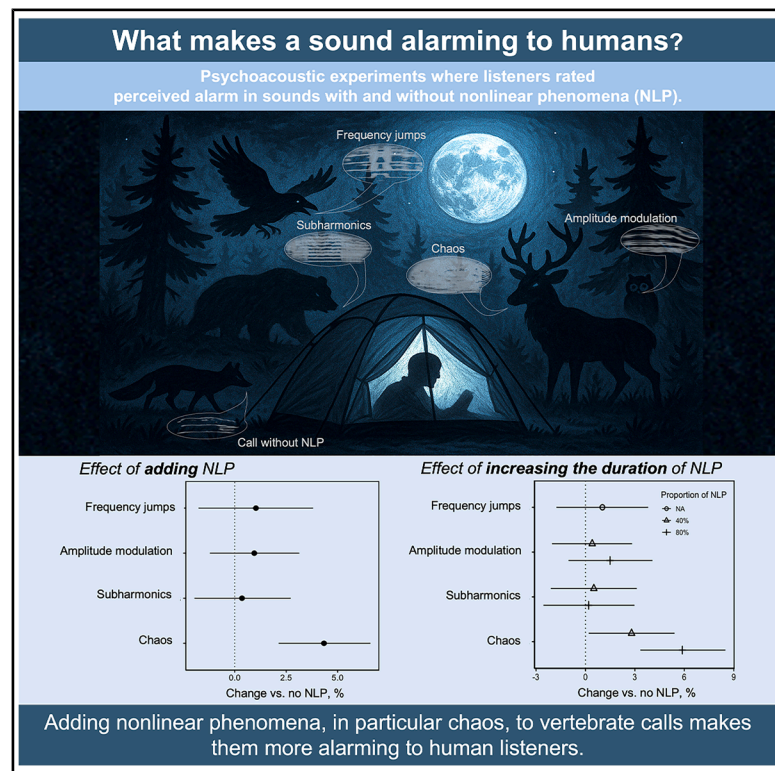


Nonlinear phenomena make animal calls alarming for human listeners

Graphical abstract



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In brief

Biological sciences; Zoology; Evolutionary biology

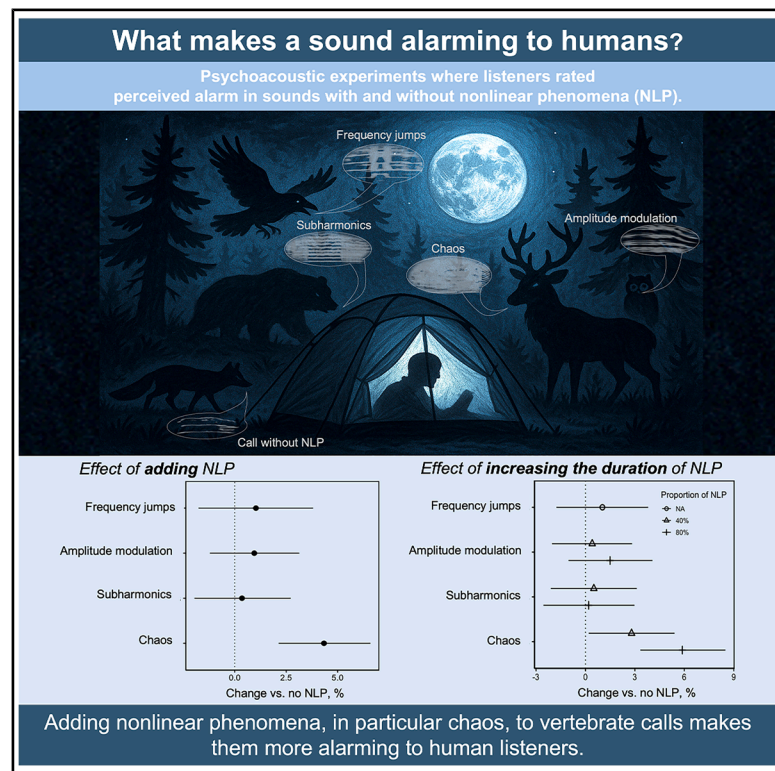
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- Deterministic chaos makes bird and mammal calls alarming to human listeners
- Increasing the proportion of chaos in animal calls makes them more alarming



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Article

Nonlinear phenomena make animal calls alarming for human listeners

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SUMMARY

Animal vocalizations are extremely diverse, and evolutionary approaches to understanding this diversity assume some mapping between their acoustic form and communicative function, with specific features serving universal roles. Here, we investigate whether irregular vocal production with nonlinear phenomena contributes to the alarming quality of vertebrate calls. We resynthesized 98 calls of birds and mammals from 18 species, adding frequency jumps, subharmonics, amplitude modulation, or chaos. Human listeners then rated how alarming they found these calls in an immersive setting mimicking a forest at night. Chaos consistently made the calls more alarming, but other tested NLP did not, confirming that chaos is particularly suitable both for signaling alarm and, potentially, for intimidation in agonistic interactions. While our results suggest that nonlinear phenomena may have a broader function in the mammalian vocal repertoire, follow-up studies should now investigate whether these perceptual effects induced by nonlinear phenomena extend to receivers in non-human species.

