whether they can provide information on the sex, size and age of the emitter, (2) evaluated whether distance calls have individual properties, from the sender’s perspective, (3) tested whether receivers discriminate distance calls depending on the emitter’s identity and (4) explored whether an individual’s response strength towards its partner’s distance call is associated with fitness-related traits (i.e. pair bond duration and average number of offspring per year). We recorded distance calls of individually marked geese, quantified the variation in call acoustic properties and carried out a playback experiment in the wild. Distance calls encoded information about the sex of the goose, but not its age or size. From the emitter’s perspective, we found some support for individuality in distance calls. From the receiver’s perspective, geese were capable of recognizing distance calls from different individuals. Finally, the response strength towards playback of the partner’s call was positively correlated with pair bond duration. Vocal recognition has been proposed to be tightly related to social structure, the evolution of sociality and vocal learning. Here, we uncovered vocal recognition of individual affiliative calls in a social bird from the most basal avian group studied so far.

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crowded social contexts (Carlson et al., 2020; Cure et al., 2011; Elie & Theunissen, 2018; Pollard & Blumstein, 2011; Robertson, 1996; Vignal et al., 2008). Individual recognition holds a key role for understanding the foundations of social structures, social transmission and social interactions such as cooperation (Gokcekus et al., 2021). Because effective pair-specific communication is expected to generate a fitness benefit (Griffith, 2019; Hall, 2009; MacLennan & Burghardt, 1993; Sánchez-Macouzet et al., 2014), the problem of vocal recognition is central in the evolution of vocal communication processes within social species.

Vocal recognition has been studied across diverse vertebrates from mammals to birds (reviewed in Carlson et al., 2020; Frommolt et al., 2003; Insley et al., 2003; Tibbetts & Dale, 2007). Within birds, an ecologically diverse group with diverse communication systems, vocal recognition has been addressed in multiple groups (e.g. Berg et al., 2011; D’Amelio, Klumb et al., 2017; D’Amelio, Trost et al., 2017). Much research attention has been focused on the role of song for social recognition and this has been studied in the context of territoriality, mainly in songbirds (e.g. Brindley, 1991; Godard & Wiley, 1995). However, the most ancient vocalizations that are common and widespread among most, if not all, bird species are innate calls (Kondo & Watanabe, 2005; Marler & Slabekoorn, 2004). Often, individual produces multiple calls that differ in function (Adreani et al., 2020; Clay et al., 2012; D’Amelio, Klumb et al., 2017; Marler, 2004; Marler & Slabekoorn, 2004; Seddon et al., 2002). A common call category is ‘affiliative calls’, which mediate social interactions between partners, kin or group members (e.g. Baker, 2000; Berg et al., 2011, 2012; Boucaud et al., 2017; D’Amelio, Trost et al., 2017; Elie et al., 2010; Kondo & Watanabe, 2009; Sharp et al., 2005; Szipl et al., 2015; Ter Maat et al., 2014). In the past decade there has been increased study of these calls, especially in the context of sociosexuality (e.g. Adreani et al., 2020; Gill et al., 2015; Kondo & Watanabe, 2009; Marler & Slabekoorn, 2004; Sewall et al., 2016). Evidence for individual vocal recognition of affiliative calls is scarce (Kondo & Watanabe, 2009). Cooperatively breeding long-tailed tits, Aegithalos caudatus, can recognize contact calls from kin and nonkin (Hatchwell et al., 2001; Sharp et al., 2005) whereas zebra finches, Taeniopygia guttata, can differentiate almost every affiliative call at the individual level (D’Amelio, Klumb et al., 2017; Elie & Theunissen, 2018; Vignal et al., 2004, 2008). Emperor penguins, Aptenodytes forsteri, birds that breed in large numbers, are also capable of recognizing affiliative calls individually (Aubin et al., 2000). Given that individual vocal recognition has been hypothesized to be relevant for the origin of vocal learning (Nowicki & Searcy, 2014 and see Nottebohm, 1972) and considered important for the evolution of sociality (Gokcekus et al., 2021), investigating vocal recognition of affiliative calls in basil bird species with socially complex life histories is especially necessary.

Greylag geese are basal birds that belong to the Galloanserae (Prum et al., 2015). They form long-lasting, socially monogamous pair bonds (Hemetsberger, 2001; Hirschenhauser et al., 2013) and live in large flocks that often exceed 100 or even 1000 individuals (McKay et al., 2006). Further, individual geese in a flock seem to have different social status depending on their sex and pairing status (Black et al., 1989; Kotschal et al., 1993; Lorenz, 1988). Male greylag geese are normally larger than females but there is no prominent difference in feather coloration between the sexes (Volodin et al., 2015). Further, it is very likely that male and female greylag geese differ in their syrinx morphology as has been described in several closely related species (Würdinger, 1976). Greylag geese communicate with unique species using several ‘affiliative call’ types such as ‘greeting calls’, ‘contact calls’ or ‘distance calls’ (Lorenz, 1988; Fischer, 1964). As in other species, connectivity over long distance and with no visual cue from the receiver can be achieved by emitting ‘distance calls’, which are often repeated loud contact calls (Elie & Theunissen, 2018; Lorenz, 1988; Marler & Slabekoorn, 2004; Vignal et al., 2008; Yoneda & Okano, 1991).

