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Acoustic context and dynamics of nonlinear phenomena in mammalian calls: the case of puppy whines

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Nonlinear phenomena (NLP) are often associated with high arousal and function to grab attention and/or signal urgency in vocalizations such as distress calls. Although biomechanical models and *in vivo/ex vivo* experiments suggest that their occurrence reflects the destabilization of vocal fold vibration under intense subglottal pressure and muscle tension, comprehensive descriptions of the dynamics of NLP occurrence in natural vocal signals are critically lacking. Here, to plug this gap, we report the timing, type, extent and acoustic context of NLP in 12 011 whines produced by Beagle puppies (*Canis familiaris*) during a brief separation from their mothers. Within bouts of whines, we show that both the proportion of time vocalizing and the number of whines containing NLP, especially those with chaos, increase with time since separation, presumably reflecting heightened arousal. Within whines, we show that NLP are typically produced during the first half of the call, following the steepest rises in pitch (fundamental frequency, f_0) and amplitude. While our study reinforces the notion that NLP arise in calls due to instabilities in vocal production during high arousal, it also provides novel and efficient analytical tools for quantifying nonlinear acoustics in ecologically relevant mammal vocal communication contexts.

This article is part of the theme issue 'Nonlinear phenomena in vertebrate vocalizations: mechanisms and communicative functions'.

1. Introduction

While typically stable and periodic, vocal fold vibration can occasionally become irregular and lead to the production of *nonlinear phenomena* (hereafter NLP) [1,2]. These include four types of common acoustic perturbations, namely frequency jumps, subharmonics, deterministic chaos, amplitude modulation and biphonation [3,4], that are responsible for perceived vocal harshness, roughness and instabilities [5,6].

Nonlinear phenomena were initially described as nonadaptive vocal features or by-products of irregular phonation [3], often characterizing pathological human voices [7,8]. Yet, NLP are ubiquitous in the vocal repertoires of healthy humans (*Homo sapiens*) [1,9,10] as well as non-human mammals from various phylogenetic groups [11], including diprotodonts such as koalas (*Phascolarctos cinereus*) [12], rodents such as yellow-bellied marmots (*Marmota flaviventris*) [13,14], primates such as rhesus macaques (*Macaca mulatta*) [3] and chimpanzees (*Pan troglodytes*) [15], carnivores such as meerkats (*Suricata suricatta*) [16]), as well as artiodactyls such as North American elk (*Cervus canadensis*) [17] and cattle (*Bos taurus*) [18]. Nonlinear phenomena have also been identified in the vocalizations of several canid species, including African wild dogs (*Lycaon pictus*) [4], red wolves (*Canis rufus*) [19], dholes (*Cuon alpinus*) [20] and domestic dogs (*Canis familiaris*) [21–23]. These observations suggest that NLP probably play a key role in the vocal communication systems of mammals and have thus led to the formulation of several hypotheses to explain the possible communicative functions of NLP. For example, it has been proposed that they serve to grab listeners' attention [14,16,24] and/or provide cues to high arousal in contexts associated with physical pain [9,10,25,26], distress [14,23,27,28] or aggression [6], with the function to elicit aid or intimidate rivals.

Because the acoustic forms of animal vocal signals are likely to reflect their functions, understanding the mechanisms underlying the production of specific acoustic features is crucial for determining their communicative value [29,30]. Previous studies investigating the vocal production of NLP used *in vivo* or *ex vivo* high-speed observations of phonating larynges (as in elephants [31], red deer [32], dogs [33] and humans [8]) and/or biomechanical simulations of vocal folds (e.g. a two-mass model [34–36]). They showed that high subglottal pressure and/or strong muscle tension on the vocal apparatus, expected to arise during heightened arousal states [37,38], can lead to vocal instabilities [32–35]. More specifically, it has been demonstrated that increasing subglottal pressure can trigger acoustic bifurcations from simple periodic to more complex vibrations associated with NLP production [32,33,36]. Furthermore, antero-posterior or left-right asymmetries in the vocal folds, which can result from involuntary changes in muscle tensions in emotionally aroused animals [37,38], can also elicit aperiodic vibration (chaos) or period doubling (subharmonics) [8,33–35].

Critically, research in this area is hampered by a lack of knowledge regarding the actual acoustic contexts (i.e. the concurrent state of other acoustic features of the call) in which NLP occur within the natural vocal communication systems of animals. Indeed, the findings from biomechanical modelling and *in vivo* or *ex vivo* experiments with phonating larynges suggest that the occurrence of NLP in calls is unlikely to be random. On the contrary, NLP within calls or within long vocal sequences may covary with other acoustic features, such as fundamental frequency (f_o, corresponding to the rate at which vocal folds vibrate), amplitude or duration [2]. Indeed, high arousal is likely to be associated with the production of long calls with high subglottal pressure leading to high f_o and amplitude [2], making calls higher-pitched and louder, as reported in alarm or distress calls of several mammal species, such as the distress calls of infant elephants [27] or infant giant pandas [28] (also reviewed in [37,38]). In such contexts, f_o (or the first harmonic) can sometimes cross the first formant frequency (vocal tract resonance), leading to nonlinear interactions between the larynx (vocal source) and the supra-laryngeal vocal tract (vocal filter) that eventually cause the production of NLP (reviewed in [39]). Nonlinear phenomena are thus expected to occur in relatively high-pitched vocalizations—a hypothesis supported by investigations of chimpanzee panthoot vocalizations and hyena *Crocuta crocuta* whoop vocalizations, where NLP occur when f_o is at its maximum [15] or close to the first formant [40].

Yet, systematic and comprehensive descriptions of the timing, type, extent and acoustic context of NLP remain rare and limited in scope. Such an understanding would enable researchers to connect the mechanisms underlying NLP production to their acoustic forms in animal calls and to ground functional hypotheses, such as the communication of high arousal, in strong physiological and behavioural foundations.

