

2 **Nonlinear vocal phenomena affect human**
3 **perceptions of distress, size and dominance in puppy**
4 **whines**

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20
21 **Abstract**

22 While nonlinear phenomena are widely reported in animal vocalisations, often causing
23 perceptual harshness and roughness, their communicative function remains debated.
24 Several hypotheses have been put forward: attention grabbing, communication of distress,
25 exaggeration of body size and dominance. Here, we use state-of-the-art sound synthesis to
26 investigate how NLP affect the perception of puppy whines by human listeners. Listeners
27 assessed the distress, size, or dominance conveyed by synthetic puppy whines with
28 manipulated NLP, including frequency jumps, and varying proportions of subharmonics,
29 sidebands, and deterministic chaos. We found that the presence of chaos increased the

30 puppy's perceived level of distress and that this effect held across a range of representative
31 f_0 levels. Adding sidebands and subharmonics also increased perceived distress among
32 listeners with extensive caregiving experience with pre-weaned puppies (e.g., breeders,
33 veterinarians). Finally, we found that whines with added chaos, subharmonics, or sidebands
34 were associated with larger and more dominant puppies, although these biases were
35 attenuated in experienced caregivers. Together our results show that nonlinear phenomena
36 in puppy whines can convey rich information to human listeners and may thus be crucial for
37 offspring survival during breeding of a domesticated species.

38

39 **Keywords**

40 Nonlinear vocal phenomena, puppy whines, human perception, interspecific
41 communication, animal communication

42

43 **Introduction**

44 There is now widespread evidence that vertebrate vocal signals communicate both static
45 information (e.g., relatively stable physical and social attributes) and dynamic information
46 (e.g., transient emotional and motivational states) about the animals that produce them
47 [1,2]. Investigating how these signals are emitted, and how mechanisms of vocal production
48 determine their acoustic structure, has enabled researchers to better understand their
49 evolution and functions [2].

50 In mammals, the production of vocalisations is initiated in the larynx by vocal fold vibration
51 [3]. The rate at which the vocal folds vibrate determines a key feature of vocal signals, their
52 fundamental frequency (f_0), which is largely responsible for their perceived pitch [3]. While
53 vocal fold vibration is typically regular, perturbations can occur, causing abrupt changes in
54 the tonal structure of acoustic signals [4,5]. This results in acoustic irregularities known as
55 nonlinear phenomena (hereafter NLP), which are widely reported in the vocalisations of
56 terrestrial mammals (e.g., koalas (*Phascolarctos cinereus*): [6]; marmots (*Marmota*
57 *marmota*): [7]; chimpanzees (*Pan troglodytes*): [8]; meerkats (*Suricata suricatta*): [9]; giant
58 pandas (*Ailuropoda melanoleuca*): [10]; dogs (*Canis lupus familiaris*): [11,12]; North
59 American elk (*Cervus canadensis*): [13]; cows (*Bos taurus*): [14] African elephants (*Loxodonta*

60 *Africana*): [15]), including humans (*Homo sapiens*) [16,17]. Generally, the presence of NLP in
61 vocalisations is responsible for perceived harshness, roughness and instability [18].
62 Four main types of NLP in animal vocalisations are frequency jumps, subharmonics,
63 sidebands, and deterministic chaos. *Frequency jumps* correspond to sudden changes in vocal
64 fold vibration [19]. *Subharmonics* can appear when one vocal fold vibrates at a period
65 corresponding to an integer fractional value of the second vocal fold (e.g., 1:2, 2:3) [20],
66 while *sidebands* (resulting from biphonation) are produced by the vibration of two
67 independent sound sources (e.g., vocal folds vibrating at two independent frequencies) [4].
68 Finally, *deterministic chaos* (hereafter chaos) usually occurs when vocal folds vibrate in
69 asynchronous nonperiodic regimes [5]. Because of their ubiquity in mammal calls, a
70 consensus is emerging that NLP are not merely by-products of vocal production but rather
71 function to communicate information about the caller [4,5]. However, it remains unclear
72 what kind of information NLP transmit.

73 It has been suggested that NLP are vocal indicators of high arousal [7,11,15,21] in contexts
74 associated with distress (e.g., during separation from conspecifics or immediate risk of
75 predation) [22]. Specifically, chaos represents the most severe and perceptually harsh form
76 of vocal nonlinearity [18] characterizing the distress vocalisations of several mammal
77 species [10,11,15,21–23], including humans [16,17]. For instance, perceptions of distress
78 increase with the presence of NLP in nonverbal vocalisations of human infants [16] and
79 adults [17]. This has led to the suggestion that a possible biological function of NLP may be
80 to reduce habituation in receivers by making these calls unpredictable and thus difficult to
81 ignore [9,24–26].

82 Aside from NLP, f_0 (perceived as pitch) and formant frequencies (vocal tract resonances that
83 influence perceived timbre) also affect the perceptual quality of vocalisations. In many
84 terrestrial mammals, formants reliably predict inter-individual differences in body size,
85 whereas f_0 is usually a better predictor of dominance status [27]. Indeed, animals in
86 aggressive motivational states commonly produce harsh low-pitched calls [28] to potentially
87 signal and/or exaggerate their size and dominance [2]. These signals can therefore play a
88 key role in determining the outcome of agonistic interactions, for instance during sexual
89 competition or territorial defence [27]. In this context, another hypothesis regarding the
90 potential functions of NLP may be to exaggerate perceived size and dominance [4,5]. Some
91 NLP can indeed lower perceived pitch, enhancing the perceptibility of vocal tract resonances

92 by increasing spectral density, and potentially, may affect perceptions of the vocaliser's size
93 and dominance [4,18]. Together, several hypotheses have thus been put forward regarding
94 the functions of NLP: attention grabbing, communication of distress, and/or size or
95 dominance exaggeration.