In this study we recorded distance calls and conducted field playback experiments on wild greylag geese. The aims of this study were to investigate the potential of distance calls to encode information on the sex, age and size of the senders, as well as to assess the individuality of distance calls from their acoustic properties (i.e. aspects of the sender) and from the response in the receiver, based on Tibbetts and colleagues’ definition of individual vocal recognition (Tibbetts & Dale, 2007; Tibbetts et al., 2008). Accordingly, for true individual recognition to take place, the sender’s signal, the receiver’s template matching and the receiver’s behavioural response must be individual specific (Tibbetts & Dale, 2007; Tibbetts et al., 2008). We combined a descriptive approach with a playback experiment in a wild population of geese to test three main hypotheses: (1) whether the acoustic properties of distance calls vary with sex, age and size of the sender, (2) whether distance calls have individually distinct acoustic properties and (3) whether greylag geese respond differently to distance calls from different flock mates. Finally, the availability of a long-term data set with information on multiple fitness-related traits of the focal geese in our experiments allowed us to address an additional exploratory question: does the response strength of a bird towards its partner’s distance call during our playback experiment relate to fitness-related traits? We considered two proxies for fitness, namely the average number of offspring per year for the focal bird and the focal bird’s pair bond duration, which in geese is a reliable fitness-related trait (Sánchez-Macouzet et al., 2014).

METHODS

Study Site

This study was carried out on 45 individuals from a free-ranging and nommigratory flock of 114 greylag geese at the Konrad Lorenz Research Centre (KLF) for Behavior and Cognition in Grünau im Almtal, Upper Austria (47°48′50.5″N 13°56′51.0″E) during September and October 2020. Geese are individually colour banded and their life histories have been monitored since 1973 (Hemetsberger, 2001). Therefore, information such as birth year, sex, pairing status and length of the relationship are known for every individual (Hemetsberger, 2001). The geese are habituated to human observers and have been supplemental fed with barley and grass pellets twice per day in outdoor feeding troughs since 1973 (Hemetsberger, 2001). Information about the tarsus length (a proxy for body size) was obtained from the long-term data set of the greylag goose monitoring project (Hemetsberger, 2001). Briefly, tarsus length was measured at the time of independence (age 5–6 months) in all juvenile geese. While juvenile birds have not reached adult size, their tarsus length was correlated with adult tarsus length (Pearson correlation: r = 0.99, P < 0.001; Frigerio et al., n.d.).

Distance Call Recordings

In total we recorded 524 distance calls from 36 greylag geese across 4 weeks before the playback experiment. To quantify the distance call’s acoustic properties, we used a subset of 29 geese for which we had more than four distance calls per goose, 501 distance calls in total (mean ± SD = 17.3 ± 13.4 calls per goose). All recordings were made with a Sennheiser MKE 600 directional microphone and a sampling rate of 44100 Hz. Calls were recorded at 5 m from the goose with an opportunistic sampling method. A distance call was defined as a repeated loud call lasting more than 300 ms, normally occurring after group movement of the flock, and after partners have been separated (Fischer, 1964; Lorenz, 1988; see Fig. 1).
Experimental Design

We conducted playback experiments on 23 adult (±1.5 years old) focal geese. Each focal goose was exposed to four types of playback tracks with: (1) partner’s distance calls, (2) nonpartner distance calls, (3) a reverse partner’s call playback (each call was reversed retaining the same call order of the nonreversed track) and (4) a white noise playback (white noise stimulus every 10 s of the playback track), a total of 92 playbacks (Fig. 2a). Nonpartner playback tracks had multiple different calls from a single individual, ordered randomly within the track. Nonpartner geese were assigned randomly to the focal geese. We designed the playback tracks with the software Audacity (Audacity Team, 2020). Each playback track consisted of (1) 1 min of pretrial silence, (2) 1 min with a distance call broadcast every 10 s (six calls), (3) 1 min of silence, (4) 3 min of a distance call every 10 s (six calls; Fig. 2b). This resulted in playback tracks lasting 3 min (Fig. 2b). To avoid pseudoreplication, we used 7.9 ± 4.2 (mean ± SD) different distance calls per playback track (in six cases we had only one distance call of sufficient quality). Each call of the playback was normalized (value of −1) to ensure the same amplitudes in the playback track and later adjusted with the speaker to the loudness of geese calling in the flock (measured 5 m away). The reverse partner call playback was included to test whether the geese can recognize the distance calls based on the acoustic properties only or whether they integrate information on the temporal sequence of the acoustic properties (partner calls and reversed partner calls have the same acoustic properties, differing only in the temporal arrangement of the call properties).

Figure 1. Spectrograms of three female and three male greylag goose distance calls showing individual variation in call characteristics.

