Behavioral Ecology and Sociobiology (2024) 78:37
https://doi.org/10.1007/s00265-024-03452-9

ORIGINAL ARTICLE

'Beware, I am large and dangerous' – human listeners can be deceived by dynamic manipulation of the indexical content of agonistic dog growls

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Received: 2 June 2023 / Revised: 9 February 2024 / Accepted: 21 February 2024 / Published online: 1 March 2024

Abstract

Dishonest vocal signals about body size are rarely encountered, however, dogs are capable of modifying indexical information in their growls. This apparent acoustic body-size manipulation could be affected by the level of threat experienced by the dog. We tested whether this natural size manipulation actually affects how listeners assess the size of the dog, thus whether it could be considered as a successful indexical information manipulation. We requested human participants to assess dog growls, originally recorded when dogs encountered various 'threatening strangers' (of different sex, stature). The participants heard several sets of growl pairs, where they had to guess, which growl belonged to the 'larger dog'. In the Control condition, dog growls originated from two different dogs in a pair; in the Test condition, growls of the same dog were presented pair by pair, always recorded in the presence of different threatening humans. Human listeners reliably picked the larger dog from two differently sized animals based on their growls alone. In the Test condition, participants thought that the dog was 'larger' when it was threatened by a female experimenter, and when the dog was growling at a larger sized human. We found that while growl length modulation was the main factor behind size-choice decisions in the case of female strangers, formant dispersion difference contributed the most when listeners chose which dog was the larger in the case of male opponents. Our results provide firsthand evidence of dogs' functionally deceptive vocalizations towards humans, a phenomenon which has not been shown before in any interspecific scenario.

Significance statement

Body size is an important decisive factor in agonistic contests, however dishonestly vocalizing about it is difficult because of the anatomical-physical constraints of voice production. In our research, human listeners had to guess which one was the 'bigger dog', based on pairs of growl playbacks, where both growls in a pair originated from the same dog, while the dog was seemingly threatened by various approaching experimenters. According to the participants' guesses, dogs showed themselves as bigger when threatened by female and larger humans. Dogs manipulated different acoustic parameters of their growls when facing male or female threatening humans; they may follow different strategies against opponents of differing apparent dangerousness. Thus far, dishonest acoustic signaling of size was an only rarely described phenomenon, especially during between-species communication. Therefore, our results represent significant discovery in interspecific vocal deception among realistic circumstances.

Keywords Dog · Human · Indexical information · Vocalizations · Signal manipulation · Deception

Communicated by C. Soulsbury.

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Introduction

The outcome of agonistic interactions is often based on the body size (difference) between the contestants, both in intraspecific (Moreno-Opo et al. 2020) and interspecific contexts (Fausch et al. 2021). Consequently, it would be advantageous if the individuals could assess their opponent's size based on such indirect clues as acoustic signals (Ladich 2004). And because these contests theoretically can be 'won' solely based on the effect of communication (e.g., vocalizations: Reby et al. 2005), it would be highly advantageous to develop increasingly effective signals. One way to achieve a higher success rate in deterring or discouraging opponents is to send deceptive signals (Bee et al. 2000). However, because of the conservative connection between sound quality and the anatomy of sound producing organs (Ghazanfar et al. 2007), the information given about body size is typically hard to manipulate in acoustic signals.

The acoustic parameters that are most often mentioned in connection with indexical size communication are the fundamental frequency (f_0) and formant dispersion (*dF*). According to the source-filter theory (Fitch 2000), these parameters are independent of each other, because while the frequency of the sound depends on the rate of vibration of the vocal folds (i.e., the 'source'), the formants will be the function of the vocal tract (i.e., the 'filter' – length and shape). This means that while f_0 is mostly a function of the weight, thickness and tension of the vocal folds, the *dF* will show a more intimate connection with the body size of the signaler, as the length of the vocal tract strongly depends on the size of the animal (Fitch 1997).

These anatomical constraints seemingly leave little room for sending dishonest (i.e., larger than actual) acoustic size information by the signaler (Fitch and Hauser 1995). This problem theoretically can be overcome by using artificial sound amplifiers as shown in tree crickets (*Oecanthus* sp.), where the smaller males cut song-enhancing holes in leaves, thus enhancing their mate-attracting success (Deb et al. 2020). Rarely, anatomical features allow the systematic manipulation of *dF* of particular calls, as we see in male red (*Cervus elaphus*) and fallow deer (*Dama dama*) (Fitch and Reby 2001), and koalas (*Phascolarctos cinereus*) (Charlton et al. 2007), that are capable of lowering their larynx via specific muscles, thus the 'elongated' vocal tract results in modified *dF*, conveying larger body size towards potential mates and competitor males. While the previous examples can be connected with pressures of sexual selection, in the yellow ground squirrel (*Spermphilus fulvus*) Matrosova et al. (2007) described the phenomenon of 'vocal mimicry' that can enhance the survival of young individuals against infanticide and selective predation. In this species, although having smaller body and skull sizes, juvenile individuals can produce alarm calls with lower f_0 than adults, thus avoiding agonistic attacks from adults and preferential attacks from predators. Still, 'dishonest' acoustic indexical signaling remains a rarely described phenomenon, especially in the interspecific domain, probably because of the coupled consequence of relative scarcity of competitive between-species encounters and the physical constraints of sound production.

In the case of dogs (*Canis familiaris*), we find a rich vocal repertoire that shows similarities with the vocabularies of closely related Canid species (Cohen and Fox 1976), and the effects of domestication (Pongrácz 2017). Growls are considered to be a conservative type of vocalization because they serve similar functions in dogs and wolves (Cohen and Fox 1976). Dogs often growl in both agonistic (e.g., resource guarding, defense, and offense) and in playful contexts (Faragó et al. 2010a). The indexical (body-size related) information conveyed by the growls is well documented. Riede and Fitch (1999) and later Taylor and colleagues (2008), showed that both the f_0 and *dF* values of defensive growls correlated negatively with the body size of the dog.

It was also found that other dogs react accordingly to the indexical content of growls. Taylor et al. (2011) showed that dogs reacted differently when approaching a hidden speaker, depending on the size-information encoded in the dog growls. In modality-matching experiments, we showed that in the case of the growls that dogs emitted during defending a bone from another dog, the information about the signaler's size was accurately recognized by other dogs (Faragó et al. 2010b). However, it was also shown that when dogs growled in a playful context, their growls conveyed indexical information about a 'larger' dog to the receiver dogs (Bálint et al. 2013). These findings indicate that dogs are most likely able to modify those parameters of their growls that indicate their size.