Here, to plug this gap, we provide a comprehensive description of the temporal distribution of NLP and of the acoustic context in which they occur (i.e. f_o, amplitude and duration of calls), using whining in domestic dog puppies as an experimental model. Nonlinear phenomena have been documented in the vocalizations of a wide range of canids [19,20], including the whines of both adult dogs [21,22] and puppies [23]. In adult dogs, it has been suggested that NLP may grab the owner's attention, for instance, when a dog is experiencing frustration [22], and/or NLP may reflect high arousal of the vocalizer in contexts associated with distress, for instance, when a dog is separated from its owner [21]. Importantly, like in adult dogs, puppy whines, which are also emitted in distress contexts such as during separation from their mother [41], often contain a large amount of NLP, such as frequency jumps, subharmonics and chaos (figure 1). In addition, whines can contain *biphonation*, which involves the simultaneous production of two frequencies that are independent and not harmonically related. The lower of these two frequencies (f_o) is laryngeal, whereas the higher frequency g_o is presumably produced by other mechanisms (e.g. an aerodynamic whistle [22,43]). Low *amplitude modulation* can also occur in puppy whines and typically results from the modulation of the laryngeal f_o by a much lower frequency j_o (presumably produced by a supralaryngeal source; see figure 1). Finally, similar to the distress vocalizations of several other mammalian species [38,44], whines are produced in sequences, and some of their acoustic features can vary dynamically with arousal, including variations in whine duration, amplitude and/or f_o (figure 1e).

We recorded the whines of Beagle puppies aged one, three, six and nine weeks ($n = 32$ puppies from six litters) during a short separation from their mother and littermates. We then extracted 12 011 whines, annotated NLP episodes (i.e. frequency jumps, subharmonics, chaos, amplitude modulation and biphonation) and measured key vocal characteristics, including the f_o, the amplitude and the duration of calls. This approach allowed us to experimentally test three key predictions based on the current state of knowledge about the mechanisms of NLP production and their functions in the vocal communication system of mammals:

(1) NLP are expected to occur in regions of the whines where amplitude and laryngeal f_o reach their maxima (e.g. as in chimpanzee pan-hoots [15] or hyena whoop vocalizations [40]), and thus, where the vocal system of puppies is predicted to be relatively unstable.

(2) NLP production should increase over the separation period along with the average f_o and duration of whines as puppies are expected to gradually become more aroused and push their vocal system into overdrive.