Figure 2. (a) Experimental design showing the exposure of the focal goose to playback tracks of different social categories ('partner distance call', 'nonpartner distance call', 'reverse partner distance call' or 'white noise'). (b) Example of a playback track with arbitrary amplitude units. The playback consisted of 12 calls of one category, played every 10 s, with 1 min of silence after six calls. (c) Playback blocks: order in which playback categories were broadcast for all 23 geese.
We conducted playbacks on 13 nonconsecutive days. The test subjects were 13 males and 10 females exposed to four playback categories. Each focal goose was exposed to one of the four different playback categories (‘nonpartner call’, ‘partner call’, ‘reverse call’ of the partner call and ‘white noise’) on one of 4 trial days per goose. The order with which focal geese were exposed to the different playback categories was quasirandomized and referred to as playback blocks. Specifically, five to six geese were randomly assigned to be tested with one specific playback category (e.g. ‘reverse call’ playback, first block), while each of the other three groups (blocks) of five to six individuals were first tested with one of the other playback categories (‘partner call’, ‘nonpartner call’ or ‘white noise’; Fig. 1c). A quasirandomized model simplified the exposure of the flock to different call categories on a trial day. Three to four geese were tested in the morning (0800–1000) and three to four individuals in the afternoon (1600–1800). The speaker was placed 5 m away from the focal goose while it was resting, to minimize both movement of the goose before the trial period and observer bias. After each trial, it took approximately 10–15 min to identify the next focal goose and to wait and be sure that it was in a resting position. One to two observers recorded the response of the focal goose by noting the behaviour on a response sheet and by filming for later confirmation. During the preplayback (1 min) and trial periods (3 min) the following response variables of the focal subject were noted: (1) number of vigilance postures (attention) defined as adopting/holding a vigilant body posture with horizontal beak position and a stretched neck (John & Inglis, 1978), (2) number of times gazing at the speaker (attention), defined as number of times a goose directs one eye towards the speaker, and (3) number of distance calls (call reply). As additional information, the distance between the focal bird and its partner was quantified before the trial began.

Acoustic and Principal Component Analyses

To quantify acoustic variation in the greylag goose distance calls, we extracted 17 acoustic features per call and the call’s duration using the R package ‘seewave’ (Sueur et al., 2008). Given that most of
the acoustic variables were correlated (Fig. A1), we decided to conduct a principal component analysis (PCA) using the function 'prcomp' from the package 'stats' (R Core Team, 2019). This is a common procedure in bioacoustics studies (e.g. D’Amelio, Klumb et al., 2017; D’Amelio, Trost et al., 2017; Vignal et al., 2004). Distance call duration was analysed independently as we restricted the common procedure in bioacoustics studies (e.g. D’Amelio, Klumb et al., 2017; D’Amelio, Trost et al., 2017; Vignal et al., 2004). Distance call duration was analysed independently as we restricted the common procedure in bioacoustics studies (e.g. D’Amelio, Klumb et al., 2017; D’Amelio, Trost et al., 2017; Vignal et al., 2004). Distance call duration was analysed independently as we restricted the

Statistical Analyses

All our analyses were performed in R (v. 3.6.1; R Core Team, 2019). Most of the statistical interpretations were carried out under a pseudo-Bayesian framework with noninformative priors (Korner-Nievergelt et al., 2015; the correlations with fitness-related traits were interpreted under a frequentist view). We used the packages 'arm' (Gelman & Su, 2020) and 'lme4' (Bates et al., 2014) and assumed a Gaussian error distribution for every model and the fit was assessed via visual inspection of the residuals’ distribution. For each model we carried out 10 000 simulations to obtain the posterior distribution of every estimate, the mean value and the 95% credible interval (CrI). Briefly, posterior distributions comprise the range of plausible parameter (and estimate) values given the data and the model. This approach allows one to obtain posterior probabilities for specific hypotheses rather than testing null hypotheses, as in a frequentist approach. For example, one hypothesis could be that hypothetical group 'A' is larger than hypothetical group 'B'. Here, one can determine the posterior probability of this difference (termed ‘p_{diff}’ between A and B as the percentage of times (out of 10 000) that the estimate for A was larger than the estimate for B. We defined a difference between groups to be statistically meaningful when 'p_{diff}' was higher than 95% and an effect to be statistically meaningful when the 95% CrI of the parameter’s posterior distribution did not overlap with zero. A threshold of 5% is equivalent to the significance level in a frequentist framework (i.e. P value of 0.05); for details on this approach and statistical inference, see Korner-Nievergelt et al. (2015).
Properties of greylag goose distance calls

To quantify the degree to which greylag goose distance calls are individually acoustically distinct, we tested three statistical models using each principal component (PC1 and PC2) as the dependent variable. Model 1 was a linear mixed-effect model with sex, age and their interaction as explanatory variables. Given that we had multiple vocalizations from each individual goose, Goose ID was set as random factor. Model 2 was a linear mixed-effect model with sex, tarsus length and their interaction as explanatory variables and Goose ID as random factor. Model 3 was a simple linear model with one explanatory variable: Goose ID. For details on each of these models see Tables A2, A3 and A4. For modelling the call’s duration, the explanatory variables were sex, age and size, with Goose ID as random factor. In all our models, dependent variables were transformed into z-scores using the function `scale()` from the ‘base’ R package (v. 3.6.1; R Core Team, 2019).