INTRODUCTION

Evolutionary approaches to understanding the diversity of mammal vocalizations typically assume that the acoustic form of vocal signals maps onto specific functions, leading to universal acoustic characteristics that can be shared among multiple species. For example, Morton's motivation-structural rules¹ propose that lower-pitched and/or harsher calls should signal aggression while higher-pitched and/or more tonal calls should advertise submission. While these rules have provided a useful framework, they mainly focused on properties of the fundamental frequency and paid less attention to Morton's second, relatively under-theorized, insight about the role of vocal harshness.

Integrating this second component of Morton's rules requires a proper understanding of how animal vocalizations are produced, and how the production mechanism affects their acoustic properties. In vertebrates, relatively stable and periodic modes of vibration of oscillators in vocal organs, such as membranes in the syrinx of birds or vocal folds in the larynx of mammals, typically result in the production of tonal acoustic signals. However, these signals may also include perceptually harsh

vocal elements—known as *nonlinear phenomena* (hereafter NLP)—that result from irregularities in the typical pattern of vibration of oscillators, often caused by a high subglottal pressure and/or strong muscle tensions on vocal sources (in birds² and in mammals³). The most commonly reported types of NLP include frequency jumps, subharmonics, amplitude or frequency modulation, biphonation, and deterministic chaos (hereafter chaos)^{2–5} (Figure 1). *Frequency jumps* correspond to sudden shifts in the vocal source vibration rate and are visible as upward or downward jumps in the contour of the call's fundamental frequency (f_0), which corresponds to the rate at which avian vocal membranes and mammalian vocal folds vibrate, and which is responsible for the perceived pitch of vocalizations. *Subharmonics* often result from a period doubling or tripling in the vocal fold vibration. They can be seen in spectrograms as spectral bands that are harmonically related to f_0 (most commonly occurring at one-half or one-third of f_0). *Amplitude or frequency modulation* results from the modulation of f_0 by a lower f_m and is visible as sidebands occurring at $m \cdot f_0 \pm n \cdot f_m$, where m and n are integers. Amplitude modulation contrasts with biphonation, where vocalizations are characterized by two independent and audible pitches. Finally, *chaos* corresponds to asynchronous and