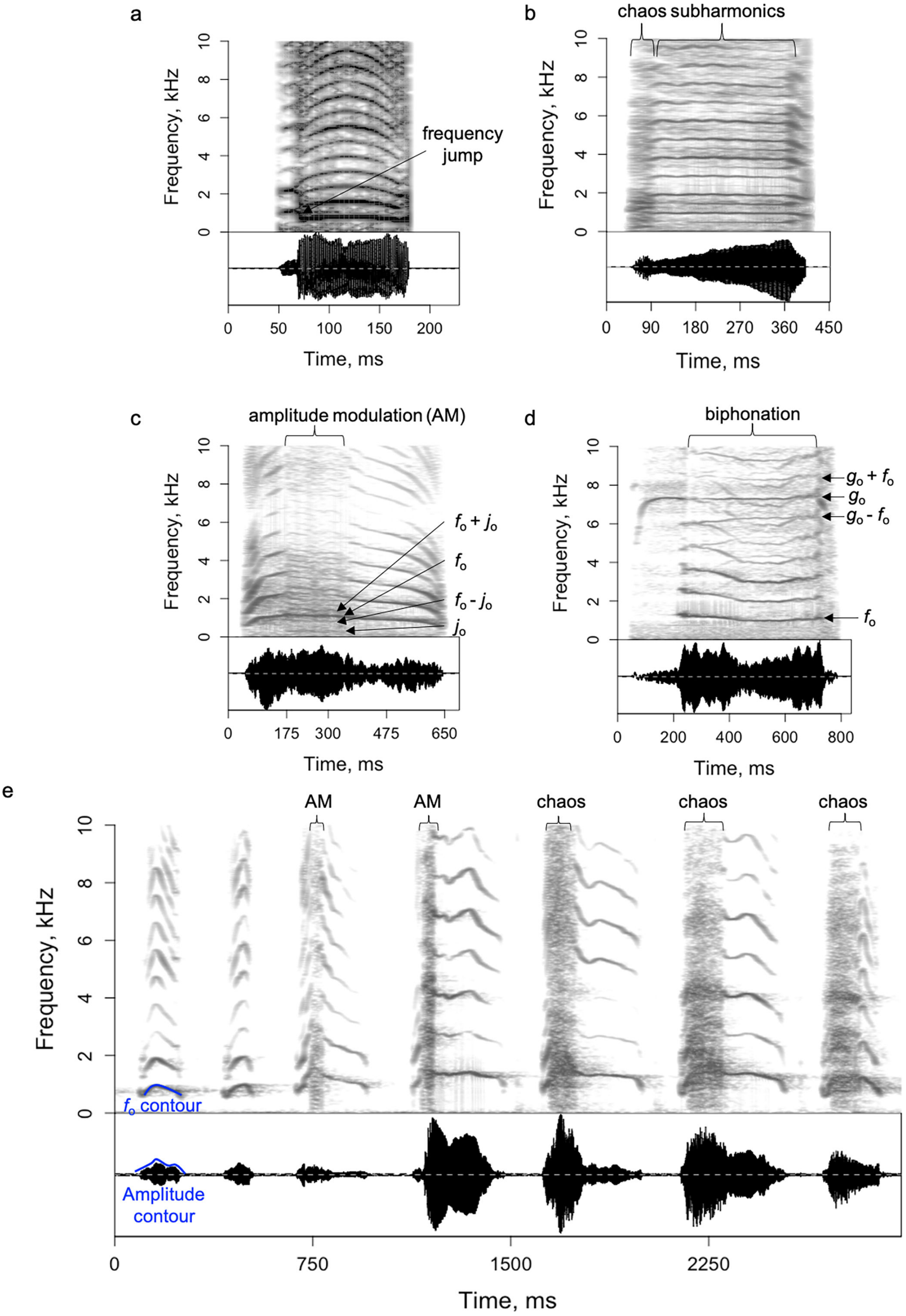

Figure 1. Examples of NLP occurring in puppy whines. Panel (a) illustrates an example of a whine containing a downward frequency jump. Panel (b) corresponds to whines characterized by a combination of two different types of NLP, chaos and subharmonics. Panels (c) and (d) show clear examples of amplitude modulation and biphonation, respectively. Sidebands are visible at a linear combination of $m^* f_0 \pm n^* j_0$ (f_0 higher than j_0 for amplitude modulation) or $m^* g_0 \pm n^* f_0$ (g_0 higher than f_0 for biphonation) where m and n are integers. Note in (e) an increase in whine duration, amplitude and f_0 coinciding with the production of NLP. Spectrograms were generated with the *spectrogram*() function from *soundgen* R package [42].

(3) NLP are expected to be more common in the whines of newborn puppies (compared with those of two-month-old puppies) as newborns are more vulnerable [45] and thus more likely to respond more strongly to a separation event.

2. Material and methods

(a) Recordings of puppy whines

We recorded whines produced by Beagle puppies (n = 32 individuals from six litters) during a short separation from their mother and littermates. Whines were recorded between March 2019 and February 2020 at two different breeding facilities (Ecole Véterinaire Maison-Alfort and Elevage des Pins de Meluzzine, both in France), where females and their litters are kept in the same enclosure during the first two months of puppies' lives. For each individual, whines were recorded at two to three of four different ages (one, three, six or nine weeks). One individual, who almost never whined, was excluded from the analyses to keep the number of calls comparable across individuals.

Each individual was carried to a separate room, placed alone in a pen (roughly 100 cm × 50 cm) and recorded for a maximum of five minutes (mean ± s.d. = 3.5 ± 2 min) using a Sennheiser MKH70 directional microphone connected to a Zoom H4n audio recorder (44.1 kHz, 24 bit). The microphone was positioned approximately 30 cm from the animal's mouth. To avoid saturation of acoustic signals, when necessary, the input level was adjusted during the recording. While this prevented us from measuring variation in whine amplitude across sequences as time since separation increased, we could still measure amplitude variation within individual whines.

At the end of each recording trial, puppies were immediately reunited with their mother. All puppies displayed normal behaviours upon being reunited, including suckling or interacting with their mother and littermates, indicating that any stress experienced during the recording had been low and temporary. No puppies showed signs of distress (e.g. excessive panting, yawning, lip licking [46,47]), which otherwise would have led to the immediate interruption of the trial. The mothers in this study were habituated to being temporarily separated from their litter (e.g. during daily walks) and accustomed to breeders manipulating puppies during daily care (e.g. weight measurements evaluating the physical condition of puppies). As a consequence, mothers did not display any signs of stress during separations from their puppies for individual recordings.

(b) Acoustic analyses

Our acoustic analysis of whines included the following steps: (i) extraction of individual whines from recordings, (ii) manual annotation of NLP, namely frequency jumps, subharmonics, chaos, amplitude modulation and biphonation, and (iii) measurement of key acoustic parameters, namely the f_0, the amplitude and the duration of extracted whines (electronic supplementary material, table S2). Our original pool of recordings consisted of 125 full-length audio recordings, each containing hundreds of individual whines. From this pool, we selected 68 recordings from a total of 31 individual puppies from six different litters to create a balanced dataset across ages (17 recordings per age class; electronic supplementary material, table S1).

The authors agreed on a nomenclature after discussing the inspection of a subsample of spectrograms. M.M. then visually inspected spectrograms of all 12 011 whines in Praat v. 6.1.26 [48] (Gaussian window, window length = 0.01 s, dynamic range = 100 dB), annotated the onset and offset times of all whines and classified them into whines without NLP (n = 6995) and whines with NLP (n = 5016). Whines were then extracted using the function *segment()* from the soundgen R package v. 2.6.2 [42] that allows their semi-automatic detection. Because the level of background noise slightly changed across recordings, settings related to the proportion of noise or to the silence-to-noise ratio were adjusted in order to improve the performance of the algorithm. Finally, M.M. manually annotated 7178 NLP episodes in the 5016 whines identified to contain one or several episodes of NLP.

All extracted whines were further acoustically analysed with the function *analyze()* (soundgen R package) to measure their f_0 and amplitude contours. Because the presence of NLP in calls can lead to f_0 tracking errors, we supervised the extraction of f_0 contours in whines that contained NLP by using the online *pitch_app* tool (soundgen R package). This was not necessary for whines without NLP, from which f_0 extraction was performed automatically. Indeed, when verifying the reliability of manual versus automatic extractions of f_0 contours on a subset of 500 whines without NLP, we found a nearly perfect correlation between these two methods (Pearson's correlation r = 0.99).

(c) Statistical analysis

We conducted our statistical analyses using Bayesian multilevel models and generalized additive models (see below for details of each model and electronic supplementary material, table S3 for their syntax). In all Bayesian multilevel models, the puppy identity was modelled as a random factor to account for multiple measurements on the calls produced by the same individual.