Greylag goose response to distance calls of different social relevance

To assess whether greylag geese were capable of discriminating distance calls from individuals of different social relevance, we used one statistical model for each of the behaviours that were quantified during the playback experiment. For ‘call response probability’, given the binary nature, we fitted a generalized linear mixed-effect model with a binomial distribution with ‘Treatment’ (nonpartner, partner, reversed call) as an explanatory variable and two random effects: (1) Goose ID, to account for within-individual variation during the trials and (2) Playback block, to account for any possible effect of the playback order. Here, we excluded the white noise control from the treatment groups because none of the geese called during this trial and its inclusion did not allow for an optimal model fit. For ‘Number of vigilance events’ and ‘Number of gazes towards the speaker’ we fitted a generalized linear mixed-effect model with a Poisson distribution, given that our dependent variables consisted of count data. As in the previous model, Treatment was the explanatory variable (including the white noise stimuli), and Goose ID and Playback block were random factors.

Response strength towards the partner’s calls in relation to fitness-related traits

To explore the idea that vocal response could be associated with fitness-related traits, we carried out Spearman correlations between the response strength (number of distance calls, number of vigilance events, number of gazes towards the speaker) per focal goose towards the partner’s playback call with two fitness-related traits: pair bond duration and average number of offspring per year. Bonferroni correction increases the probability of type 2 error, and whether its application is helpful remains under discussion (Nakagawa, 2004). For this reason, we report both the original P values and Bonferroni-adjusted P values.

Ethical Note

This study complies with all current Austrian laws and regulations concerning work with wildlife. Observing the animals and checking their nests were performed under Animal Experiment Licence Number 66.006/0026-WFV/3b/2014 by the Austrian Federal Ministry for Science and Research (EU Standard, equivalent to the Animal Ethics Board). Data on tarsus length used in this study were obtained from banding during previous years as part of the long-term monitoring of the greylag goose population. We confirm that the owner of the land, the Duke of Cumberland, gave permission to conduct the study on this site. All data collected in 2020 for this study were obtained using noninvasive methods. Birds were habituated to the presence of humans. We adhered to the ASAB/ABS Guidelines for the use of animals in research.

RESULTS

Acoustic Variation in Distance Calls

We found differences by sex in distance call acoustic properties (i.e. PC1 accounting for 54% of the variance in our data; Fig. 3a, Table A2; mean PC1 score ±SE: female = −1.15 ± 0.51; male = 1.64 ± 0.50). Based on PC1 loadings (Table A1), compared with males, females had lower mean frequency (female = 2518 ± 120 Hz; male = 3081 ± 120), fundamental frequency (female = 1036 ± 20 Hz; male = 1267 ± 50 Hz) and spectral entropy (female = 0.67 ± 0.01; male = 0.73 ± 0.01). We found no relationship between acoustic properties of the call and age (Fig. 3a, Table A2). Within each sex, acoustic properties did not vary with body size (Fig. 3b, Table A3). In addition, there was some degree of individual variation in acoustic properties in PC1 (Fig. 3c, Table A4).

For PC2, which accounted for 13% of the variance in our data, we did not find an effect of age, sex or body size (Tables A2 and A3), and PC2 was qualitatively less variable among individuals than PC1 (Fig. A3, Table A4). Finally, distance call duration did not vary with age, sex or size (Table A5).

Greylag Goose Response to Distance Calls of Different Social Relevance

During the playbacks, the distance between the focal goose and its partner did not differ between treatments (Table A6). Greylag geese were more likely to respond to their partner’s calls (Fig. 4a) than to nonpartner calls (p_{diff} = 99.98%) or reversed partner calls (p_{diff} = 99.87%). For details on the model estimates see Table A7.

Greylag goose adopted more vigilant postures during the playback of the partner’s calls than to calls from the nonpartner (p_{diff} > 99.99%), the reversed call (p_{diff} = 99.73%) and the white noise (p_{diff} = 99.93%; Fig. 4b). Further, greylag goose adopted less vigilant postures during the nonpartner calls than to calls from their partner (p_{diff} > 99.99%), the reversed call (p_{diff} > 99.99%) or the white noise (p_{diff} = 99.98%; Fig. 4b). There were marginally more vigilant postures during the reversed partner calls than during white noise (p_{diff} = 94.00%) but fewer than during the partner’s calls (p_{diff} = 95.91%) and more than during the nonpartner calls (p_{diff} = 99%; Fig. 4b). For details on the model estimates see Table A7. The number of gazes towards the speaker during the playbacks of the partner’s calls was similar to that towards the reversed partner calls (p_{diff} = 76.5%) and white noise (p_{diff} = 57.59%; Fig. 4c). Finally, there were fewer gazes towards the speaker during the broadcast of nonpartner calls than towards the partner’s call (p_{diff} = 99.97%), the reversed call (p_{diff} = 99.99%) or the white noise (p_{diff} = 99.96%; Fig. 4c) For details on the model estimates see Table A7.