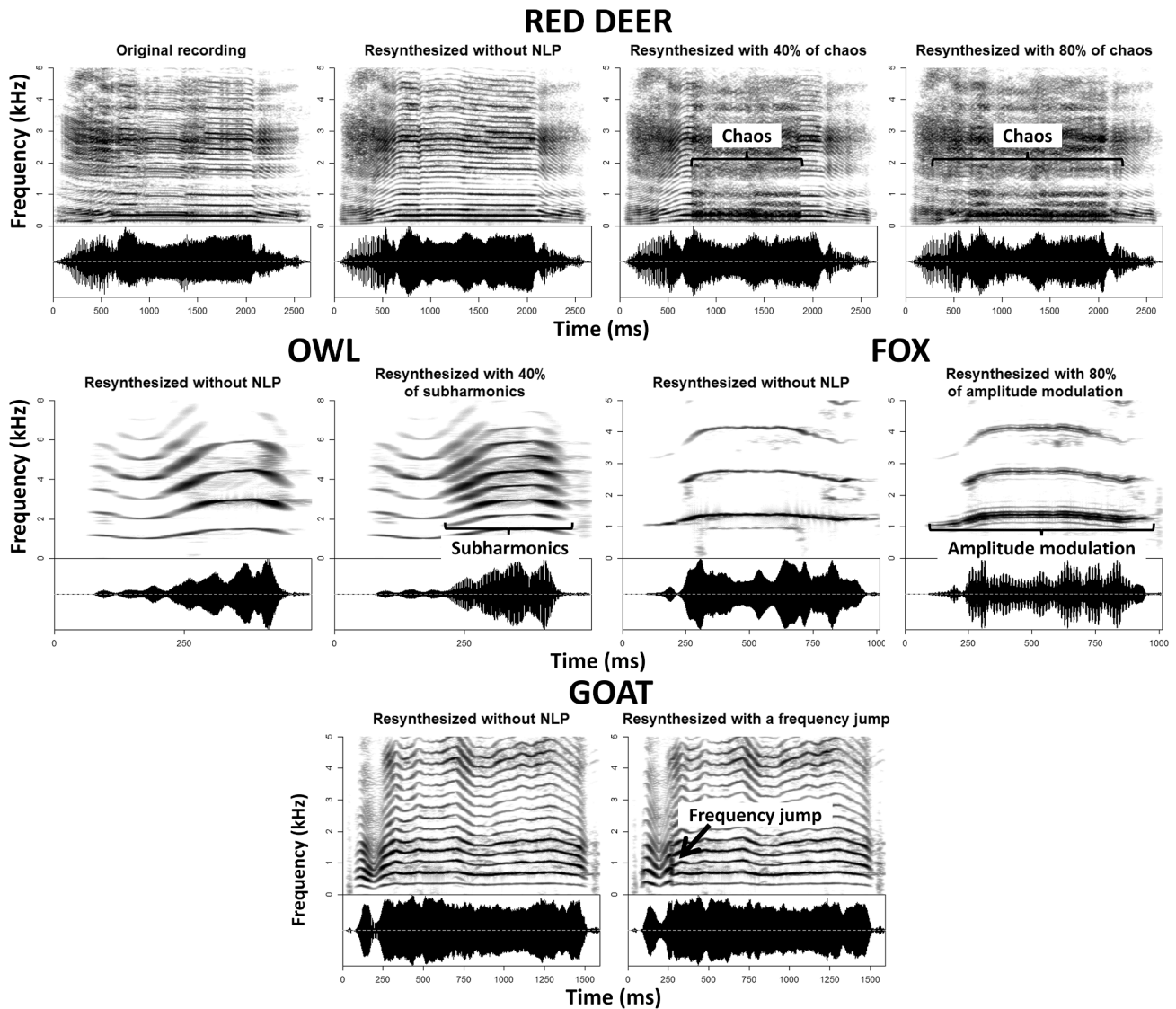


Figure 1. Examples of spectrograms showing the original, natural call, and resynthesized calls with added nonlinear phenomena of various types (chaos, subharmonics, amplitude modulation, and frequency jumps)

A variety of species were included, here a red deer (*Cervus elaphus*), tawny owl (*Strix aluco*), fox (*Vulpes vulpes*), and goat (*Capra hircus*). These calls were resynthesized with different proportions of NLP (40% and 80%). Spectrograms were generated with the `spectrogram()` function from `Soundgen` R package.⁶

nonperiodic vibrations of the vocal folds and is identifiable as noisy sections in animal calls.

In a wide range of vertebrates, NLP are produced in contexts associated with extreme arousal, including aggression and distress: for example, when vocalizers perform agonistic displays,^{7,8} experience extreme pain,^{9–12} separation from conspecifics,¹³ or a predation threat.¹⁴ It has thus been suggested that NLP may function to signal relatively high levels of urgency (because they are produced in contexts associated with danger) and ultimately grab the attention of receivers to elicit adequate behavioral responses, such as helping or fleeing (in birds^{15,16} and in mammals^{14,17–19}). For example, in birds, NLP appear particularly aversive for white-crowned sparrows (*Zonotrichia leucophrys*)¹⁶ and great-tailed grackles (*Quiscalus mexicanus*).¹⁵

Playback experiments indeed revealed that presenting these two bird species with synthetic sounds containing downward frequency jumps or white noise (a perceptual proxy of chaos²⁰) elicit relatively strong vigilance. Furthermore, in mammals, NLP, and particularly chaos, are a common feature of high arousal calls, such as distress or alarm vocalizations.^{13,17–19} One example is found in the whines of domestic dog puppies (*Canis familiaris*): individuals emit more NLP as the separation time from their mother and littermates increases.¹³

There is also evidence that listeners interpret NLP as cues to high arousal and/or distress. The addition of NLP to synthetic puppy whines also considerably enhances human perception of distress compared to those without NLP.²¹ Just as observed in the “cries” of puppies, those of human babies (*Homo sapiens*)

can contain high levels of NLP. This is particularly true when the baby is experiencing pain: pain cries emitted during vaccination contain more NLP than discomfort cries emitted during bath.¹¹ The addition of NLP—and again particularly chaos—to synthetic baby cries increases perceived pain as rated by human listeners.¹¹ Similar results were obtained for the pain vocalizations of human adults. A recent study demonstrated that the amount of NLP in childbirth nonverbal vocalizations (emitted without epidural anesthesia) increases as the labor progresses, and that screams given during the final, most painful stage of labor are rated as expressing extreme pain by human listeners.¹² Also, in contexts of aggression, it has been reported that the presence of NLP is typically associated with higher levels of perceived size and formidability.^{7,22} Finally, NLP may have inherent perceptual properties (unpredictability and roughness) that make them startling and unpleasant and thus ideal for generating a sense of alarm in receivers.¹² Together, the above observations support the view that the communicative functions of NLP may serve as a common acoustic feature across vertebrates, potentially facilitating the expression and detection of distress and danger both within and across species.