Our first aim was to provide a comprehensive description of whines containing NLP (models 1–7 in electronic supplementary material, table S3). To achieve this, we used Bayesian multilevel models to investigate whether the duration of NLP in whines (absolute and relative durations, modelled as lognormal response variables) varied across the different types (models 3–4 in electronic supplementary material, table S3). We also analysed the position of NLP within individual whines with a Bayesian generalized additive multilevel model that evaluated the probability of finding NLP (modelled as a 0/1 response variable) within each temporal bin of calls, with a separate smoothing function for each type of NLP (model 5 in electronic supplementary material, table S3). Finally, because NLP are typically produced in relatively high and loud calls [15,27,40,49,50], we ran two generalized additive models to examine which acoustic changes (f_0 and amplitude) preceded the onset of NLP within whines. The outcome variable in these models encoded whether or not an episode of NLP commenced in a particular frame as a smooth function of f_0 or amplitude in this frame and their slopes in the preceding frame, again separately for each type of NLP (models 6—7 in electronic supplementary material, table S3 for amplitude and f_0, respectively).

Our second aim was to investigate how the vocal production of whines and their acoustics vary with increasing time since the puppy's separation from its mother. To test whether the whining activity of puppies increased with time since separation, we used a Bayesian multilevel model to assess the presence of any whine as a linear function of time since separation (modelled as temporal bins over the separation period; model 8 in electronic supplementary material, table S3). In this model, we also controlled for possible age variation in puppy whining activity. In addition, because we expected to find more NLP as a puppy's distress mounted, we modelled the type of whine (i.e. whine without NLP, with a single type of NLP, with a combination of NLP) as a categorical response variable (model 9 in electronic supplementary material, table S3) and the probability of finding each type of NLP as a smooth function of time since separation (models 10–11 in electronic supplementary material, table S3). Finally, to verify the prediction that f_0 and duration of whines would increase with time since separation, we fitted Bayesian models with these two acoustic parameters as response variables (modelled as a Gaussian distribution; model 12 in electronic supplementary material, table S3).

Our last aim was to describe how NLP change with development, from birth to two months of age. We thus ran a Bayesian multilevel model examining the relationships between the production of NLP in whines (presence/absence) and the puppy's age (model 13 in electronic supplementary material, table S3).

Bayesian multilevel models were fitted with the *brms* R package (*brm()* function) using default priors [51]. A total of 4000 iterations were run over two Markov Chain Monte Carlo chains. These iterations included 500 warm-up iterations to improve the convergence of each model and thus their prediction. We verified the convergence of each model, evaluating that rhat values were approximately 1 and ESS values were approximately 2000 [52]. For each model, we also visually inspected that *observed* and *a posteriori* predictions overlapped using the function *pp_check()* (brms R package) [52]. Generalized additive multilevel models were fitted with the *mgcv* R package (*gam()* function [53]). Our results are summarized by the medians and 95% credible intervals (CIs) calculated on the posterior distributions of the effects of interest. Summary tables for all reported models and convergence checks are available at https://osf.io/qfdup/ in the folder 'analysis_html'.

3. Results

(a) Acoustics of whines with nonlinear phenomena

We found that puppy whines include all key types of NLP, namely frequency jumps, subharmonics, chaos, amplitude modulation and biphonation. Chaos and frequency jumps were the two most common types, occurring in 37% and 36.5% of calls, respectively. In comparison, subharmonics, amplitude modulation and biphonation were less common: they were present in 26.5%, 17.7% and 15.9% of whines with NLP, respectively. Furthermore, while in most cases NLP occurred as a single episode (n = 3351 out of 5016 whines with NLP), we also found that 1665 whines contained multiple NLP episodes, ranging from two to six episodes per whine, most commonly with different NLP types (1450/1665). Specifically, we identified 78 different NLP combinations in puppy whines, the most common of which was chaos followed by subharmonics after about 150 ms [124.6, 179.6] (n = 291 out of 1450 whines; models 1–2 in electronic supplementary material, table S3, also see electronic supplementary material, table S4 and figure S1a). As frequency jumps are discrete and instantaneous events, we did not measure their duration. While in most cases f_0 jumped down, on average by −245.2 ± 153.2 Hz (mean ± s.e.) (corresponding to −3.9 ± 2.6 semitones), it also jumped up, on average by 205.1 ± 157.9 Hz (mean ± s.e.; corresponding to 3.1 ± 2.1 semitones) (electronic supplementary material, figure S2). When present, the different types of NLP affected variable proportions of the whine: biphonation affected more than half of its duration (57% [53, 62]), whereas episodes of subharmonics, amplitude modulation and chaos were shorter (i.e. 26% [24, 28], 26% [24, 28] and 34% [31, 37] of call duration, respectively; model 4 in electronic supplementary material, table S3 and figure S3b). Absolute durations of NLP within whines averaged 61 ms [56, 65] for amplitude modulation, 64 ms [60, 69] for subharmonics, 82 ms [76, 88] for chaos and 114 ms [105, 124] for biphonation (model 3 in electronic supplementary material, table S3 and figure S3a).

(b) Nonlinear phenomena co-occur with increases in f_0 and amplitude within whines

We investigated the temporal dynamics of NLP within individual whines and found that NLP often occurred early in whines, typically during the first half. Indeed, the posterior probability of NLP occurrence peaked sharply at 10% of a whine's duration for frequency jumps. The distribution of other NLP across the duration of a typical whine was more uniform, but their probability also reached its maximum in the first half of a whine, at 14% (from the beginning of whines) for subharmonics, 29% for amplitude modulation, 35% for chaos and 40% for biphonation (model 5 in electronic supplementary material, table S3 and figure S4).

As reported in chimpanzee pant-hoot calls [15] or hyena whoop vocalizations [40], we expected NLP to occur in calls when both amplitude and f_0 of whines would have reached their maxima. Our results partly support this prediction, as we found that NLP typically occurred when the amplitude and f_0 of whines were rising (before reaching their maximum values; figure 2a,b), which possibly reflects instabilities in the puppy vocal apparatus. In addition, f_0 slopes were also steeper in whines containing NLP than in those without (figure 2b), indicating that the stronger increase in f_0 might favour stronger destabilizations in the vocal system of puppies when they produce calls with NLP.