However, besides the indexical content, dogs' vocalizations primarily convey affective information, in other words, their acoustic layout mostly depends on the inner state of the signaler (Faragó et al. 2017). The vocal expression of inner states can be described along two main dimensions: arousal (or intensity) and valence (i.e., positive vs. negative). While the acoustic fingerprint of arousal seems to be fairly similar across a wide variety of species, the encoding of valence shows stronger species-specificity (Briefer 2020). However, it is also suspected that higher levels of matching valence-signals can be expected when two species are routinely engaged in mutual social interactions (Faragó et al. 2014), for example, in the case of dogs and humans. As inner states can rapidly change (Ferretti and Papaleo 2019), one can expect that the affective content of dog growls would change more dynamically than the indexical information they convey. For testing the effect of the inner state on the acoustic parameters of dog growls, in our original study (Bálint et al. 2016) we chose to modify the intensity of the same inner state (defensive aggression), while we recorded the growls that dogs emitted during an encounter with a threateningly behaving human ('Threatening Stranger Test', Vas et al. 2005). To elicit various levels of fear, we used male and female 'strangers', who were also of different body size ('large' and 'small' adult men and women). Each dog was tested with two threatening strangers (depending on the experimental condition, either two men, different size; two women, different size; or one man and one woman), on different days, who slowly approached them until the dog started to growl. The main question was whether dogs would modify those acoustic parameters that affect the apparent body size conveyed by the growls during the various levels of threat/fear (Bálint et al. 2016). In that study we showed that dogs growled with lower f_0 and lower *dF* at threatening men. This means that (if we consider an approaching male as a more serious threat than a female would be), dogs may sound 'larger' in their growls when they experience more intense fear. The study of Bálint and colleagues (2016), was the first that indicated that dogs may react with dynamically changing indexical signaling in an inter-specific interaction with humans, depending on the experienced level of threat. In other words: graded changes in the inner state caused adjustments in the indexical acoustic information communicated by the dog.

Dogs are considered to be a domesticated species with extreme levels of adaptation to their anthropogenic niche, including such socio-cognitive skills that make the coexistence of the two species smooth and mutually complex (Miklósi and Topál 2013). Inter-specific communication plays an important role in this, with a strong emphasis on acoustic communication (Pongrácz 2017). It was found that humans can use dog vocalizations as a rich source of information about the inner state of dogs (barks: Pongrácz et al. 2005, 2006; Jégh-Czinege et al. 2020; growls: Faragó et al. 2017). It has also been proven that humans can evaluate the intensity and valence of dog emotions based on the same acoustic rules that are being used when we assess human emotional vocalizations (Faragó et al. 2014). Besides the emotions, human listeners were also found to be sensitive to the indexical content of dog growls (based on the f_0 and *dF*, Taylor et al. 2008). There is also evidence that human listeners attribute stronger apparent aggressiveness to those growls that at the same time convey larger body size (Taylor et al. 2010b).

So far the only experiments in which human listeners were asked about the apparent size of dogs based on their vocalizations, the researchers used growl playbacks with artificially modified acoustic parameters to identify which cues affect size assessment (Taylor et al. 2008, 2010b). Based on the experiments of Bálint and colleagues (2016), we had the opportunity to create a playback experiment with genuine, unaltered dog growls originating from simulated agonistic encounters. Each dog provided two sets of samples, where the threat level could be different, according to the different size and sex of the opponent human. Our main goal was to test whether the acoustic differences between these growls can be regarded as manipulative communication, where dogs tried to show themselves acoustically larger. For this, we had to prove that the indexical information that might be different between two growls from the same dog, would truly affect the size assessment made by human listeners. To our best knowledge, this would be the first empirical study investigating the above-mentioned phenomena of 'dishonest' or 'deceptive' acoustic communication between dogs and humans. The relevance of this approach is highlighted by the fact that dishonest indexical acoustic communication has been rarely described, and especially in the interspecific dimension, it is thus far, an almost unprecedented phenomenon.

Goals, hypotheses

Although there are several indications that acoustic signaling is an effective interspecific form of communication (Pongrácz 2017), so far we do not have evidence that humans would be sensitive to the potential manipulation of indexical (body-size related) information in the vocalizations of other species. Similarly, there are no such studies that would directly indicate that humans would recognize the dynamic change of dogs' inner state based on their vocalizations.

We devised an online playback experiment, which used the dog growls originally recorded by Bálint et al. (2016). The participants listened to pairs of growls, and based on the growls only, they had to decide which dog was the larger. We analyzed these answers in relationship with the true size of the dogs (Control condition), and additionally, whether the same dog was threatened by a male or female experimenter of large or small body size (Test condition).

We hypothesized that dogs would growl themselves 'larger' in the case of a stronger experienced threat. Therefore, we predicted that dogs that encountered male opponents, and also those dogs that were threatened by 'larger' experimenters, would emit growls that are perceived by human listeners as coming from a larger individual, thus (dishonestly) showing the individual dog to be acoustically 'bigger'.

Materials and methods

Playback sounds and original recording conditions (according to Bálint et al. 2016) To minimize observer bias, data collection has been performed through an online system, where the participants have been offered with the sound samples by an algorithm. Throughout the data analysis, researchers followed blinded methods, where they were not aware, which sound samples the participants evaluated. We used the growl recordings from the study of Bálint et al. (2016). In the original study we used the 'Threatening Stranger' protocol, developed by Vas et al. (2005), to create a mildly stressful context where we recorded an average of 20–30 s vocalizations from the subjects. Each dog was tested twice, with at least 3 days in between, by two different 'strangers'. Depending on the experimental group, these were either two men, two women, or a man and a woman in case of the individual subjects. To avoid pseudoreplication, a substantial number (N_{female}=N_{male}=8) of adult female and male 'strangers' participated in the original experiment (their age ranged between 24 to 60 years (men), and between 24 to 32 years (women). With the help of a formula ([height of person (cm)] × 3√[mass of person (kg)])we calculated the 'frontally visible body surface' of each stranger and based on this value, sorted them into 'small' and 'large' categories separately in case of male and female 'strangers'. We considered a person as being 'small' or 'large' if their values were below or above the gender-specific median frontally visible body surface. In this way, we had 4 'small' and 4 'large' strangers from each gender.

The original collection contained N = 1496 growls, each of these were recorded in the 'Threatening Stranger Test'. The total number of tested dogs was 138 in the original study, from these only 96 dogs were tested with both strangers, and finally, only 64 dogs emitted growls during both test occasions. We narrowed down the original set of growls according to the following prerequisites: (i) a dog had to have growl(s) from both tests (i.e., encounters with both threatening strangers); (ii) the recordings should not contain strong background noise; (iii) as a maximum, each dog could provide four growls to the final database (two from each test). The intensity of the selected growls was set to 0.073 Pa in Praat software. In the final set of growls we had 215 individual growl recordings from N = 56 dogs. From these, N = 106 growls were recorded in the first tests of the subjects, and N = 109 growls originated from the second tests. We assembled 206 pairs of growls where both recordings originated from the same dog, always from its first and second tests, respectively.

The sex ratio of the 56 dogs was 30/26 (males/females). Besides mongrels, the sample contained individuals from 22 different breeds. Average age: 3.70 years (SD = 2.45 years); average height at the withers: 45.24 cm (SD = 11.54 cm); average body weight: 18.04 kg (SD = 9.16 kg). From these 56 dogs, originally tested in the experiment of Bálint and colleagues (2016), 15 individuals were tested with two male strangers of different size, 18 dogs were tested with two female strangers (of different size), and 23 dogs were tested with a male and a female stranger.