96 Previous investigations of the perceptual effects of NLP in nonhuman animal vocalisations
97 have focused on a single type (e.g., chaos in lizards (*Liolaemus chiliensis*): [29]; chaos in
98 marmots: [24]; subharmonics in meerkats: [9]; chaos in red deer (*Cervus elaphus*): [26]).
99 Past studies also typically relied on NLP variation in natural vocal sounds (frogs (*Odoranna*
100 *tormota*): [30]; meerkats: [9,25]; marmots: [24]; red deer: [26]), and hence, could not
101 control for potentially covarying acoustic parameters (e.g., f_o , intensity). It thus remains
102 crucial to understand the biological function(s) of each type of NLP by testing their
103 independent perceptual effects across different species, call types, and behavioural
104 contexts. Yet, until recently, a major limitation in the experimental study of NLP has been
105 the absence of tools to synthesise naturalistic sounds with controlled levels of NLP.

106 Here, we take advantage of recent advances in parametric sound synthesis, thus far used
107 only on human nonverbal vocalisations [18,31,32], to systematically add NLP to synthetic,
108 yet highly realistic, nonhuman animal vocalisations. More specifically, we applied this
109 method to investigate how the presence and duration of NLP in distress whines, produced
110 by 1- to 9-week-old domestic dog puppies, affect their perception by humans. Whines are
111 high-pitched tonal calls considered to signal distress, typically given by puppies during
112 separation [33] or aggression by their mother [34]. Like adult dog whines [11,12], puppy
113 whines also often contain NLP (see electronic supplementary material), particularly when
114 the dog's emotional arousal increases (personal observation). Although puppies' survival
115 mainly relies on mothers, who intensively breastfeed, groom, and warm them [34], the
116 intervention of human caregivers is sometimes required for breeding in this domesticated
117 species [35]. As such, NLP in whines may be important to attract the attention of the
118 mother, but also of humans, ensuring that puppies receive care. Indeed, the common
119 presence of NLP across vertebrate infant distress calls suggests that these shared vocal
120 features may support the interspecific vocal communication of need to human caregivers
121 [22]. Therefore, to investigate the possible function of NLP as vocal indicators of distress in
122 human-puppy interactions, we performed playback experiments using synthetic puppy
123 whines in which we manipulated the presence, and duration, of NLP (frequency jumps,

124 subharmonics, sidebands, chaos) across f_0 levels (low, medium, high). We predicted that
 125 NLP added to whines, particularly chaos, would increase human perceptions of the puppy's
 126 distress, and that higher proportions of NLP would enhance these perceptual effects.
 127 Moreover, because NLP affect perceptions of size and dominance in synthetic human
 128 vocalisations [18,32], we tested whether these perceptual effects generalize to other
 129 mammal vocalisations. Indeed, dominance-like behaviours have been described as a trait of
 130 individual temperament in dogs [36,37], and can occur during the early development of pre-
 131 weaned canids, including puppies (e.g., during play with littermates) [36,38]. We thus
 132 predicted that NLP would increase perceived size and dominance. Finally, under the
 133 assumption that the interspecific function of infant distress vocal signals may be particularly
 134 important in caregiving contexts (e.g., for breeders and veterinarians), we replicated our
 135 experiment on a distinct sample of professionals with extensive experience in puppy
 136 caregiving to test whether such experience modulates the perceived effects of NLP.
 137

138 **Materials and Methods**

139 Our experimental protocol included: (1) audio recording natural distressed puppy whines,
 140 (2) creating synthetic whine stimuli based on these recordings of natural vocalisations, and
 141 (3) online playback experiments in which we respectively tested 200 and 217 human
 142 listeners from the general population (Experiments 1 and 2), and 55 listeners selected for
 143 their extensive experience in puppy caregiving (Experiment 3). All participants judged the
 144 perceived level of distress, body size, and dominance conveyed by each synthesized puppy
 145 whine. While the first and third playback experiments tested the perceptual effects of the
 146 presence or absence of NLP, the second experiment also tested the perceptual effects of
 147 their duration (Table 1).
 148

	Playback Experiment 1 (N=200) and Experiment 3 (N=55)	Playback Experiment 2 (N=217)
Total number of original synthetic prototypes	20	40

Manipulations	Types of NLP	none, frequency jumps, subharmonics, sidebands, chaos	none, subharmonics, sidebands, chaos
	Duration of NLP (% of whine duration)	20-40%*	50% or 80%
	Levels of f_0	low, medium, high	low, medium, high
Total number of synthetic stimuli		300	840

149 **Table 1:** Overview of the experimental design used for playback experiments. Level of
150 manipulation ‘none’ indicates vocal stimuli without NLP. * Values drawn at random within
151 this range, derived from the peak of the observed distribution of NLP durations.

152 Experiments 1 and 3 shared an identical design and identical whine stimuli.

153

154 *Acoustic recordings*

155 We recorded whines of 32 Beagle puppies from 6 different litters at roughly 1-, 3-, 6-, and 9-
156 weeks of age (Table S1) at two different breeding facilities (France). We used a Sennheiser
157 MKH70 directional microphone connected to an audio recorder Zoom H4n (44.1kHz, 24bit)
158 and positioned at approximately 30 cm from the animal’s mouth.