Response Strength Towards the Partner’s Calls in Relation to Fitness-related Traits

The mean number of offspring per year was positively correlated with the pair bond duration (Spearman correlation: r_{S} = 0.42, P = 0.04). The number of distance calls given in response to experimental broadcast of the partner’s distance calls was not correlated with the average number of offspring per year per pair (Fig. 5a; Spearman correlation: r_{S} = 0.35, P = 0.06, adjusted P = 0.18), but was positively correlated with the duration of the pair bond (Fig. 5b; Spearman correlation: r_{S} = 52, P = 0.01, adjusted P = 0.03). Vigilance events and gazes towards the speaker were not correlated with the average number of offspring per year per pair or the duration of the pair bond (Fig. A4).
DISCUSSION

In this study, we investigated the distance call of greylag geese in the wild. First, we analysed the acoustic properties of distance calls to assess whether they can provide social information on sex, age and size of the sender. Second, we quantified individual acoustic variation in distance calls to assess whether calls can transmit individual identity information. Third, we carried out a playback experiment to assess recognition response in greylag geese towards distance calls from different individuals. Finally, we compared the strength of a paired bird’s response towards broadcast of their partner’s calls with fitness-related traits. We showed that distance calls in greylag geese can encode information about the sex of the sender and individual information, and that individual geese had differentiated responses to broadcast of distance calls depending on the sender. Finally, the magnitude of response to the partner’s calls was positively correlated with pair bond duration.

Acoustic properties of greylag geese distance calls differed between the sexes but variance in acoustic properties was not explained by the age or size of the calling bird. Sex differences in acoustic parameters of calls seem to be widespread in birds (Vicario et al., 2001; Volodin et al., 2009, 2015). For example, in vermilion flycatchers, Pyrocephalus rubinus, females show a higher level of entropy in ‘peent’ calls than males (Rios-Chelén et al., 2020), and in little spotted kiwis, Apteryx owenii, males call not only more tonally, but also at higher frequencies than females (Digby et al., 2013). In most cases, this difference can be explained by differences in size, where it is expected that larger individuals produce lower frequency sounds than smaller individuals (Medina-García et al., 2015; Morton, 1977; Pfefferle & Fischer, 2006). In greylag geese, males are larger than females and yet produce higher frequency sounds; we found no effect of size on acoustic parameters of distance calls within each sex. Thus, the differences between male and female call structure may have their origin in sexually dimorphic membrane and sac structures of the syrinx, which has been measured for three other closely related species, namely greater white-fronted goose, Anser albiﬁrons, pink-footed goose, A. brachyrhynchos, and taiga bean goose, A. fabalis (Würdinger, 1970). In the study of Würdinger (1970), female geese called with lower fundamental frequencies than males, similar to greylag geese. Sex differences in call characteristics could be shaped by sexual and/or natural selection given that female and male greylag geese behave differently during courting, breeding and rearing of goslings, which may therefore expose each sex to different selection pressures (Lande, 1980; Lorenz, 1988).

Vocal recognition can occur at different levels from general categorical recognition (e.g. social recognition, kin recognition and unfamiliar) to individual recognition (reviewed in Carlson et al., 2020; Tibbetts & Dale, 2017). Understanding how vocal recognition and social organization interact will generate insights into feedback mechanisms and evolutionary drivers of sociality with a dual focus on individual behaviour and social associations (Gokcecus et al., 2021). Tibbetts et al. (2008) have suggested that for ‘true’ individual recognition to take place, the sender’s signal, the receiver’s template-matching and the receiver’s behavioural response must be individual specific. From the sender’s perspective, we found some evidence for signal individuality in the acoustic properties measured in greylag goose distance calls. While present, the acoustic differences were modest between individuals although visual inspection of spectrograms hints at more pronounced individual variability in distance calls (Fig. 1). It is possible that our acoustic measurements did not capture the complexity of the calls as seen in the spectrograms. However, there might also be other aspects of distance calls that provide additional ‘individual’ features that we did not account for. For example, zebra finches can recognize certain call types individually, despite the calls being almost indistinguishable from their measurable acoustic properties (Elie & Theunissen, 2018). Something similar could be occurring in geese but needs to be explored in more detail. Additionally, individuality could result from an underlying syntactic structure in greylag goose distance calls, which has been shown in birds (Suzuki et al., 2019). The potential for individuality in greylag goose calls from the sender’s perspective certainly merits further investigation. From the receiver’s perspective, during the playback experiment, goose calling increased towards their partner’s calls and, notably, calls, vigilance events and gazes to the speaker decreased during nonpartner calls. It is possible that these results only reflect a form of categorical or social recognition. It is also possible that ‘true’ individual vocal recognition could be occurring if reversed calls were perceived as calls from unknown specifics (they have the exact same acoustic properties of a greylag goose distance call). This idea is supported by our findings because some geese responded with calls and vigilance events to the reverse call, more strongly than their response to white noise and nonpartner calls (and weaker than their response to partner calls). The flock of greylag geese observed in this study has about 130 individuals and has had roughly the same adult group composition for at least 5 years. Therefore, the familiarity factor should not play a central role in determining how the geese responded to the playbacks as all geese should be equally familiar with flock members. Clearly, follow-up experiments are necessary to test more robustly whether ‘true’ individual recognition is occurring. Vocal responses almost disappeared (only three of 23 birds vocalized) when the geese heard the reverse of their partner’s call. In the field of neuroscience this test is commonly used to unequivocally determine whether auditory or vocal-production neurons are specific towards the stimuli’s temporal sequences and as an indication of recognition (e.g. Amador et al., 2013; Dave & Margoliash, 2000; Prater et al., 2008). Our results suggest that goose vocal recognition is not based on the call’s acoustic properties per se, but rather on the temporal arrangement of these properties which may have individual signatures.