The average f_0 of the 215 growl samples was: 122.26 Hz (SD = 46.39 Hz); average dF: 1113.50 Hz (SD = 325.33); average duration: 1.45 s (SD = 1.23 s).

Questionnaire and participants of the online survey

The survey was completed by 311 participants (male/female = 77/234). Average age: 33.69 years (SD = 11.50 years). On average it took 10.9 min (SD = 10.41) to complete the survey.

The participants could access the online survey at this link (https://growl1.elte.hu/). The questionnaire is additionally placed to the Electronic Supplementary Material. It started with a brief explanation of the study. Then it continued with basic (partly optional) demographics, and then we asked a few questions about the participants' experience with, and attitude towards dogs (Table 1). After completing these questions and confirming their informed consent, the participants reached the actual online playback experiment.

Table 1 The list of those questions that we used to survey the dog-related experiences of the participants. The whole questionnaire can be seen in the Electronic Supplementary Material

Question	Answer type
Have you ever lived with a dog in the same household for more than one month?	Yes, I live presently with dog(s) / Yes, I have lived with dog(s) / No, never
Have you ever owned a dog?	Yes / No
On average, how many dogs do you have interaction with in a week (Excluding your own dog)?	'number'
Have you ever had a bad experience with dogs?	'Multiple choice' – "Yes, a dog bit me"/ "Yes, a dog attacked me" / "Yes, a dog attacked my dog" / "Yes, I saw that a dog attacked my relative/friend/ a stranger." / "Yes, a dog frightened me" / "No, I never had"
How much do you like dogs?	Continuous scale between − 1 (strongly dislike) and + 1 (like a lot)
How do you respond to an unknown dog?	Continuous scale between − 1 (surely avoid it) and + 1 (pet it)

Procedure

The task was simple: after listening to the two growls one by one, they had to decide which one of the two growling dogs was the larger. They had to continue with this until all the presented growl pairs were assessed accordingly.

Following the completion of the demographic part of the questionnaire, the participants continued with the practice phase, where they were familiarized with the survey interface (Fig. 1).

We provided each participant with two practice tasks in which we played back a cat's meow and a lion's roar. To help the participants choose the correct button (lion – the bigger animal), it was highlighted with yellow color. The program only allowed the participants to proceed if they clicked on the yellow button in both training trials.

The test itself consisted of 45 pairs of growl playbacks. In 30 pairs, the same dog's two growls were played back, which were originally recorded in two different 'Threatening Stranger' trials (Bálint et al. 2016). From these, 10 growl pairs were from a test group, where there were two different size males, 10 pairs from two different size females, and 10 growl pairs were from a test group, where the dog was facing one male and one female stranger. The remaining 15 pairs of growls served as controls. In each of the control pairs we sorted growls from two different dogs. More importantly, within a pair, the growls had to originate from the same test group (male-male; female-female, or male-female). Furthermore, the growls had to be elicited by the same size male, or female strangers in the case of a given pair of growls. In the case of dogs that were originally tested in the male-female group, within a given pair of growls, the dogs had to be tested by same sex experimenters. The weight difference between the two dogs was not taken into consideration when forming the control growl pairs.

The 45 pairs of growls were played back in a randomized order. In a set of 45 pairs the exact same growl pair was included only once (i.e., each growl pair was unique within a set of 45 pairs). It was also randomized whether the playback started with the sound from the left or the right-side pictogram. The color of the icon on the actual playback side changed to green to highlight the identification of sound-button pairs (Fig. 2).

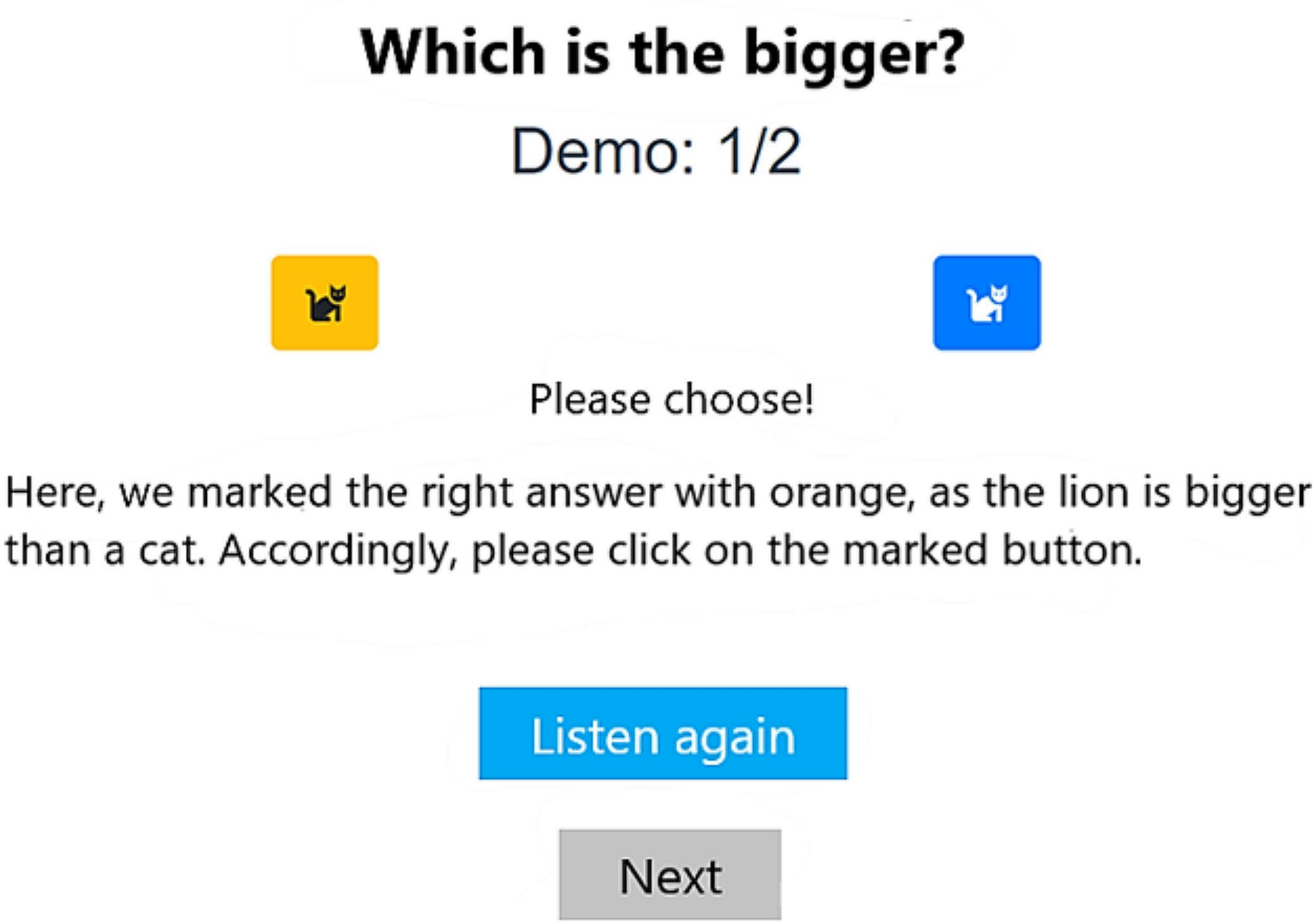

Fig. 1 Actual layout of the first practice task

If the participants could not decide after listening to both growls, or they did not hear the playbacks well, they had the option to listen to the growls again. If they clicked on the 'Listen again' button, the pair of growls was automatically played back, with 2s between the two sound samples. The repeated playback always started on that side where it was started before.