159 Mothers and their litter stayed in the same enclosure during the 9 first weeks of the
160 puppies’ lives. To record natural whines, each puppy was placed alone in a pen in a separate
161 room (roughly 100 x 50cm). Each puppy was thus recorded in a separation behavioural
162 context, without visual and acoustic contact with its mother and littermates. This method of
163 recording distress vocalisations has been widely applied in vertebrates [22]. Our recordings
164 started once the puppy had produced its first whine and did not last for more than 5
165 minutes to limit stress potentially induced by our experimental conditions. At the breeding
166 facilities, bitches are habituated to being temporarily separated from their litter (e.g., during
167 daily walks) and accustomed to breeders manipulating puppies during daily care (e.g.,
168 weight measurements evaluating physical condition of puppies). It was thus unlikely that we
169 induced stressful behaviours in mothers while recording their puppies. In addition, when
170 bringing the puppy back to its mother, the observation of normal maternal behaviours such
171 as grooming or breastfeeding [34] indicated low stress levels.

172

173 *Stimulus creation*

174 From this pool of acoustic recordings of natural puppy vocalisations, we used 10 whine
175 sequences at each age category (i.e., 1-, 3-, 6-, 9- week-old, 40 sequences in total) from 26
176 different individuals as templates to create their associated fully synthetic copy (hereafter
177 synthetic prototype). We choose whine sequences composed of three repeated whines
178 without NLP to facilitate their synthesis with the R package *soundgen* [31].

179 For each synthetic prototype, we prepared sets of vocalisations with systematic
180 manipulations of NLP and f_o (Table 1) for playback experiments. Specifically, we created
181 synthetic whine stimuli at low, medium, and high levels of f_o , with or without different types
182 of NLP added at each f_o level, based on those that naturally occur in puppy whines, including
183 frequency jumps or varying proportions of subharmonics, sidebands, and chaos (Fig. 1).
184 Manipulations of NLP and f_o were applied to the three repeated whines composing the
185 entire synthetic prototype.

186 To inform these manipulations, we first performed detailed acoustic analyses on our
187 recorded whines to characterise the natural vocal variation in puppy whines (see electronic
188 supplementary material). We manually measured onset time and proportion of NLP as well
189 as the f_o of 4841 natural whines containing NLP. This allowed us to create highly realistic
190 variants that remained within the range of natural production, thus increasing the ecological
191 validity of our experimental method and reliability of our results.

192 In total, there were 300 stimuli in Experiments 1 and 3: 20 prototypes * 5 NLP conditions
193 (none, frequency jump, subharmonics, chaos, sidebands) * 3 f_o levels (low, medium, high).
194 Experiment 2 included 840 stimuli: 40 prototypes * 7 conditions of NLP duration (none +
195 50% or 80% of the whine duration affected by subharmonics, sidebands, chaos = 1+ 2*3 = 7)
196 * 3 f_o levels. All audio stimuli and R code for their synthesis are available for download at
197 <https://osf.io/rp7m8/>.

198

199 *1- Manipulations of nonlinear phenomena*

200 Experiments 1 and 3 tested perceptual effects of the presence or absence of NLP in puppy
201 whines. We manually coded frequency jumps as instantaneous changes in f_o occurring at
202 the maximum f_o slope. Indeed, as the production of NLP is typically associated with
203 increases in subglottal pressure, leading to a relatively high f_o and amplitude, and ultimately,

204 to an unstable vocal system [3,39], NLP are expected to occur in sections of calls where f_o is
205 relatively high [40]. We also added sidebands, subharmonics, and chaos to whines by
206 randomly selecting the onset time from the observed natural distribution. Durations of
207 these types of NLP were selected at random within an interval corresponding to the most
208 commonly produced NLP durations in natural whines, i.e., 20% to 40% of the whine's
209 duration (Fig. S1).