In line with our above observations, when mapping whines' variation in amplitude (i.e. amplitude slope) before the onset of NLP, we also found that NLP were often preceded by rising amplitude (model 6 in electronic supplementary material, table S3, figure 2c). As for f_0 variation, NLP typically occurred just after an episode of rising f_0 (model 7 in electronic supplementary

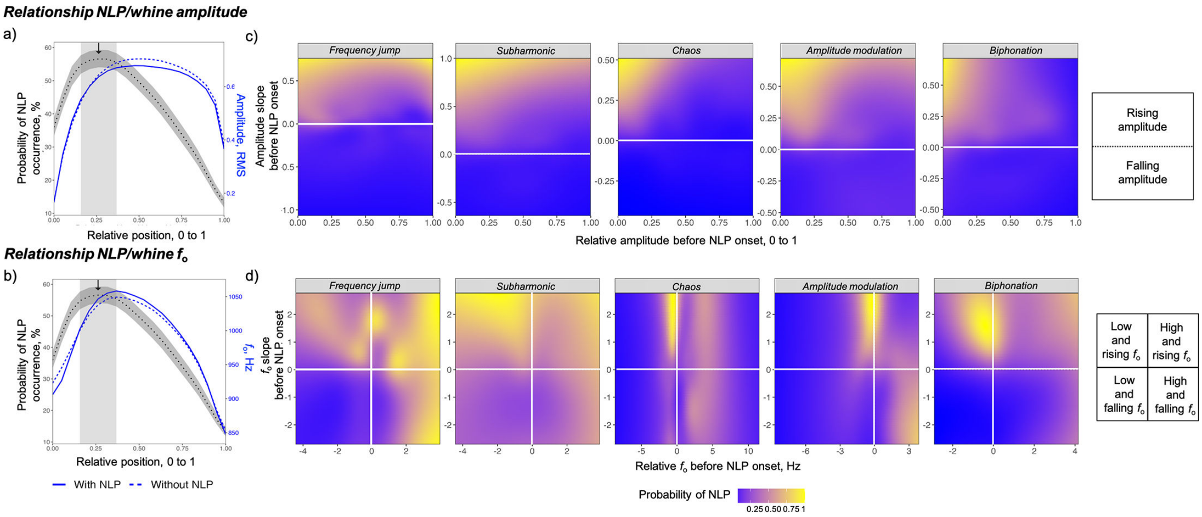

Figure 2. Acoustic correlates of NLP occurrence within whines. Average (a) amplitude contours and (b) f_0 contours in whines with NLP (blue dashed lines) and without NLP (blue solid lines), and the probability of NLP occurrence (black dotted lines). Each line corresponds to fitted values extracted from the posterior distribution. The shaded rectangle shows the highest density interval of NLP posterior probability, corresponding to the region in which NLP most commonly occur in whines. The arrow indicates where, in an average whine, NLP occur with the highest probability. Panels (a) and (b) show that NLP occur while amplitude and f_0 slopes are at their steepest rising phase, just before they peak. This observation is confirmed by our model predictions (models 6–7 in electronic supplementary material, table S3) represented in panels (c) and (d). Panels (c) and (d) show the probability of NLP occurrence modelled as a smooth function of (c) amplitude or (d) f_0 and its slopes just before the onset of NLP. Overall, NLP have the highest probability to occur immediately after a rapid increase in the amplitude and f_0 of whines (yellow regions).