In the test growl pairs, the only difference between the two growls was the treatment (sex or size of the 'stranger', while the dog was the same). In the control growl pairs, the main relevant difference between the two growls was the size of the dog (treatment was the same). According to the core hypothesis of our study, the sex and/or the 'threatening strangers' had an effect on the acoustic parameters of dog growls that could affect the apparent indexical information about the caller's size. Therefore, we predicted that the participants should have enough information to make a decision about which one was the 'bigger dog', thus we used the 'forced choice' paradigm in the case of each pair of playbacks. The participants had to choose one of the icons as the 'bigger dog', because there was no option for 'same size' (Fig. 3). The software only allowed to step forward to the next pair of growls when the participant clicked on one of the icons.

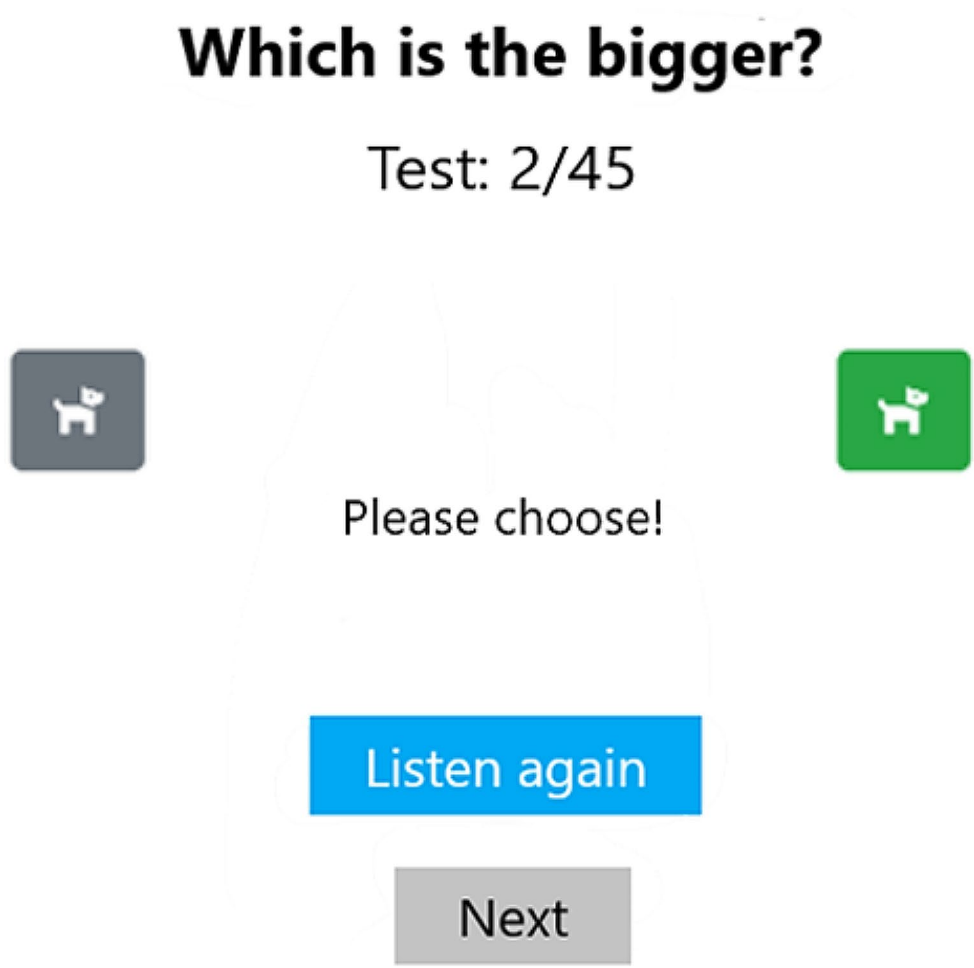

Fig. 2 Example for the outlay of a testing task. The icon on the right side is changed to green, indicating that the growl that is actually being played belongs to the right side

Statistical analysis

All analyses were performed in R Statistical environment with R Studio (version 1.2.1335). We used binomial Generalized Linear Mixed Models with logit link function (lme4 package, glmer function) with participant ID as random intercept. Response variable was the choice of the participant. We analyzed whether the participants could correctly find out which one was the larger dog in the control growl pairs (these always came from two different dogs), using an intercept only model including only participant ID as random intercept. In such models the exponentiated estimate of the intercept gives the odds ratio of correct choices. Then a second model was used to test the potential effects of demographic variables (age, sex) and dog-related experience of

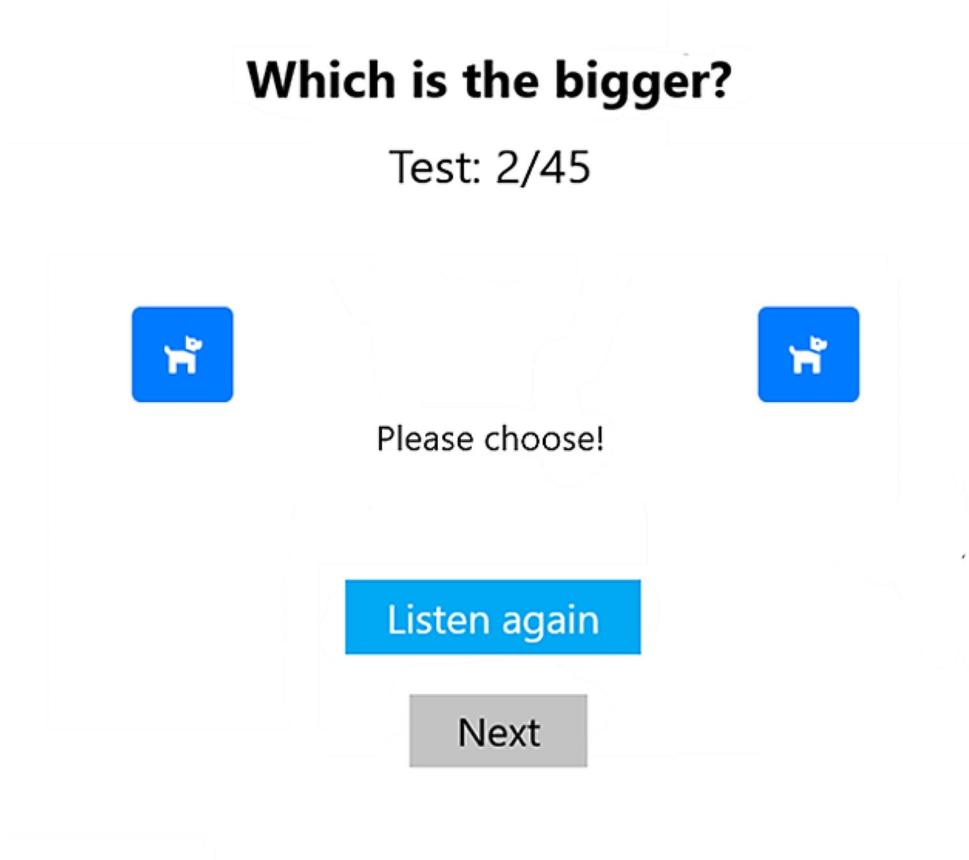

Fig. 3 Testing task, the moment of choice for the participants. After listening to both growls, the participant had to choose one of the icons as the 'bigger dog'

the participants. A third model was used to test the effects of difference between the heights and weights of the dogs in the control growl pairs; difference between the f_0, dF and duration values of the growls within the growl pairs. Finally, to test the participants' overall acoustic preferences we included their choice for longer, lower pitched or lower formant growls in three separate intercept-only models (like in case of correct choice).