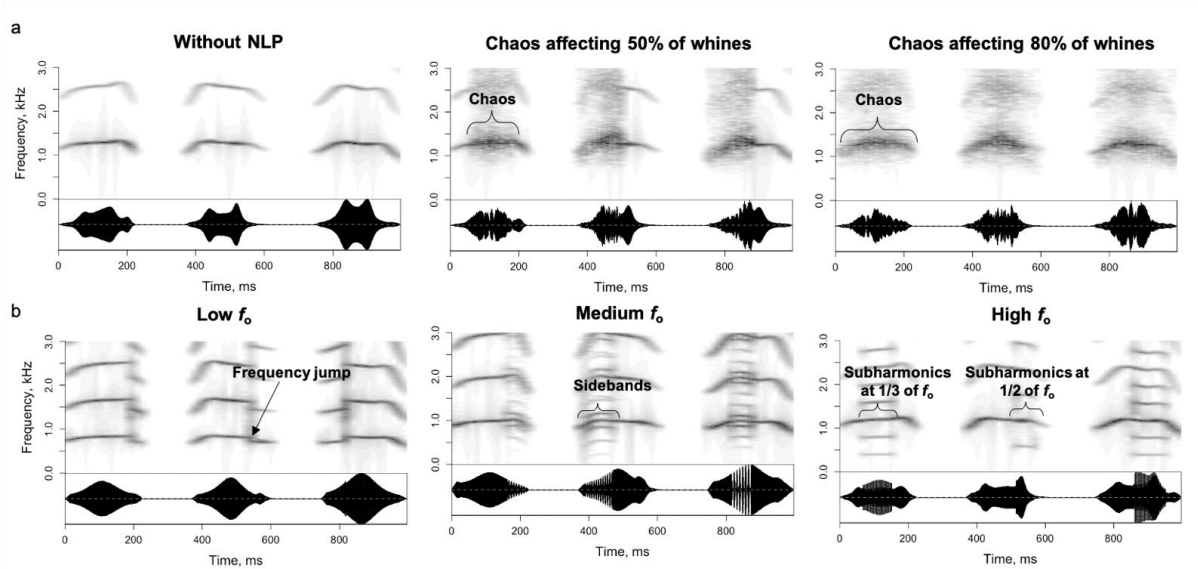
210 Experiment 2 tested perceptual effects of NLP duration. Here, the duration of NLP was fixed
211 at either 50% (hereafter medium proportion) or 80% (hereafter high proportion) of the
212 variant's duration (Fig 1.a), both of which remained within the natural range (Fig. S1). The
213 onset time of NLP was also randomly selected from the observed natural distribution, but
214 under the constraint that the onset time should be within a specific interval (medium
215 proportion: [0; 50] % of the whine duration, high proportion: [0; 20] % of the duration).
216 We synthesized subharmonics, sidebands, and chaos using a method allowing for natural
217 variability. Specifically, to synthesise subharmonics, the integer ratio of subharmonic
218 frequencies to f_o was drawn from a truncated Poisson observed distribution (mean=1 and
219 range= [2, 5]), typically resulting in additional spectral components (subharmonics) at $f_o/2$ or
220 $f_o/3$. We created sidebands by adding amplitude modulation, the frequency of which was
221 selected from a Gaussian distribution (mean \pm SD = 170 \pm 20 Hz) characterizing sidebands in
222 natural puppy whines. The amplitude of subharmonics and sidebands, expressed as the
223 proportion of the amplitude of f_o , was randomly selected from a Gaussian distribution with
224 a mean \pm SD of 50% \pm 10% [3] and 80% \pm 10%, respectively. Finally, we created chaos by
225 adding jitter (i.e., changes in f_o periodicity) with values of 3 \pm 0.6 semitones in Experiments 1
226 and 3, and 1.2 \pm 0.3 semitones in Experiment 2, such that chaotic episodes sounded natural.

227

228 *2- Manipulations of f_o*

229 Because variations in f_o can affect perceptions of distress [41–44], size [45,46], and
230 dominance [47], we also tested whether perceptual effects of NLP vary across f_o levels.
231 From our f_o measurements of natural whines containing NLP, we identified three main f_o
232 categories that roughly correspond to quartiles of the natural distribution with a mean \pm
233 semitones/2 of 790 \pm 27 Hz (low f_o), 972 \pm 27 Hz (medium f_o), and 1170 \pm 27 Hz (high f_o),
234 hereafter termed target region. We thus synthesised stimuli at each f_o level by first
235 randomly selecting a target f_o value from each target region. This allowed for natural

236 variability in f_0 across variants within each target region. Second, we calculated a coefficient
 237 of correction as the ratio between the target f_0 value and average f_0 across whines in the
 238 original synthetic prototype. Third, the f_0 of the prototype was corrected by this coefficient,
 239 such that the average f_0 of the new variant reflected the target f_0 value.



240
 241 **Figure 1:** Spectrograms of variants of the same whine prototype synthesized with or without
 242 NLP (frequency jumps, subharmonics, sidebands, chaos) at different levels of (a) NLP
 243 duration (NLP affecting 50% or 80% of the whine's duration, as illustrated with the addition
 244 of chaos) and (b) f_0 (low, medium, high). While every NLP manipulation was tested at every
 245 f_0 level, here we show a range of NLP manipulations at each f_0 level as examples.

246
 247 *Playback experiments with human listeners*

248 We performed online playback experiments on 487 human adult listeners ($N= 206$
 249 Experiment 1; $N= 221$ Experiment 2; $N= 55$ Experiment 3). Before each experiment,
 250 participants completed a short questionnaire indicating their sex, age, profession, level of
 251 comfort with puppies and experience with puppy-ownership. They were also informed that
 252 they would hear distressed puppy whines recorded during separation from mothers and
 253 littermates. Because the term "puppy" can refer to both pre- and post-weaned dogs, we
 254 defined a puppy as a dog younger than 3 months of age in our online questionnaire.
 255 Participants first listen to three natural whine sequences containing NLP to familiarise
 256 themselves with nonlinear puppy whines and to adjust their sound level to a comfortable

257 volume, which was then kept constant for the experiment. We asked participants to use
258 headphones when completing the experiment in a quiet environment.
259 Playback experiments comprised three blocks testing perceived distress, size, or dominance.
260 The order of blocks and stimuli within blocks were randomized. Each block contained 20
261 (Experiments 1 and 3) or 40 (Experiment 2) whine stimuli, such that each prototype was
262 tested once per block with a randomly chosen level of f_o and NLP condition for a given
263 participant who listened to a total of 60 stimuli (Experiments 1 and 3) or 120 stimuli
264 (Experiment 2). Following each whine exposure, participants rated the whine by indicating
265 how distressed/dominant/large the puppy sounds, using a continuous sliding scale ranging
266 from 0 (Not at all distressed/dominant or extremely small) to 100 (Extremely
267 distressed/dominant/large). Participants could listen to stimuli several times and could
268 adjust their rating if needed.
269 In Experiments 1 and 2, we respectively excluded 6 and 4 participants who completed less
270 than 80% of the experiment or otherwise failed to engage with the study. No participant
271 from Experiment 3 was excluded. Statistical analyses were thus performed on 472
272 participants ($N= 200$ Experiment 1, $N= 217$ Experiment 2, $N= 55$ Experiment 3), aged 28 ± 11
273 years old (mean \pm SD) (range [18-74]), of whom 40% self-reported as female, 60% as male,
274 and less than 1% as 'other'. Nearly all participants in Experiments 1 and 2 (409/417) did not
275 professionally work with puppies but felt comfortable in their presence (381/417), and 65%
276 had owned a puppy within the past 5 years. In Experiment 3, we specifically selected
277 participants for their extensive experience in puppy caregiving, and thus their regular
278 exposure to whines. Most of these participants professionally worked with puppies, as out
279 of 55, 40 were dog breeders, 12 were veterinarians, and 2 were dog trainers.