The fitness benefits of social recognition in geese have not been tested, but one can reasonably expect that recognition of alliance partners could be favoured by natural selection, for example during rapid group movement. Given the differentiated response to the broadcast of the partner’s distance calls and hence evidence that geese appear capable of distinguishing at least some flock members as shown in this study, we predict that greylag geese should be able to locate their partner acoustically in a flock, especially after or during group movements when partners get lost in or separated from the group. Given partner-specific response patterns, our study shows social recognition of innate affiliative calls in the most ancient avian species with a complex social structure studied so far. In Neovolles, call differentiation has been investigated experimentally, and several social species of this large group seem to be capable of differentiating between conspecifics of different social relevance via acoustic signalling: zebra finches, Magellanic penguins, Spheniscus magellanicus, green-rumped parrotlets, Forpus passerinus, jungle crows, Corvus macrorhynchos, superb fairy-wrens, Malurus cyaneus, European starlings, Sturnus vulgaris, chestnut-crowned babblers, Pomatostomus ruficeps, etc. (Berg et al., 2011; Chalik, 1992; Clark et al., 2006; Colombelli-Negrel & Evans, 2017; Crane et al., 2015; Elie &
Theunissen, 2018; Kondo et al., 2010). All these examples, together with our results, underscore the need for broader taxonomic research across basal and recent lineages to disentangle more fully the evolutionary history of vocal recognition across birds (and other vertebrates) and its relationship with sociality.

Greylag geese responded more intensively towards their partner’s playback the longer the pair had been bonded. There was a positive, but not statistically significant, correlation between average number of offspring produced and call responsiveness. Given the exploratory nature of these analyses, we are aware that these results could be spurious, but feel they are worth presenting, not least given the rarity of data relating vocal behaviour to fitness-related traits. There could be selection on cooperation and vocal coordination between pairs that might improve the quantity and/or quality of offspring. Only a few acoustic studies have included relationship duration proxies because the life history of the individual study animals must be known (Clark et al., 2006). The finding that geese with longer pair bond duration responded more strongly to each other stands in contrast to a study in Magellanic penguins, where female response to the partner’s playback was weaker in pairs with longer pair bond duration (Clark et al., 2006).

Cooperation and coordination in socially monogamous birds and the value of good partnerships rather than sexual conflict over mate choice is gaining more research attention (Griffith, 2019). We cannot disentangle cause and effect in our observation, and it is possible that more responsive individuals remain together for longer in greylag geese. On the other hand, the correlation may arise from a mate familiarity effect, where familiarity with the mate improves social display quality over time (Black, 1996). In Japanese quails, Coturnix japonica, offspring survival improved with age due to higher maternal investment (Pittet et al., 2012). In greylag geese, acoustic connectivity might promote offspring survival. The age of an individual can also influence vocal or auditory systems and therefore trigger a stronger behavioural response in the receiver; for example, in zebra finches, middle-aged individuals have a louder song, which was proposed to occur due to increased sub-syringeal air sac pressure (Badwal et al., 2020). Our data do not support this mechanism in the greylag goose system as we found no significant effect of age on distance call characteristics. In general, future research could test whether senescence or cooperation influence vocal response patterns within pair bonds.

Author Contributions

S.K., N.A. and M.G. designed the research; M.G. collected the data; N.A. and M.G. conducted the statistical analysis; N.A. and M.G. wrote the manuscript, and all authors discussed the results, provided critical analysis and feedback and commented on the manuscript. N.A. and M.G. share first authorship.

Data Availability

Data reported in this paper are available in the Dryad Digital Repository at http://doi.org/10.5061/dryad.vdcj5sx4.