In case of the test growl pairs (these came from the same dog within a pair) we analyzed the associations between the participants' choices (which dog they considered as being 'bigger'), we tested for different preferences (first or second encounter with the 'threatening strangers', longer, lower pitched or lower formant growls, body size of the 'threatening strangers' in case of same-sex cases, gender of the stranger in the different gender cases) of the participants again using intercept only models.

To test for possible confounding factors (side preferences or playback order) on the models containing independent factors we used AIC based backwards stepwise model selection (drop1 function) to find the parsimonious models (Initial models reported in as Supplementary tables, parsimonious model details are reported in the Results). To check model assumptions and assess fit quality we used check_model function, and to calculate odds ratios and confidence intervals from the model summaries we used model_parameters function, both from the easystats package.

Results

Descriptive results of the dog-experience related questions.

Of the participants, 230 fully completed the survey, 81 individuals only partially finished it (their responses, in the case of the completed growl-pair evaluations, were also included to the analysis, thus the full dataset contains 11,166 responses). Among the participants, 197 people lived with dogs at the time of the study, 65 participants lived together with dogs in the past, and 49 participants never had a dog. Majority of the participants reported that they usually met with 2 dogs a week. We also asked them whether they liked dogs (the continuous scale ranged between − 1 ("I definitely dislike dogs") and + 1 ("I like dogs a lot")). Here, the participants' average score was 0.80 (SD = 0.35). When we asked the participants whether they would interact with an unknown, neutrally behaving dog, the continuous scale again ranged between − 1 ("I would surely avoid the dog") and + 1 ("I would pet the dog"). Here we received an average 0.41 score (SD = 0.51).

Control growl pairs

In the case of the control growls, there was an actual size difference between the two dogs that originally emitted the growls. Therefore, we could test whether participants (N = 296 with 3724 responses) could correctly guess which dog was truly the bigger. Average success rate was 59.85% (SD = 19.18). We found that the participants significantly more often picked the truly larger dog as being the 'bigger' one (OR[95%CI] = 1.496[1.397–1.602]; z = 11.541, $p < 0.001$; Table S1).

Individual effects

Among individual-specific factors (age, gender, attitude towards and experiences with dogs) only age had a significant effect on the correct size assessment: younger participants were significantly more successful in choosing the truly bigger dog (OR[95%CI] = 0.926[0.863–0.993]; z=-2.149, $p = 0.032$; Table S2).

Growl-specific effects

Not only the body mass and the height at the withers differences between the two dogs showed a significant association with the correct 'bigger dog' choice, but also the absolute differences between the growls' acoustic parameters (Table 2), f_0 and dF difference had effect, growl length difference not.

We found that the larger was the difference between the two dogs within a growl pair in the aforementioned parameters, the easier it was for the participants to choose which dog was truly the bigger (Fig. 4).

Regarding the association between the acoustic features of the growls and the participants' choices, we found that the dog was thought to be bigger if its growl had lower f_0 (OR[95%CI] = 1.943[1.797–2.101]; z = 16.683, $p < 0.001$, Table S3), lower dF (OR[95%CI] = 1.336[1.252–1.426]; z = 8.753, $p < 0.001$; Table S4), and longer duration (OR[95%CI] = 1.339[1.251–1.433]; z = 8.418, $p < 0.001$; Table S5).

Test growl pairs

In the case of the growl pairs that came from the same dog, we checked whether the original test order had an effect on the participants' choices (N = 310, with 7442 responses). We found that the first recorded growl (i.e., the growl that came from the first in order 'Threatening Stranger' test of the given dog in the Bálint et al. (2016) study) was 6% more often chosen as the 'bigger dog' (OR[95%CI] = 0.939[0.897–0.982]; z=-2.735, $p = 0.006$; Table S6).

Overall, within-dog acoustic effects

We found that each acoustic parameter showed a significant association with the choices of the participants. They thought that the growls with lower f_0 (OR[95%CI] = 1.407[1.331–1.489]; z = 11.931, $p < 0.001$; Table S7) and longer duration growls (OR[95%CI] = 1.115[1.066–1.167]; z = 4.704, $p < 0.001$; Table S8) came from the 'bigger dog'. However, in the case of the formant dispersion, participants chose the growls with higher dF as the 'bigger dog' (OR[95%CI] = 0.888[0.847–0.930]; z=-5.027, $p < 0.001$; Table S9).

Same sex strangers

We analyzed whether the size of the 'Threatening Stranger' was associated with the participants' choices (N = 305 with 4401 responses). This comparison was possible in those cases when the dog was tested on both occasions with

Table 2 The results of the full model, in the case of the Control group of growl pairs (two different dogs' growls in a pair)

	Effect of difference between growls and dogs			
Predictors	Odds Ratios	CI	Statistic	p
(Intercept)	1.607	1.491–1.731	12.456	**< 0.001**
weight	1.120	1.033–1.214	2.734	**0.006**
height	1.095	1.007–1.191	2.120	**0.034**
growl length	1.037	0.968–1.112	1.037	0.300
f_0	1.696	1.544–1.862	11.060	**< 0.001**
dF	1.169	1.070–1.278	3.455	**0.001**
Random effects				
σ^2	3.29			
$\tau_{00\ ID}$	0.03			
ICC	0.01			
N_{ID}	296			
Observations	3672			
Marginal R^2 / Conditional R^2	0.119 / 0.128			
log-Likelihood	-2332.461			