280

281 *Data analysis*

282 Data from playback experiments were analysed using Bayesian multilevel models fitted with
283 the *brms* R package [48] using default priors. The response variable of models corresponded
284 to ratings re-coded from 0 to 1 and modelled with zero-one-inflated beta distribution [49].
285 To investigate whether the presence of NLP affected human perceptions of puppy whines,
286 and whether these effects of NLP varied with whine f_o , we first fitted a model including data
287 from Experiments 1 and 2, testing the general population ($N=417$ participants). This model
288 included a three-way interaction between the tested perceptual scales (3 levels), NLP

289 condition (5 levels) and f_o (3 levels). We allowed effects of NLP on each scale to vary across
290 participants and prototypes by fitting the interaction between NLP and scale as random
291 slopes for all participants and prototypes. We also assumed that each stimulus would have
292 its unique rating on each scale. This model resulted in the following *brms* syntax:

293 Rating response \sim scale*NLP* f_o + (NLP * scale | participant) + (NLP * scale | prototype) +
294 (scale | stimulus)

295 To examine whether experience in puppy caregiving influences the effects of NLP, we fit an
296 analogous model to the data collected from experienced caregivers ($N=55$ participants in
297 Experiment 3). Finally, we tested whether the duration of NLP reinforced their perceptual
298 effects by fitting a second model with data from Experiment 2 ($N= 217$ participants). This
299 model included a two-way interaction between rating scales and duration of NLP (7 levels).

300 The model followed this *brms* syntax:

301 Rating response \sim scale*duration + (scale*duration | participant) +
302 (scale*duration | prototype) + (scale | stimulus)

303 In this model, we captured an assumed variability of predictors *scale* and *duration* across
304 participants and prototypes and allowed for ratings of each scale to vary across each unique
305 stimulus. Posterior distributions of model parameters were summarized by their median and
306 95% credible interval.

307

308 Results

309 We predicted that the presence and duration of NLP in puppy whines would increase
310 perceptions of distress, size, and dominance by human listeners. With the exception of
311 frequency jumps, all NLP affected listeners' ratings on one or more of these perceptual
312 scales (Fig. 2.a, Fig. 3, Fig. S2.a).

313 Specifically, in the general population (Experiments 1 and 2), we found that perceptions of
314 distress were primarily affected by chaos, which increased distress ratings by 5.6% [3.8, 7.4]
315 compared to identical whines without NLP. In contrast, distress ratings were not noticeably
316 affected by the addition of subharmonics (-0.7% [-2.1, 0.7]) nor sidebands (1.3% [0, 2.6]).

317 Experienced puppy caregivers (Experiment 3) also rated whines with chaos as more
318 distressed-sounding, but unlike the general population, they furthermore associated

319 sidebands and subharmonics with higher distress (see electronic supplementary material for
320 details, Fig. S2.a).

321 Moreover, we predicted that longer episodes of subharmonics, sidebands, and chaos in
322 puppy whines would increase their perceptual salience and thus, enhance their effects on
323 perceived distress. Surprisingly, we found that increasing the duration of chaos from 50% to
324 80% of the whine's duration did not further increase perceived distress (-0.4% [-3.0, 2.3]),
325 and that increasing the duration of subharmonics and sidebands reduced perceived distress
326 by 4.8% [2.2, 7.5] and 3.1% [0.8, 5.4], respectively (Fig. 3).

327 While effects of NLP were relatively stable across each f_o level, our results confirm an
328 independent effect of f_o on distress ratings in participants for all three experiments (Fig. 2.b
329 and c; Fig. S2.b and c). Indeed, puppies producing whines with higher levels of f_o were rated
330 as more distressed (9.3% [8.1, 10.6]), compared to the same whines synthesized at lower f_o
331 levels (Fig. 2b).