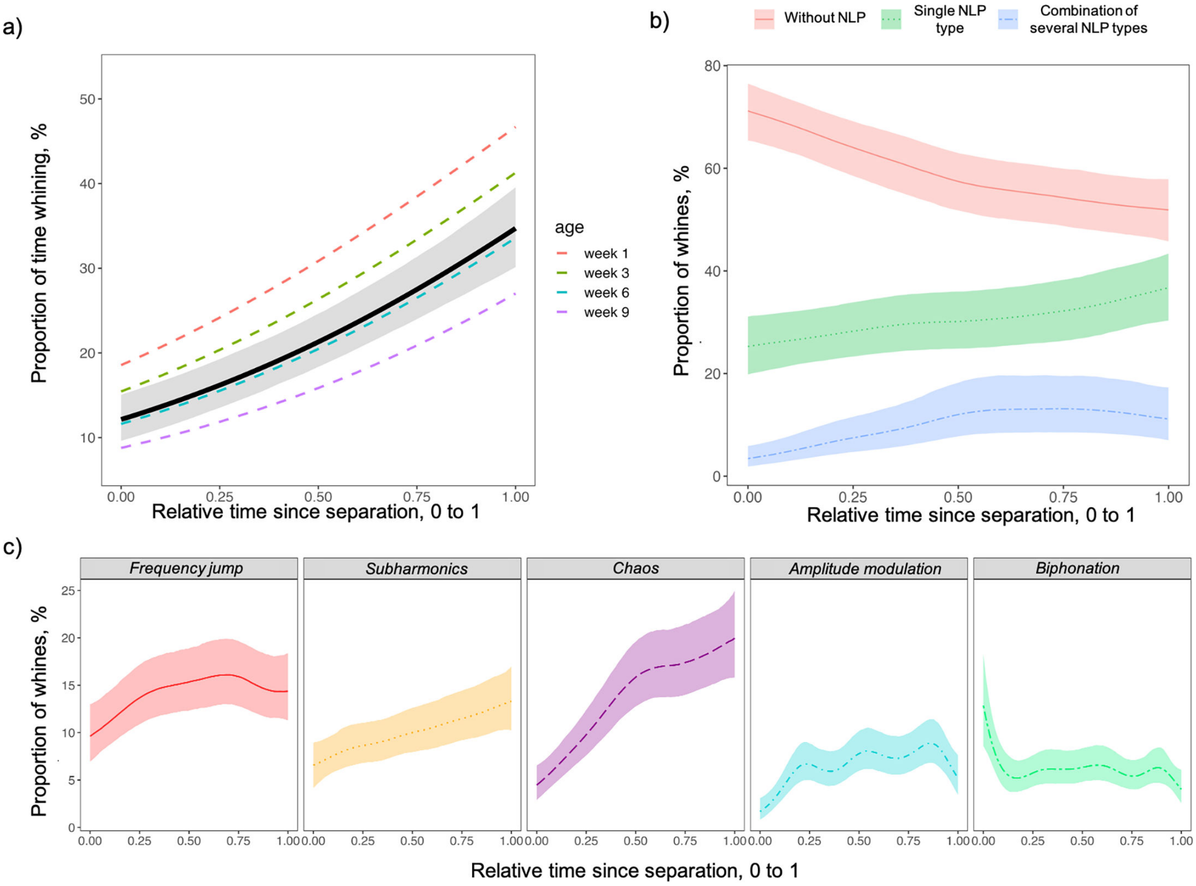

Figure 3. Production of whines with and without NLP since puppy separation from the mother. Because the duration of separation varied by ± 2 min between individuals, we converted the absolute time of separation as a relative time ranging from 0 to 1. Lines correspond to fitted values extracted from the posterior distribution, and ribbons indicate 95% credible intervals (models 8–10 in electronic supplementary material, table S3). In panel (*a*), the black solid line corresponds to fitted values averaged across all puppy ages, whereas the coloured dashed solid lines show model predictions for each age class. We found an overall increase in the production of whines with time since separation, although older puppies spent 21% less time whining compared to younger puppies (model 8 in electronic supplementary material, table S3). This general intensification of whining is accompanied by an increase in the production of whines containing NLP (a single type or a combination of several) (see panel b, model 9 in electronic supplementary material, table S3), particularly those containing chaos, frequency jumps and subharmonics (see panel c, model 10 in electronic supplementary material, table S3).

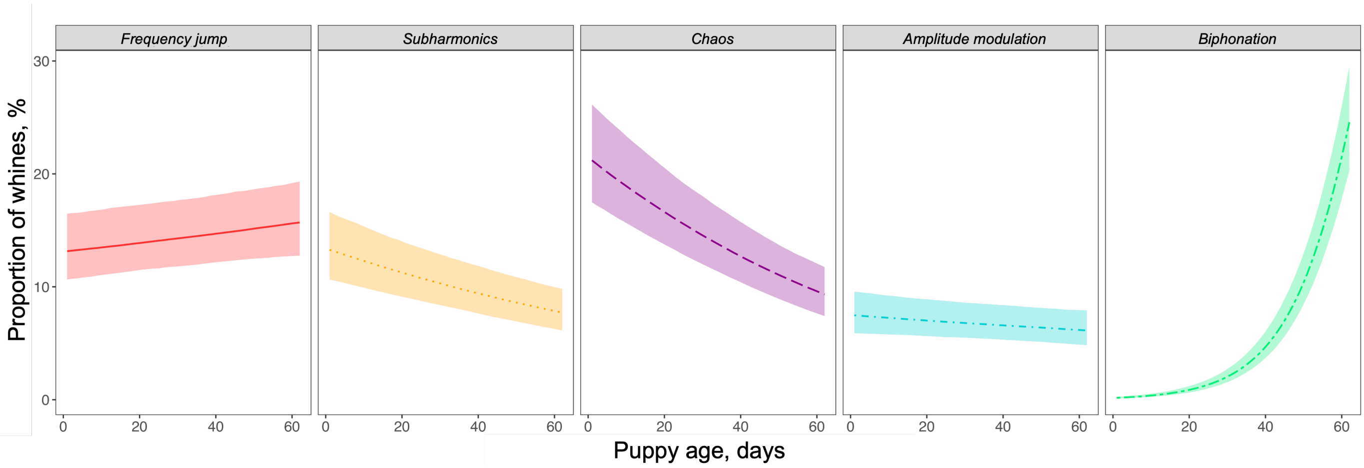

Figure 4. Ontogeny of whines containing NLP expressed as the proportion of whines with at least one episode of NLP. Lines correspond to the fitted values extracted from the posterior distribution, and ribbons to the 95% credible interval (model 13 in electronic supplementary material, table S3). This figure shows that the proportion of whines containing subharmonics and chaos decreased over puppies' development, whereas the occurrence of biphonation increased with age.

material, table S3, figure 2d). The main exception was frequency jumps, which could appear in two different 'scenarios', preceded either by a relatively high and rising f_0 or by a relatively high and falling f_0. Finally, while f_0 was usually rising just before the onset of subharmonics, chaos, amplitude modulation and biphonation, absolute f_0 values did not considerably differ from the average f_0 of whines before the onset of chaos, amplitude modulation and biphonation. In contrast, f_0 values preceding subharmonics could be either lower or higher than average f_0 (figure 2d).

(c) Nonlinear phenomena in whines increase with time since separation, but f_0 and duration remain stable

We found that whining increased the longer the puppies were separated from their mother and littermates (model 8 in electronic supplementary material, table S3, figure 3a). Indeed, whines with NLP occurred more often towards the end of a separation period, thus explaining why the proportion of whines without NLP decreased with time since separation (model 9 in electronic supplementary material, table S3, figure 3b). Specifically, while the proportion of whines without NLP decreased during separation (odds ratio at the end versus the beginning of a recording session = 1.2 [1.1, 1.4]), the proportion of whines containing a single type of NLP or a combination of several types of NLP increased (odds ratio = 1.2 [1.1, 1.4] and 2.9 [2.0, 4.4], respectively). This was mainly driven by an increase in chaos (odds ratio = 3.7 [2.7, 5.5]) and, to some extent, by an increase in amplitude modulation, subharmonics and frequency jumps (odds ratio = 3.0 [1.6, 6.0], 1.9 [1.5, 2.8] and 1.4 [1.1, 1.9], respectively) from the beginning to the end of the separation period (model 10 in electronic supplementary material, table S3, figure 3c). In contrast, the proportion of whines containing biphonation rapidly dropped from 12.9% [8.6, 18.3] to 5.2% [3.8, 7.1] at the beginning of the separation period and then remained relatively stable until the end (model 10 in electronic supplementary material, table S3, figure 3c). Furthermore, although we predicted that proportions (or durations) of NLP affecting whines would increase during separation, we did not find noticeable changes in NLP durations over time (model 11 in electronic supplementary material, table S3 and figure S5).