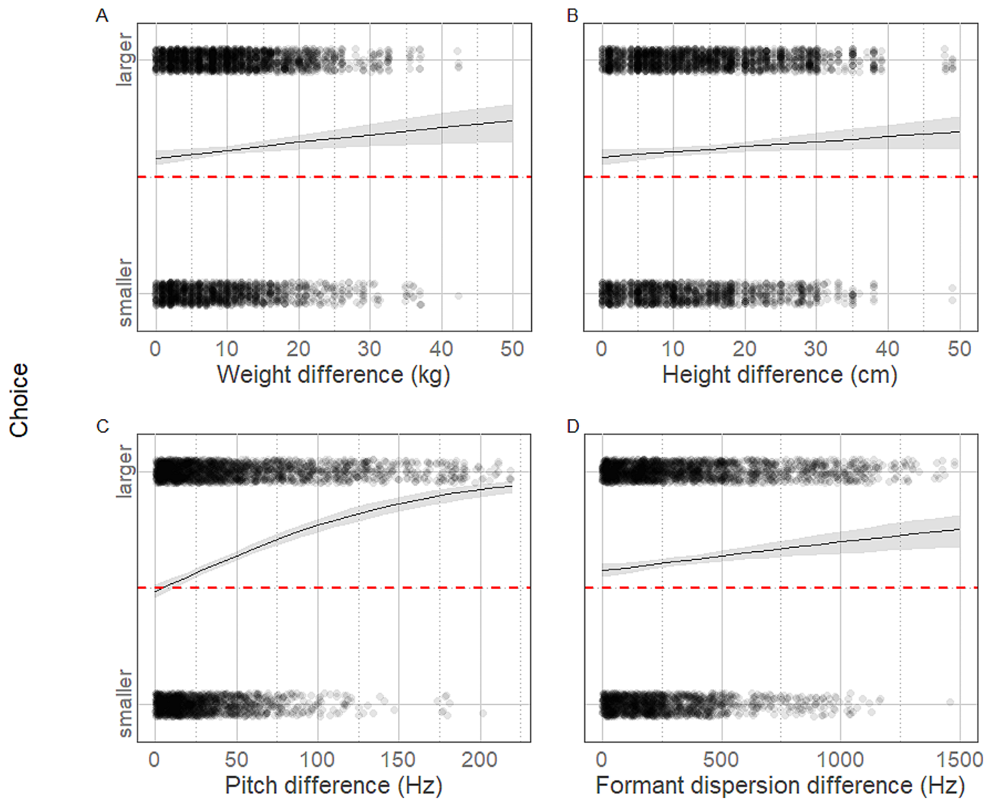

Fig. 4 The results of the model testing for dog and growl related effects in case of the control growl pairs coming from different individuals. The Y axis shows whether the subjects choose the growl originating from the smaller or larger dog as larger. X axis shows the difference between the particular growl pair regarding the dogs' actual size and the growls' acoustic parameters. Trend lines show the model estimates, representing the change in the chance of choosing the correct growl with the shading representing 95% confidence intervals. Dashed line represents the 50% random level. The greater was the difference between the dogs in weight (**a**) and height at withers (**b**); and the more the fundamental frequencies (**c**) and formant dispersions (**d**) differ between the growls, the more likely the participants made the correct choice

same-sex strangers (of different body size). We found a near-significant trend, as participants more often thought those growls belonged to the 'bigger dog' that were emitted towards the larger size 'Threatening Stranger' (OR[95%CI] = 0.948[0.894–1.006]; z=-1.763, p = 0.078; Table S10).

Individual effects From individual features, only the gender of the participant had a weak significant effect on the choice preference for threatener size: female participants chose the growl evoked by the larger threatening person significantly more likely (OR[95%CI] = 1.148[1.004–1.312]; z = 2.018, p = 0.044; Table S11).

Growl specific effects We found that the gender of the threatening stranger influenced the choice of the subjects. In case of growls evoked by two male strangers we found no bias, while in case of two female strangers we found that the participants more likely thought that the dog was 'bigger' if it encountered a bigger stranger (OR[95%CI] = 0.833[0.738–0.940]; z=-2.974, p = 0.003; Table 3). We found a significant effect of the difference between the f_0 values – as according to this, the larger was the difference between the two growls' f_0 values, the participants chose more frequently the growl as if it would come from the 'bigger dog', which was elicited by the larger stranger (OR[95%CI] = 0.911[0.858–0.968]; z=-3.027, p = 0.002, Fig. 5).

Different gender strangers

We analyzed whether the sex of the stranger was associated with the choices made by the participants in the case of those test growl pairs where the dog originally encountered a male and a female threatening stranger respectively (N = 299 with 3041 responses). We found a significant effect, the participants chose those growls as belonging to the 'bigger dog' with 14% higher chance, which were elicited by female strangers (OR[95%CI] = 1.148[1.069–1.232]; z = 3.787, p < 0.001; Table S12).

Individual effects From individual features, the age of the participant had a trend-like effect: younger participants choose the growl evoked by the female threatening stranger slightly more often (OR[95%CI] = 0.935[0.870–1.004]; z=-1.849, p = 0.064). In contrast, experiences with dogs, specifically the number of encountered dogs had an effect of the choice. Subjects that met more dogs showed a tendency to choose the growl evoked by a male stranger as com-

Table 3 The results of the full model, in the case of the Test group of growl pairs

	Growl specific effects on choosing the growl evoked by the larger stranger			
Predictors	Odds Ratios	CI	Statistic	p
(Intercept)	1.073	0.980–1.175	1.523	0.128
Stranger gender [female]	0.825	0.730–0.933	-3.056	**0.002**
growl length	1.034	0.969–1.104	1.010	0.313
f_0	0.917	0.863–0.975	-2.762	**0.006**
d*F*	1.023	0.960–1.090	0.711	0.477
Random effects				
σ^2	3.29			
$\tau_{00\ ID}$	0.00			
ICC	0.00			
N_{ID}	305			
Observations	4308			
Marginal R^2 / Conditional R^2	0.005 / 0.006			
log-Likelihood	-2975.706			

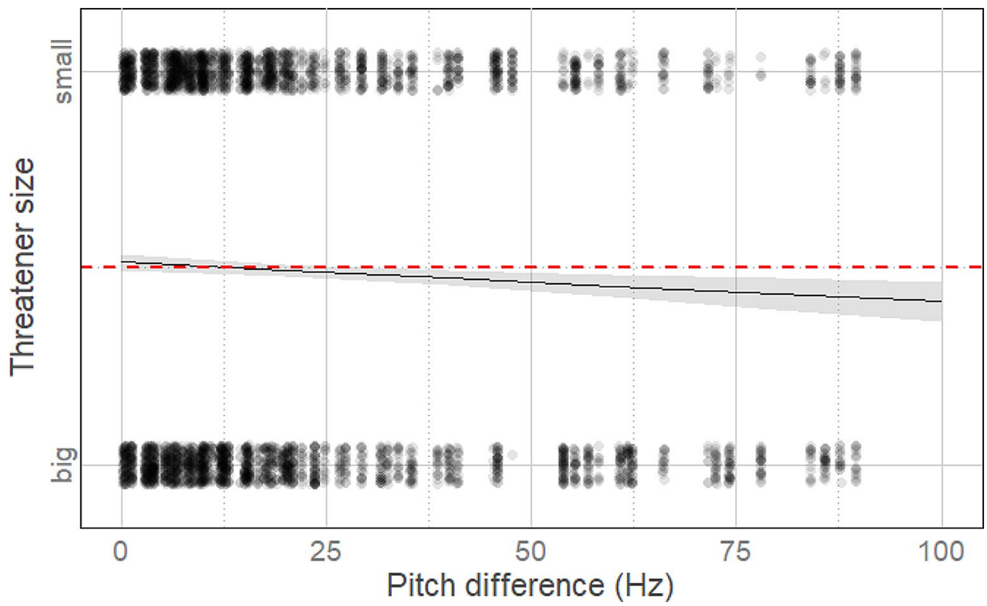

Fig. 5 The effect of the difference in fundamental frequencies within a growl pair on the choice for the growl as coming from the 'bigger dog' elicited by the larger threatening stranger in the case of same-sex threatening strangers. Trend line shows the model estimate, representing the change in the chance of choosing the correct growl with the shading representing 95% confidence intervals. Dashed line represents the 50% random level