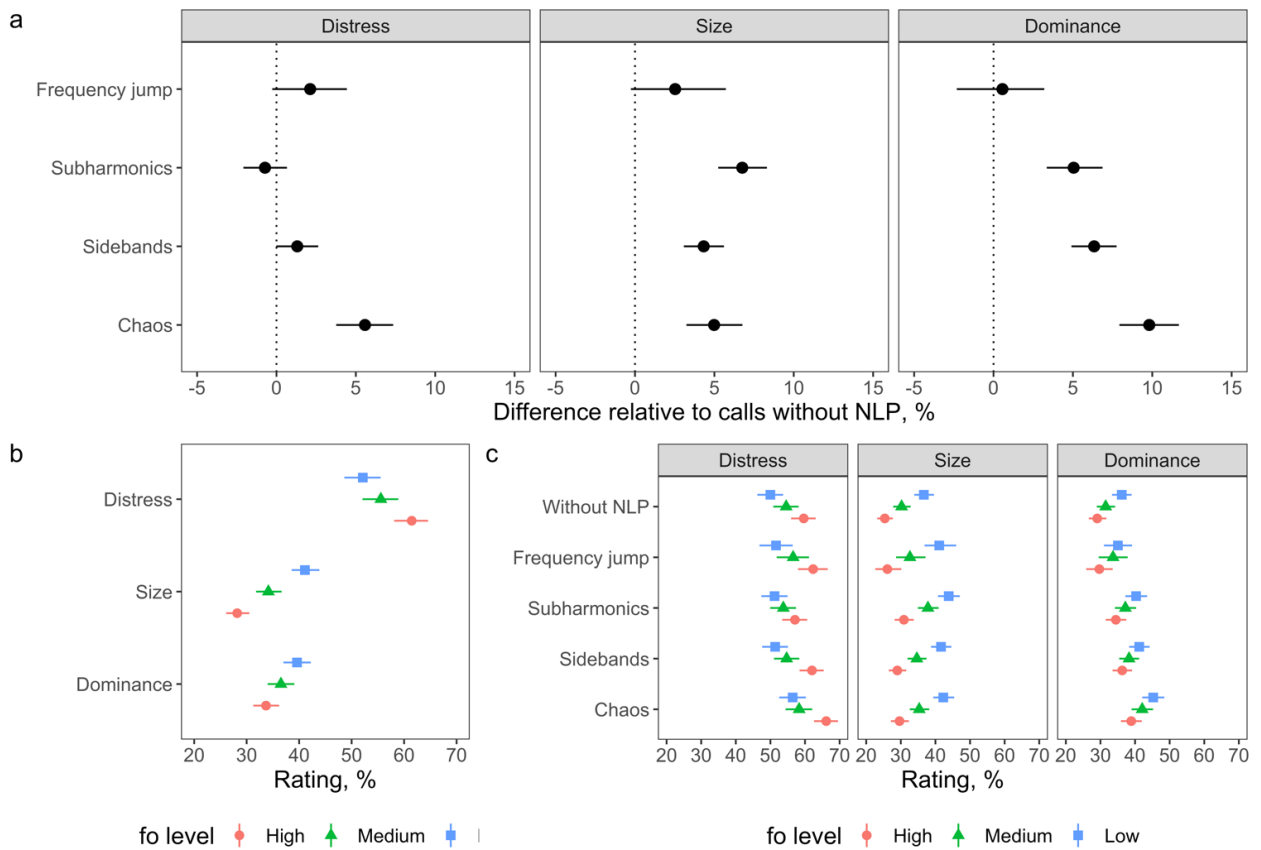
332 In addition to effects on perceived distress, our results show that the general population
333 (Experiments 1 and 2) rated size and dominance about 4% to 6% higher in whines containing
334 subharmonics, sidebands, or chaos, compared to whines without NLP (Fig. 2.a). However,
335 these effects were absent or limited in experienced puppy caregivers (Fig. S2.a).

336 We also predicted that increasing the duration of subharmonics, sidebands, or chaos from
337 50% to 80% of the whines' durations would reinforce their effects on perceived size and
338 dominance. Our results indeed show that whines containing 80% of subharmonics (but not
339 chaos and sidebands) increased perceived size by 6% [3.0, 8.9] and perceived dominance by
340 5.1% [2.3, 7.7] compared to the same whines with only 50% of these NLP (Fig. 3).

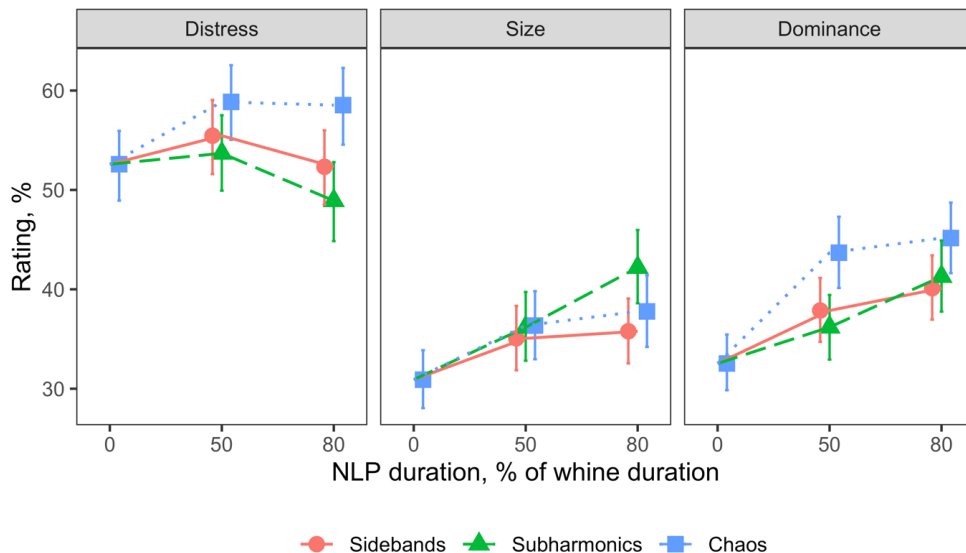
341 Finally, we found no interactions between NLP and f_o levels in the general population
342 (Fig.2c), instead confirming an independent effect of f_o on perceived size and dominance
343 (Fig.2b): whines with a lower f_o were systematically associated with larger (12.9% [14.1,
344 11.7]) and more dominant (5.9% [-7, -4.8]) sounding puppies, relative to the same whines
345 synthesized at higher levels of f_o . Similar results were found for experienced puppy
346 caregivers (Fig. S2.b and c).

347

348



349
 350 **Figure 2:** Main effects of (a) NLP, (b) f_0 , and (c) interactions between NLP and f_0 on perceived
 351 distress, size, and dominance (N=417, Experiments 1 and 2). Solid markers correspond to
 352 medians of posterior distribution with their 95% credible intervals.