We also investigated whether other acoustic parameters of whines varied with separation time. We predicted higher f_0 and longer duration in whines produced towards the end of separation than those produced at the beginning. Unexpectedly, we found no change in whine f_0 (4.3 Hz [−172.3, 106.7]) or duration (6.3 ms [−118.4, 63.0]) between the beginning and the end of recording sessions (model 12 in electronic supplementary material, table S3 and figure S6).

(d) The production of nonlinear phenomena changes with puppy age

Because our dataset includes whines produced by puppies at different ages (electronic supplementary material, table S1), our final aim was to investigate how the whining behaviour associated with NLP production varied with age during the first two months of puppies' lives.

While we found an increase in the puppies' vocal activities over the separation period, which was held for each age class (one, three, six and nine weeks of age), there was also a noticeable effect of age on the intensity of whining behaviour. One-week-old puppies exhibited stronger whining behaviour, spending 21% [14, 29] more time vocalizing compared to nine-week-old puppies (model 8 in electronic supplementary material, table S3; figure 3a). In addition, NLP occurrence decreased from birth to two months of age with an odds ratio of 0.6 [0.5, 0.7] and 0.5 [0.4, 0.6] for whines containing subharmonics and chaos, respectively (model 13 in electronic supplementary material, table S3; figure 4). In contrast, the proportion of whines affected by biphonation increased greatly from one to nine weeks of age (odds ratio of 107.9 [73.8, 157.8]). The occurrence of frequency jumps and amplitude modulation in whines, however, tended to be stable throughout the first two months of puppies' development, as their respective odds ratios were relatively close to 1 (odds ratios for week nine versus week one: 1.2 [1, 1.3] for frequency jumps and 0.8 [0.7, 1] for amplitude modulation).

4. Discussion

Using fine-grained acoustic and statistical analyses, we quantified the within-sequence and within-call temporal distribution of nonlinear phenomena (NLP) and described the acoustic context in which they occur, using an unprecedentedly large set of over 12 000 puppy whines. Our results provide further support for the contention that NLP, which make vocalizations sound harsh and rough [5,6], are vocal indicators of high arousal (here in a behavioural context associated with distress), as indicated by biomechanical models and *in vivo*/*ex vivo* investigations of the mechanisms of NLP production [8,31,33–36,54].

(a) Do nonlinear phenomena occur within whines when f_0 and amplitude peak?

Partly. We found that NLP commonly occur in the first half of the whine, often after a rapid rise in f_0 and amplitude, just before they peak. A possible explanation for the timing of NLP within whines can be related to subglottal pressure. Indeed, increasing subglottal pressure typically leads to an increase in vocal fold vibration rates until they are eventually destabilized [31,33]. This is often observed during the production of loud, high-frequency calls that can contain NLP [15,27,40,49,50]. As such, these mechanistic predictions based on biomechanical modelling and *in vivo*/*ex vivo* experiments suggest that the rapid increase in f_0 and amplitude preceding NLP occurrence in whines may reflect strong increases in the puppies' subglottal pressure, which drives their vocal folds from stable, periodic oscillations to unstable, aperiodic vibrations. In addition, it is also possible that whine f_0 coincides and reaches values close to the first vocal tract resonance (formant) and creates interactions between the vocal source (i.e. larynx) and the vocal filter (i.e. supra-laryngeal vocal tract) [39], as, for instance, suggested in spotted hyena vocalizations [40]. Yet, because puppy whines are high-pitched vocalizations, we could not reliably measure formant frequencies in these calls. Future work could predict the position of vocal tract resonances using morphological data, for instance, from CT imaging (as in [55]).

(b) Does the production of nonlinear phenomena increase with time since separation and correlate with the f_0 and duration of whines?

Partly. We found that the proportion of whines containing NLP (except biphonation) increased over the separation period independently of variation in whine f_0 and duration, which remained stable. This observation suggests that NLP in calls produced in a negatively valenced context may be stronger vocal cues to high arousal than f_0 or duration. This is consistent with several studies in which the pain cries of human babies emitted during vaccination contained more NLP [25], but did not have a higher f_0 or longer duration compared to discomfort cries emitted, for example, during a bath [10,56]. In addition, the observation that f_0 does not increase with putative arousal may be a consequence of NLP occurring systematically when f_0 approaches a threshold close to its observed maximum value and that this threshold is reached more often in higher arousal whines emitted towards the end of the separation period. In other words, the vocal apparatus of highly aroused puppies may reach its limits for stable phonation, leading to the production of NLP rather than to a further increase of f_0.

More specifically, we found that the increase in the proportion of whines containing NLP was disproportionately driven by chaos. While this may be a byproduct of the effect of high arousal on vocal production, it may also reflect an adaptive specialization of distress calls to exploit receiver perception and to communicate urgency. Indeed, perceptual studies show that the presence of chaos in synthetic puppy whines strongly increases assessments of distress levels by human listeners [23]. Interestingly, while we show that the proportion of whines with chaos increased with time since separation, its duration within whines remained stable, here again, consistent with previous observations that perceived distress by human listeners is affected by the presence, but not the duration, of chaos events in puppy cries [23]. Chaos—a key contributor to perceptual harshness or roughness [6]—may also be selected in distress calls for its attention-grabbing and/or habituation-limiting properties [24].