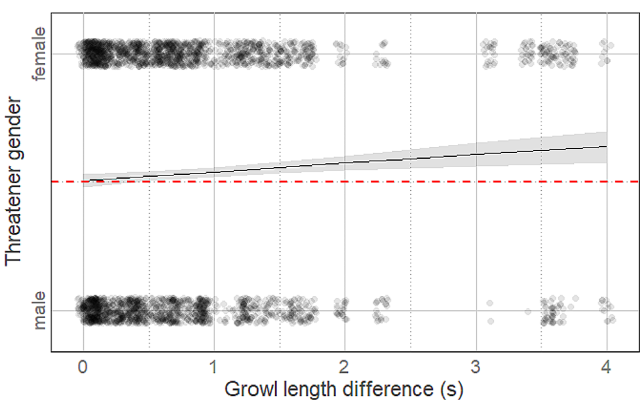

Fig. 6 The effect of the difference in lengths of the growls elicited by different sex strangers on the choice for 'bigger dog'. Trend line shows the model estimate, representing the change in the chance of choosing the correct growl with the shading representing 95% confidence intervals. dashed line represents the 50% random level

ing from a larger dog (OR[95%CI] = 0.915[0.851–0.984]; z=-2.409, $p = 0.016$, Table S13).

Growl-specific effects As the difference between the length of two growls increased, participants (N = 298 with 2974 responses) were more likely to think that the growl elicited by the female stranger belonged to the 'bigger dog' (OR[95%CI] = 1.133[1.051–1.220]; z=3.282, $p = 0.001$; Fig. 6; Table 4).

As the difference between the *dF* values of growls increased, the more likely participants chose the growl as coming from the 'bigger dog', which originally was elicited by a male stranger (OR[95%CI] = 0.893[0.830–0.961]; z=-3.019, $p = 0.003$; Fig. 7).

Table 4 The results of the full model, in the case of the Test group of growl pairs

	Acoustic effects on choosing the growl evoked by the female stranger			
Predictors	Odds Ratios	CI	Statistic	p
(Intercept)	1.175	1.093–1.263	4.357	**< 0.001**
growl length	1.125	1.044–1.212	3.102	**0.002**
f_0	1.019	0.947–1.096	0.500	0.617
dF	0.924	0.857–0.997	-2.033	**0.042**
Random effects				
σ^2	3.29			
$\tau_{00\ ID}$	0.00			
$N_{\ ID}$	298			
Observations	2974			
Marginal R^2 / Conditional R^2	0.007 / NA			
log-Likelihood	-2042.975			

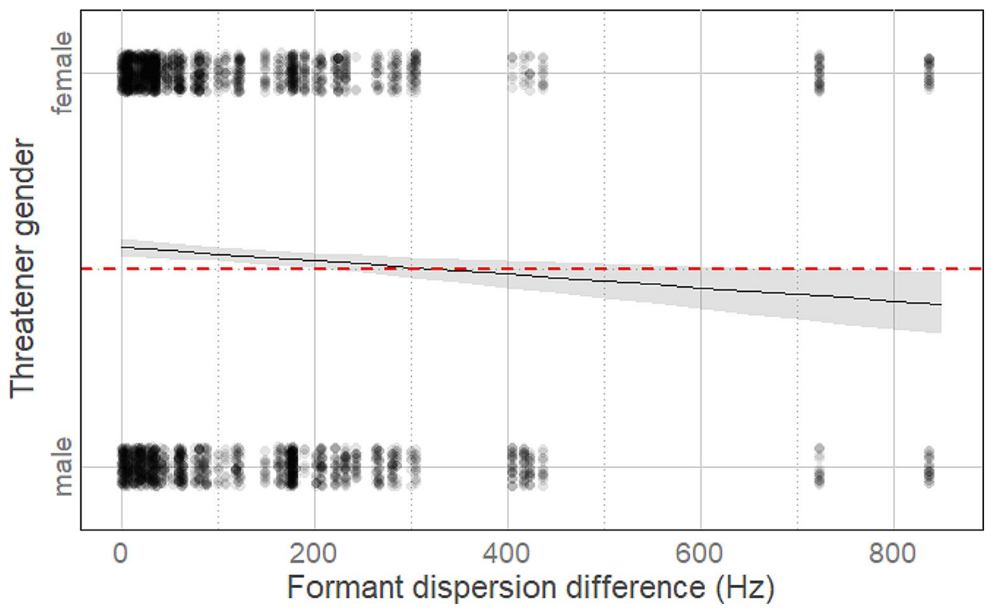

Fig. 7 The effect of the difference in formant dispersions of the growls elicited by different sex strangers on the choice for 'bigger dog'. Trend line shows the model estimate, representing the change in the chance of choosing the correct growl with the shading representing 95% confidence intervals. Dashed line represents the 50% random level

Other possible confounding effects

We checked the control and test growl pairs together (N = 311 with 11166 responses) whether the side (left vs. right side of the screen) or the order (1st vs. 2nd playback) affected the participants' choice. We did not find significant side preference (OR[95%CI] = 0.984[0.948–1.021]; z=-0.871; p = 0.384; Table S14). The order effect was significant, participants chose the second playback 16% more often as being the 'bigger dog' (OR[95%CI] = 1.163[1.110–1.218]; z = 6.316; $p < 0.001$; Table S15). A possible explanation for this effect could be that participants might found it difficult to concentrate to the task after listening to several growl pairs in a consecutive manner and they remembered better the second (more recent) growl in each pair, thus chose it more likely as belonging to the 'bigger dog'.

Discussion

In this playback study, we investigated whether human listeners are sensitive to the indexical information content of defensive dog growls. Furthermore, we wanted to know if the threateningly approaching human opponent's sex and body size affects the indexical cues of the elicited dog growl, based on the responses of human listeners to these growls.

In the case of those growls that were originally produced by the same dog, against a male and a female threatening stranger respectively, we found intriguing results. Contrary to our expectations, listeners thought that those growls belonged to a bigger dog which were elicited by threatening female opponents. A more detailed picture has unfolded by examining the differences between the acoustic parameters of these growl pairs (always originating from the same dog within a pair): the larger the difference was between the lengths of the growls, the participant was more likely to choose the growl elicited by the female stranger as the 'bigger dog'. Contrarily, in the case of a more pronounced difference between the formant dispersions, a bias occurred in the choices towards those dogs as being 'bigger' that were encountered by the male stranger.