353
 354 **Figure 3:** Effects of NLP duration on perceived distress, size, and dominance in Experiment 2
 355 (N=217). A duration of zero corresponds to whines without NLP. Solid markers correspond
 356 to medians of posterior distribution with their 95% credible intervals.

357

358 Discussion

359 We investigated the independent perceptual effects of nonlinear phenomena (NLP) that
360 occur naturally in a non-human animal vocalisation, namely in distressed puppy whines. By
361 applying an innovative method of parametric sound synthesis in the context of interspecific
362 vocal communication, we show that the presence and duration of different NLP types in
363 puppy whines generally increase their perceived distress, size, or dominance, as judged by
364 human listeners.

365

366 *Deterministic chaos increases perceptions of distress*

367 We found that the presence of chaos in puppy whines, but not the addition of frequency
368 jumps, sidebands, or subharmonics, increased perceptions of distress in human listeners
369 representing the general population. From a biomechanical perspective, the production of
370 NLP, particularly chaos, is typically associated with high subglottal pressure and strong
371 muscle tension on vocal folds [39] - configurations of the vocal apparatus that are likely to
372 arise in distressed animals with highly aroused physiological states [1]. Chaos is indeed a
373 characteristic of calls associated with distress in a wide range of mammals ([10,15,16,21,23],
374 this study). Additionally, at the perceptual level, Blumstein and Récapet (2009) [24] have
375 shown that white noise (which shares some perceptual elements with deterministic chaos
376 [50]) added to natural alarm calls of marmots induces potentially costly responses in these
377 animals (reduced foraging activity). An earlier study also showed that chaos added to
378 human nonverbal vocalisations increases the intensity of perceived negative, rather than
379 positive, affective states [51]. Together, our findings thus support that chaos is perceived as
380 a vocal indicator of higher levels of distress in mammals.

381 As increases in subglottal pressure, characterised by high amplitude and f_o , often lead to
382 vocal instability [3,39], NLP are expected to occur when f_o is relatively high. For instance, the
383 onset of NLP corresponds with the maximum f_o in chimpanzees' calls [40]. As such, it is
384 difficult to disentangle the effect of f_o from the effect of NLP when performing playback
385 experiments using natural calls [9,24,25], as these acoustic parameters may covary. To
386 overcome this limitation, we used synthetic stimuli varying in the presence and duration of
387 NLP at different f_o levels. While we confirmed that perceived distress increases

388 independently with f_o , as reported in numerous previous studies [41–44], the effect of NLP
389 on the perception of distress was relatively stable across all f_o levels. This suggests that
390 perceptual effects of f_o and NLP are independent and cumulative, and that both are salient
391 vocal indicators of distress.

392 Contrary to our prediction, whines containing relatively longer episodes of chaos did not
393 increase perceived distress compared to whines with less chaos, suggesting that a ceiling
394 effect may have been attained with chaos affecting only half of the call duration. Indeed,
395 listeners may have applied a categorical decision (no chaos = relatively low distress, chaos =
396 relatively high distress) when exposed to whines with or without chaos. Moreover, for
397 sidebands and subharmonics (whose presence did not affect perceived distress in the
398 general population), we found that perceived distress was lower in variants containing
399 longer episodes of these NLP. We suggest that bifurcations between the tonal and non-tonal
400 sections of the calls may be less salient in calls with a largely dominant non-linear regime. In
401 a recent study, we showed that subharmonics and sidebands added to human nonverbal
402 vocalisations lowered their perceived pitch [18]. As such, when exposed to subharmonics or
403 sidebands affecting 80% of the whine duration, listeners may have perceived these calls
404 with a relatively high tonality at a lower f_o and may thus have associated these lower-
405 pitched sounds with behavioural contexts of aggression, rather than distress. This would
406 follow Morton’s motivation-structural rules stating that aggressive animals typically produce
407 low-pitched sounds, whereas distressed, fearful animals produce high-pitched sounds [28].

408

409 *Nonlinearities increase perceptions of size and dominance*

410 Experimentally adding subharmonics, sidebands, and chaos - but not frequency jumps – to
411 whines increased the puppy’s perceived body size and dominance. Increasing the duration
412 of subharmonics further increased perceived size and dominance. These results are
413 consistent with recent work on human nonverbal vocalisations [18,32]. Our results also
414 confirm the well-established perceptual effect of f_o on size and dominance [45–47] – whines
415 with a relatively low f_o were systematically perceived as produced by larger and more
416 dominant-sounding puppies, independent of the effects of NLP on perceived size and
417 dominance. Although we show that f_o directly affects perceptions of size and dominance,
418 we cannot completely rule out the possibility that NLP independently lower the perceived
419 pitch of whines (as they do in human vocalisations) [18]. This pitch-lowering effect may thus

420 be one of the perceptual mechanisms whereby NLP cause puppies to sound larger and more
421 dominant. This prediction could be directly tested in future work by simultaneously
422 assessing the effect of NLP manipulations on auditory (pitch, timbre) and ecological
423 (distress, dominance, etc.) dimensions.

424 The pitch-lowering effect of NLP has been hypothesised as a possible strategy for animals to
425 exaggerate perceived size and dominance [4,5]. Indeed, frequency components such as
426 formant frequencies and/or f_0 mediate the vocal communication of size and dominance,
427 which are crucial factors affecting the outcome of social interactions, such as mating, sexual
428 competition, or territorial defence [2]. Many species have developed strategies to
429 exaggerate their apparent size and, potentially, also their dominance (reviewed in [27] and
430 [52]), with specific adaptations to their vocal apparatuses such as a descended and mobile
431 larynx [53]. Because there is no clear biological function for a puppy to sound larger and
432 more dominant to humans while producing a distress vocalisation, we suggest here that the
433 perceptual effects of NLP on size and dominance are likely the consequence of a general
434 perceptual bias linking “harsh” with “large and dominant” [18].