Interestingly, in puppies older than one month, we also found that the production of whines containing biphonation first quickly dropped as the puppy started whining and then remained stable until the end of the separation period. In canids, this type of biphonation (i.e. when f_0 modulates a higher g_0) is common and often occurs in behavioural contexts associated with attention-seeking or frustration [19,22,57]. We propose that biphonation may serve to grab receivers' attention at the beginning of a separation period and that the later production of relatively more perceptually harsh types of NLP, particularly chaos [6], may reinforce this attention-grabbing effect and signal a higher level of urgency.

Finally, a non-exclusive explanation as to why the occurrence of NLP increases with the time since separation might be short-term vocal fatigue, as has been suggested in chimpanzee pant-hoots [58] and indri songs [59,60]. However, the fact that we observed a continuous increase in vocal activity, combined with the fact that the proportion of whines containing NLP was mainly driven by an increase in the presence of chaos (typically associated with high subglottal pressure [33]), suggests that the reported increase in NLP was mainly a consequence of heightened arousal rather than fatigue.

(c) Does the production of nonlinear phenomena change with age?

Yes. As reported in several mammals [61–63], we also found that the production of NLP varied with puppy age (with the exception of frequency jumps and amplitude modulation). During the first two months of puppies' lives, biphonation increased after six weeks of age, whereas chaos and subharmonics decreased as puppies aged.

In canids, biphonation typically corresponds to the production of high-frequency whistles that occur simultaneously with ordinary, laryngeal whines [4,21,43,64]. While in several mammal species biphonation involves the vibration of specialized anatomical structures, such as vocal membranes in bats and some primate species [65,66], in a closely related canid, the dhole, this phenomenon results from the vibration of supra-laryngeal vocal structures that do not appear to have specifically evolved to support it [43]. Specifically, these supra-laryngeal structures vibrate when subglottal pressure is relatively high [67], which corroborates our observation that biphonation occurs in the highest frequency whines compared with those containing other types of NLP (electronic supplementary material, figure S7). We suggest that the absence of biphonation in whines produced by younger puppies may be due to their relatively small lung capacities: newborn puppies may not be able to efficiently increase their subglottal pressure to produce vibration of the second supra-laryngeal sound source.

Finally, we suggest that the decreasing production of chaos and subharmonics with age may reflect the maturation of neuro-motor control, accounting for the high rate of nonlinear dynamics in vocal fold vibrations (responsible for chaos and subharmonics, as in human babies [1]) and for the absence of vibrations in the supra-laryngeal vocal structures (responsible for biphonation) in newborn puppies. Alternatively, because newborn puppies also whined more than older puppies as time since separation increased, their higher production of chaos and subharmonics could also reflect higher distress levels experienced by newborn puppies. Indeed, puppies are born blind, deaf and without a fully functional thermoregulation system, making newborns more vulnerable and thus more reliant on their mothers' care than weaned puppies of nine weeks of age [45,68]. The intensity of whining, including the presence of NLP, may thus inform mothers, who are highly sensitive to whines [69], about the urgency of their puppies' needs [23]. Future studies could use playback experiments, exposing mothers to synthetic offspring calls with or without NLP, to experimentally test the communicative functions of NLP as possible vocal cues to high urgency in the context of mother–offspring vocal interactions.

5. Conclusion

As predicted by *in vivo*/*ex vivo* experiments and biomechanical modelling, our results indicate that the production of nonlinear phenomena within calls and in whining sequences reflects increasing distress. We suggest that, as such, NLP are prime candidates for the vocal communication of high arousal, particularly in negatively valenced vocalizations such as distress whines of puppies. Indeed, the non-random, graded combination of biphonation, amplitude modulation, frequency jumps, subharmonics and chaos may constitute a complex system for the communication of increasing arousal. Such a communicative function is already supported by perceptual studies involving human listeners that have shown that NLP, and especially chaos, affect perceived distress in puppy whines [23] as well as perceived arousal in human non-verbal vocalizations (aggressive calls [6], distress calls [70] or pain calls [25, 26]). The extent to which NLP also encode high arousal in the positively valenced vocalizations of canids, such as in red wolf affiliative vocalizations [19], and in other mammals, such as human sexual pleasure vocalizations [71], should be investigated in future work. Developmental and comparative studies may also investigate the extent to which NLP result from the vocalizers intentionally or unintentionally overdriving their vocal system under high arousal (as suggested in [72]), and may examine when such abilities arise during development and/or evolution.

Our systematic description of the temporal distribution and acoustic context of NLP contributes to a much-needed ecological background for understanding the mechanisms and functions of NLP in mammalian vocal communication systems. While the level of granularity in the acoustic analyses reported here requires a larger amount of annotated audio recordings and more sophisticated statistical modelling than has been customary in bioacoustic studies of NLP to date, the rewards are correspondingly richer. We therefore advocate adopting a similar methodological approach, as applied to puppy whines in this study or to Indri songs [60], for future acoustic studies of other vertebrate vocalizations.

Ethics. Acoustic recordings of puppies were performed under the ethical approval no. E-42-218-0901 (ENES Bioacoustics Research Laboratory agreement, Direction Départementale de la Protection des Populations, Préfecture du Rhône).

Data accessibility. All recordings, datasets as well as R codes for analysing data can be downloaded from https://osf.io/qfdup/.

Supplementary material is available online [73].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.M.: conceptualization, data curation, formal analysis, methodology, writing—original draft; K.P.: writing—review and editing; K.R.: writing—review and editing; N.M.: writing—review and editing; D.R.: conceptualization, methodology, writing—review and editing; A.A.: conceptualization, formal analysis, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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