To resolve this seeming contradiction, we should remember that the length and formant dispersion of growls are not equally good predictors of the true body size of the signaler (i.e., *dF* is more closely connected to body size, Taylor et al. 2010a), and they are also most probably not equally as easy to modulate by dogs. According to Faragó et al. (2017), longer growls are characteristic of higher levels of aggression, and it was also found that longer calls are connected with more negative emotions in both humans and canine vocalizations (Faragó et al. 2014). Our present results fall in line with earlier findings, showing that the dynamically changing inner states of the signaler are probably more readily manifested in the flexibly adjustable growl lengths. When the dogs were threatened by a female stranger, they possibly showed stronger aggression, which in turn manifested in longer length values in their growls. This response might be adaptive because women are more sensitive to emotional signals (Mestre et al. 2009; Christov-Moore et al. 2014), and perhaps the dog also expected from previous experience that a female opponent could be repelled more easily by ostensive aggression (Wells and Hepper 1999). On the other hand, formant dispersion, a more salient indexical cue regarding body size (Fitch 1997), might be more adaptive to modify in the case of the 'more serious' threat (i.e., men). In this case, dogs would use indexical deception by communicating a larger body size (Bálint et al. 2016).

In those cases when the same dog encountered two same-sex strangers, participants tended to choose those growls as belonging to the 'bigger dog' that were elicited by the larger body size threatening stranger. With a more detailed analysis it turned out that when the strangers were females, human listeners chose more frequently those growls as apparently emitted by a 'bigger dog' that were elicited by a larger woman. Related to this result, differences between the f_0 values of the same dog's growls made the decision easier for the participants. As we saw in the case of the growls elicited by different-sex strangers, modulating the f_0 may be a specific response to female opponents, thus in the case of two female opponents, dogs might more pronouncedly diverge in their levels of aggression and consequently emit deeper pitch growls in the case of larger (more frightening) female strangers.

In the case of the control growl pairs (originating from different dogs that received the same type of experimental treatment in the original 'Threatening Stranger' test, Bálint et al. 2016), we verified the results of Taylor and colleagues (2008), who also found that people were able to guess which was the larger dog, based on the acoustic parameters of their growls. However, this is the first time that human listeners were provided genuine (i.e., non-manipulated) growls and they were reliably able to select the larger dog based on the indexical cues in its growl. The importance of acoustic parameters in the decision of the participants is underlined by our finding that the extent of acoustic differences between the two growls of the two dogs was in a positive correlation with the difference in body size of the two dogs in the same pair, resulting in a more successful recognition of the larger dog by the participants.

In the case of the control growls, we also found an effect of the participants' age – younger listeners were more successful in guessing which dog was truly the bigger one. We cannot exclude the possibility that older participants were less sensitive to the indexical acoustic cues because of their deteriorating hearing capacity (Fogerty et al. 2012). However, there are also such indications that younger adults are affected more intensely by attention-eliciting (alarming) types of dog vocalizations (Jégh-Czinege et al. 2020). Although those earlier results were connected to dog barks, there is a strong possibility that especially in agonistic contexts, it would be adaptive that younger (i.e., reproductive age) adults would react more readily to acoustic signals that convey aggression/defensive threat (Jégh-Czinege et al. 2020).

We also found an order effect, according to this, participants chose the second growl in the pairs more often as belonging to the 'bigger dog'. However, as in each playset the growls were randomly assigned to the first or second position of the pairs, the order effect's influence on our results could be negligible.

In the case of the test growl pairs (growls from the same dog in a pair) we found another sort of order effect. Here, the participants picked more often those growls as being the vocalizations of the 'bigger dog' that were originally recorded in the first testing occasion of Bálint and colleagues' (2016) study. As in that research the authors randomized the sex and size of the threatening strangers across the two testing occasions, this result might be related to a more general effect. Dogs could be more scared of the threatening strangers during their first encounter, therefore here they emit defensive growls that convey a larger body size (Bálint et al. 2016).

Conclusions

This study provides novel information about the dynamic and parallel change of the acoustic parameters of growls related to the dogs' inner state and body size. By our knowledge this is the first time it was proven that human listeners are sensitive to the context-dependent modulations of dog vocalizations related to the signalers' body size. Perhaps the most interesting result tells that different acoustic parameters (such as the formant dispersion and growl length) of the defensive/deterrent growls can be modulated separately, according to the level of perceived threat (i.e., the sex of the threatening human). This finding is unique because by our knowledge, this is the first indication that humans as receivers can be misled by the naturally occurring manipulations of the indexical content of dog growls. The interspecific nature of how dog growls can deceive human listeners of course can be regarded as an 'incidental' phenomenon. Humans respond to the same body size-related acoustic parameters as the conspecific receivers would, thus the effect of these growls on humans may be a byproduct of intraspecific communication.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-024-03452-9.

Acknowledgements The authors are thankful to the expert Reviewers for their insightful and supportive advice throughout the peer-review process. Celeste R. Pongrácz provided proofreading of the manuscript.

Author contributions Conceptualization: PG, TF; Methodology: PG, TF, BF; Programming: BF; Validation: TF, BF, BZ; Formal Analysis: TF, BZ; Investigation: BZ; Resources: TF, BF; Data Curation: BZ, TF; Writing – Original Draft Preparation: PP, PD; Writing – Review and Editing: TF, BF, BZ; Visualization: PD, BZ, TF; Supervision: PP; Project Administration: BZ.

Funding Open access funding provided by Eötvös Loránd University. PP and PD were supported by the Hungarian National Research, Development and Innovation Office (NKFIH, Grant # K143077). PD was supported by the New National Excellence Program of the Ministry for Innovation and Technology (ÚNKP-23-2-II-ELTE-164). BF was supported by ELKH-ELTE Comparative Ethology Research Group (grant no. F01/031). TF was supported by the Hungarian Academy of Sciences via the János Bolyai Research Scholarship (BO/751/20), ÚNKP-22-5 New National Excellence Program of the Ministry for Innovation and Technology from the source of the National Research, Development and Innovation Fund (ÚNKP-22-5-ELTE-475) and the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (950159).

Data availability All data generated or analyzed during this study are currently included in the electronic supplementary material of this published article.

Declarations

Ethical approval The sound recordings (dog growls) used for constructing the online playback survey were originating from an earlier study (Bálint et al. 2016). The testing protocol of that study was done in accordance with the Hungarian regulations on animal experimentation and the Guidelines for the use of animals in research described by the Association for the Study Animal Behaviour (ASAB). Ethical approval was obtained from the National Animal Experimentation Ethics Committee, and the Animal Welfare Committee of the Eötvös Loránd University reviewed and accepted the protocol of the experiment (Ref. No.: ELTE-AWC-014/2015).

Informed consent In the current questionnaire study, we did not collect any personal data about the human participants that would reveal their identity as participation was anonymous. The participants were asked at the beginning of the questionnaire for their informed consent and agreement to participate in a scientific study, as well as to acknowledge that their responses will be used for scientific purposes only. The Research Ethics Committee of the Eötvös Loránd University has confirmed that no specific human ethical approval is required for this type of investigation in Hungary.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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