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Appendix

Table A1
Loading values of the different parameters to principal components (PC) 1 and 2

| Acoustic variable          | PC1 (54% variance explained) | PC2 (13% variance explained) |
|---------------------------|-----------------------------|-------------------------------|
| Mean fundamental frequency| 0.21                        | -0.32                         |
| SD fundamental frequency  | 0.09                        | -0.55                         |
| Starting fundamental frequency | 0.15                     | -0.33                         |
| Ending fundamental frequency | 0.05                      | -0.36                         |
| Mean peak frequency       | 0.26                        | 0.27                          |
| SD peak frequency         | 0.26                        | -0.09                         |
| Starting peak frequency   | 0.21                        | 0.18                          |
| Ending peak frequency     | 0.17                        | 0.34                          |
| Total entropy             | 0.29                        | -0.05                         |
| Mean frequency            | 0.31                        | 0.11                          |
| SD frequency              | 0.25                        | -0.10                         |
| Median frequency          | 0.31                        | 0.14                          |
| Modal frequency           | 0.19                        | 0.28                          |
| Skewness                  | -0.30                       | 0.03                          |
| Kurtosis                  | -0.29                       | 0.03                          |
| Spectral flatness         | 0.27                        | -0.06                         |
| Spectral entropy          | 0.31                        | -0.04                         |

Table A2
Effect of age and sex on principal components (PC) 1 and 2

| Fixed effects (β) (95% CrI) | PC1        | PC2        |
|-----------------------------|-----------|-----------|
| Intercept (Female)          | -1.81 (-3.06; -0.58) | 0.21 (-0.40; 0.81) |
| Age                         | -1.15 (-2.43; 0.13)  | -0.16 (-0.78; 0.47) |
| Sex (Male)                  | 3.38 (1.83; 4.96)    | -0.24 (-1.00; 0.53) |
| Sex*Age                     | 0.86 (-0.69; 2.42)   | 0.27 (-0.48; 1.02)  |
| Random factors (σ²) (95% CrI) | Goose ID | 3.27 (2.60; 4.26)   | 0.72 (0.52; 0.98)  |

CrI: credible interval. Statistically meaningful effect is marked in bold. Models 1: PC1=Age*Sex + (1 Goose ID); PC2=Age*Sex + (1 Goose ID).

Table A3
Effect of size (tarsus) and sex on principal components (PC) 1 and 2

| Fixed effects (β) (95% CrI) | PC1        | PC2        |
|-----------------------------|-----------|-----------|
| Intercept (Female)          | -0.84 (-2.66; 0.99) | -0.02 (-1.25; 1.21) |
| Tarsus                      | -0.51 (-2.33; 1.27) | -0.63 (-1.86; 0.58) |
| Sex (Male)                  | 3.04 (0.49; 5.53)   | 0.38 (-1.35; 2.07)  |
| Sex*Tarsus                  | 0.44 (-2.32; 3.20)  | 0.35 (-1.51; 2.21)  |
| Random factors (σ²) (95% CrI) | Goose ID | 2.50 (1.60; 3.86)   | 1.18 (0.81; 1.78)  |

CrI: credible interval. Statistically meaningful effect is marked in bold. Model 2: PC1=Tarsus*Sex + (1 Goose ID); PC2=Tarsus*Sex + (1 Goose ID).

Table A4
Individual variation of principal components (PC) 1 and 2

| Fixed effects (β) (95% CrI) | PC1        | PC2        |
|-----------------------------|-----------|-----------|
| Intercept (Goose 1)         | -4.13 (3.21; 5.06) | 3.49 (2.83; 4.17) |
| Goose 2                     | -4.55 (-6.30; -2.81) | -3.36 (-4.61; -2.11) |
| Goose 3                     | -3.46 (-5.02; -1.87) | -3.18 (-4.02; -2.31) |
| Goose 4                     | -6.36 (-7.72; -4.99) | -3.01 (-4.11; -1.89) |
| Goose 5                     | -6.06 (-7.23; -4.82) | -3.75 (-4.51; -3.02) |
| Goose 6                     | -4.68 (-5.91; -3.45) | -2.83 (-3.95; -1.75) |
| Goose 7                     | -6.04 (-7.23; -4.83) | -2.81 (-3.75; -1.85) |
| Goose 8                     | -7.31 (-8.35; -6.27) | -2.95 (-3.93; -1.98) |
| Goose 9                     | -5.54 (-6.80; -4.25) | -4.81 (-5.69; -3.93) |
| Goose 10                    | -5.50 (-7.21; -3.71) | -2.83 (-4.06; -1.58) |
| Goose 11                    | -5.46 (-6.77; -4.13) | -3.86 (-4.78; -2.96) |
| Goose 12                    | -5.22 (-6.59; -3.84) | -3.72 (-4.68; -2.74) |
| Goose 13                    | -5.58 (-7.11; -4.03) | -3.75 (-4.83; -2.68) |
| Goose 14                    | -8.21 (-9.82; -6.64) | -3.89 (-4.98; -2.82) |
| Goose 15                    | 0.39 (-0.86; 1.67)   | -2.02 (-3.33; -0.69) |
| Goose 16                    | -0.04 (1.90; 1.82)   | -3.96 (-4.90; 3.03)  |
| Goose 17                    | 0.37 (-0.76; 1.48)   | -2.80 (-3.62; -1.99) |
| Goose 18                    | -1.67 (2.83; -0.52)  | -4.30 (-5.12; -3.52) |
| Goose 19                    | -2.23 (-3.55; -0.89) | -2.57 (-3.46; -1.66) |
| Goose 20                    | -2.62 (-3.87; -1.36) | -3.62 (-4.55; -2.69) |
| Goose 21                    | -3.20 (-4.51; -1.90) | -3.70 (-4.97; -3.15) |
| Goose 22                    | -2.60 (-3.89; -1.29) | -3.44 (-4.40; -2.58) |
| Goose 23                    | -0.48 (-2.36; 1.33)  | -3.70 (-4.46; -2.95) |
| Goose 24                    | -4.27 (-5.86; -3.16) | -2.98 (-4.26; -1.68) |
| Goose 25                    | -2.39 (-4.27; -0.48) | -3.83 (-4.64; -3.03) |
| Goose 26                    | -5.35 (-6.57; -4.14) | -3.82 (-5.12; -2.51) |
| Goose 27                    | -3.27 (-4.73; -1.79) | -3.27 (-4.43; -2.10) |
| Goose 28                    | -4.40 (-6.03; -2.74) | -4.27 (-5.23; -3.33) |
| Goose 29                    | -5.51 (-6.56; -4.45) | -4.04 (-5.10; -2.99) |