435

436 *Effect of experience on listener perception of puppy whines*

437 While infant distress calls conveying need to parents are ubiquitous in vertebrates [22], in
438 the context of domestication, these distress calls may also function to communicate need to
439 heterospecific caregivers. Indeed, human baby pain cries are often characterised by very
440 high levels of NLP [16] and human listeners pay attention to these acoustic features to
441 assess a baby’s level of distress and need [16]. As such, the production of whines, and within
442 them the production of NLP, may have been encouraged by dog domestication, with
443 puppies exploiting human sensitivity to chaos in offspring calls. Breeders indeed do
444 intervene and provide care to puppies [35], e.g. in the case of mother neglect, aggression, or
445 rejection [34]. Consistent with this, when asked to characterise how they react when
446 exposed to puppy whines in their normal professional activities, more than 50% of our
447 experienced puppy caregivers reported being negatively affected by whines, paying
448 attention to their harshness and roughness, and using these acoustic features as cues to
449 distress in order to adjust the level of care they provide to the puppies. Interestingly, while
450 experienced caregivers were as sensitive to chaos as the general population when rating
451 perceived distress, they also associated subharmonics and sidebands with higher levels of

452 distress (unlike the general population), as also observed in other species (e.g.,
453 subharmonics in meerkats: [9]). Together these results suggest that human sensitivity to
454 chaos, the most severe form of NLP, has a universal base when assessing distress in puppy
455 whines, but that sensitivity to other NLP can also arise with extensive experience. To further
456 investigate the possibility that domestication may have emphasised whining and NLP within
457 puppy whines as a consequence of sensory exploitation of caregivers (or as a consequence
458 of relaxed predation pressures [54]), future studies should contrast the production of NLP
459 within the whines of domestic dog puppies and wolf pups (*Canis lupus*).
460 Finally, NLP had little effect on perceptions of size and dominance in experienced caregivers,
461 suggesting that their extensive experience allows them to correct for the perceptual bias
462 identified in our general population. At the same time, experienced caregivers remained
463 sensitive to whine f_0 when assessing distress, size and dominance. This suggests that f_0 may
464 function as a reliable index of these traits in puppy vocalisations, as identified for distress
465 and size in adult dog whines [55,56]) and in the calls of other mammals [1,2], a hypothesis
466 that we are currently investigating.

467

468 *Perspectives*

469 It remains to be established whether NLP signal distress information in puppy-mother vocal
470 interactions, as they do to human listeners. Indeed, a recent study reports a positive
471 relationship between the level of jitter (“noisiness”) in natural distress puppy whines and
472 the strength of adult dogs’ behavioural responses [57]. Furthermore, although whines are
473 typically associated with distress contexts, the domestic dog’s vocal repertoire also includes
474 vocalisation types that are produced in both positive (e.g., playful) and negative (e.g.,
475 agonistic) contexts, such as growls or barks [58,59]. In addition to signalling relatively stable
476 physical attributes (e.g., size) [60], these vocalisations can vary acoustically between positive
477 and negative behavioural contexts [56,61]. For example, high-pitched and tonal barks are
478 produced in playful contexts whereas low-pitched and harsh, chaotic barks are more
479 commonly produced during territorial defence [56]. Nonlinear phenomena in barks or
480 growls may thus function to communicate aggressive intent (rather than play) and, in such
481 an agonistic context, may also function to exaggerate size and dominance. This prediction
482 may be tested in the contexts of both inter- and intra-specific vocal communication. We
483 thus suggest that using methods of parametric sound synthesis, as reported here, could be

484 generalised to a wider range of species and contexts to directly test the communicative
485 function of NLP in animal vocal communication.

486

487 **Ethics**

488 Acoustic recordings of puppies were performed under the ethical Approval no. E-42-218-
489 0901 (ENES lab agreement, Direction Départementale de la Protection des Populations,
490 Préfecture du Rhône). All human participants provided informed consent, and ethical
491 approval for performing perceptual experiments with human subjects was provided by the
492 Comité d’Ethique du CHU de Saint-Etienne (IRBN692019/CHUSTE).

493

494 **Data accessibility**

495 All audio stimuli, R codes for synthesizing stimuli, html code for running psychoacoustic
496 experiments, datasets as well as R codes for analysing data can be downloaded from
497 <https://osf.io/rp7m8/>.

498

499 **Author’s contributions**

500 All authors designed the study. M.M. collected the data; M.M. and A.A. created the stimuli
501 and performed the data analyses; M.M. wrote the original draft. All authors reviewed and
502 edited the manuscript and gave their final approval for publication; D.R. Supervised the
503 study.

504

505 **Competing interests**

506 The authors declare no competing interests.

507

508 **Funding**

509 M.M. and D.R. were supported by the University of Lyon IDEXLYON project as part of the
510 ‘Programme Investissements d’Avenir’ (ANR-16-IDEX-0005) to D.R. A.A. was supported by
511 grant 2020-06352 from the Swedish Research Council. D.R & N.M. were supported by the
512 Institut Universitaire de France. Funding was provided by LabEx CeLyA, CNRS, INSERM,
513 University of St-Etienne.

514

515 **Acknowledgments**

516 We thank Professor Alain Fontbonne for kindly putting us in contact with his network of dog
517 breeders. We also thank the dog breeders who allowed us to record puppies at their
518 facilities.

519

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