CrI: credible interval. Model: PC1=Age*Sex + (1 Goose ID); PC2=Age*Sex + (1 Goose ID).

Table A5
Effect of sex, age and size on call duration

| Fixed effects (β) (95% CrI) | Distance call duration (ms) |
|-----------------------------|-----------------------------|
| Intercept (Female)          | 880 (-156; 1887)            |
| Sex (Male)                  | -56 (-225; 113)             |
| Age                         | 8 (-2; 18)                  |
| Size                        | -36 (-144; 76)              |
| Random factors (σ²) (95% CrI) | Goose ID | 10 236 (6185; 16476) |

CrI: credible interval. Model: Duration=Sex*Age*Size + (1 Goose ID).

Table A6
Effect of playback treatment on distance between the focal goose and its partner

| Fixed effects (β) (95% CrI) | Square root (Distance to partner) |
|-----------------------------|-----------------------------------|
| Intercept (Nonpartner call) | -2.16 (1.55; 2.76)                |
| Partner call                | -0.07 (-0.80; 0.63)               |
| Reverse call                | -0.52 (-1.21; 0.19)               |
| White noise                 | -0.31 (-1.00; 0.40)               |
| Random factors (σ²) (95% CrI) | Goose ID | 0.63 (0.37; 0.98) |

CrI: credible interval. Model: sqrt(DistanceToPartner)=Treatment + (1 Goose ID).
Table A7

|                | Vocal response probability | Vigilance events | Gazes to the speaker |
|----------------|---------------------------|------------------|----------------------|
| **Fixed effects (β) (95% CrI)** |                           |                  |                      |
| Intercept (Nonpartner call)       | -2.63 (-4.34; -0.97)      | -0.08 (-0.54; 0.37) | 0.27 (-0.11; 0.65)   |
| Partner call                      | 3.14 (1.37; 4.92)         | 1.43 (0.98; 1.87)  | 0.77 (0.35; 1.19)    |
| Reverse call                      | 0.47 (-1.48; 2.46)        | 1.17 (0.72; 1.63)  | 0.89 (0.47; 1.31)    |
| White noise                       |                           |                  |                      |
| **Random factors (σ²) (95% CrI)** |                           |                  |                      |
| Goose ID                          | 0.31 (0.16; 0.53)         | 0.26 (0.15; 0.44)  | 0.12 (0.07; 0.20)    |
| Playback block                    | 0.39 (0.04; 1.42)         | 0.00 (0.00; 0.00)  | 0.00 (0.00; 0.00)    |

CrI: credible interval. Values depicted as ‘0.00’ represent values smaller than 0.001. Statistically meaningful effects are marked in bold. Visualization of these models corresponds to Fig. 4a (vocal response probability), 4b (no. of igilance events) and 4c (no. of gazes to the speaker).

Figure A1. Graphic representation and correlation coefficient (Pearson r) of the correlation matrix among the 17 acoustic parameters measured in each distance call. Asterisks indicate statistically significant correlation: *P < 0.05; **P < 0.01; ***P < 0.001.
Figure A2. Contribution of the different acoustic properties that were measured to principal components (PC) 1 (accounting for 54% of the variance in our data) and 2 (accounting for 13% of the variance in our data).

Figure A3. Sources of variation in the acoustic properties of male and female greylag goose distance calls (PC2). (a) Age, (b) body size (tarsus length) and (c) individuals. Dashed and solid lines in (a) and (b) and black symbols in (c) present the model estimates; grey shading in (a) and (b) and vertical bars in (c) represent the 95% credible intervals. Coloured symbols represent the raw data. Age and tarsus length are both z scores. In (c) geese 1–14 are females and geese 15–29 are males.
Figure A4. Relationship between (a, c) gazes at the speaker and (b, d) number of vigilance events during the playback of partner calls and (a, b) average number of offspring per year and (c, d) pair bond duration in years. Coloured symbols represent the raw data (magenta/triangles – females; green/circles – males).