Here, to test the hypothesis that NLP encode alarm information that can be perceived across vertebrate species, we conducted a series of psychoacoustic experiments, in which we asked human listeners to indicate how alarmed they felt upon hearing animal calls with versus without NLP. Specifically, we presented human listeners with natural and resynthesized vocalizations of various birds and mammals, independently adding different types and amounts of NLP. Such direct manipulation is more powerful than relying on correlational approaches, which use natural sounds as stimuli and therefore cannot control for potentially covarying acoustic parameters such as f_0 or intensity.^{14,23} For instance, NLP are more common in loud, high-pitched vocalizations, and such vocalizations are often associated with high arousal,²⁴ but it is difficult to determine to what extent NLP contribute to the perception of distress or alarm in these vocalizations without being able to manipulate NLP in a targeted manner. We predicted that the addition of NLP to animal calls would increase the sensation of alarm experienced by human listeners, particularly when adding longer episodes of subharmonics, amplitude modulation and chaos. Finally, to verify that the manipulated resynthesized stimuli sounded authentic and that the effect of NLP on perceive alarm was not a by-product of resynthesis artifacts, we also collected ratings of the naturalness of both original and resynthesized recordings.

RESULTS

The aim of the perceptual experiment was to evaluate the effect of inserting different types of NLP, namely frequency jumps, subharmonics, amplitude modulation and chaos, in animal calls on human listeners' sensation of alarm. To make the task more realistic and ecologically relevant, testing occurred in an immersive audiovisual environment designed to create the impression of camping in a forest at night. We used 98 vocalizations of eighteen species of birds and mammals ranging widely in size and formidability: loons (*Gavia Immer*), owls (*Tyto sp.*, *Strix aluco*, *Asio flammeus*, *Asio otus*, and *Athene noctua*), ravens (*Corvus*

corax), martens (*Martes martes*), hedgehogs (*Erinaceus europaeus*), armadillos (*Dasypus novemcinctus*), foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), goats (*Capra hircus*), sika deer (*Cervus nippon*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), cows (*Bos taurus*), and bears (*Ursus arctos*). All these vocalizations were selected as potentially threatening or eerie, and all could potentially be encountered while camping.

Chaos enhances the alarming nature of calls

Of the tested NLP, only chaos had a noticeable perceptual effect on listeners' sensation of alarm. Chaos made calls 5% (2, 7) (median posterior distribution and 95% confidence interval) more alarming compared to the versions resynthesized without any NLP (Figure 2B). Breaking down the effects of NLP by their relative duration, which was either 40% or 80% of the call's duration, longer episodes of chaos were perceived as considerably more alarming (+7% [4, 10] relative to the same call without NLP) than shorter ones (+2% [0, 5]; Figure 2C). The addition of frequency jumps, subharmonics, and amplitude modulation had no pronounced effect on the ratings of alarm or naturalness (Figure 2B), regardless of their duration (Figure 2C).

Effect of NLP on call naturalness

In this psychoacoustic experiment, original, unmanipulated calls were presented to listeners together with the resynthesized versions. Some original recordings contained NLP and others did not, so it is not meaningful to compare the originals with each NLP condition. Averaging across all resynthesized versions, however, we found that the original recordings were rated as slightly more natural overall (+8% [4, 12]), with no clear difference in alarm ratings (+1% [-1, 4]). Crucially, the manipulation of NLP had no noticeable effect of naturalness in any condition, apart from a slight loss in authenticity after adding subharmonics at 80% of the call's duration (-5% [-9, -1]) (Figure 2C). The difference in naturalness between the original and resynthesized versions varied considerably depending on the animal and the type of added NLP. For example, original and resynthesized goat calls were rated as equally natural, whereas the original raven calls sounded more natural than their resynthesized versions, probably because the characteristic "croaking" amplitude modulation of the original was not reproduced (Figure 2D). In contrast, the perceptual effect of chaos on alarm ratings was consistently positive and hovered around 5% for all species (Figure 2D).

DISCUSSION

We found that the addition of deterministic chaos to calls given by birds and mammals from various species consistently increased human listeners' sensation of alarm. While previous work has shown that "noisy" calls from conspecifics can induce fear and lead to antipredator behaviors in several vertebrate species (e.g., in marmots,^{19,25} birds,²⁶ and lizards²⁷), to our knowledge, this is the first experimental demonstration that NLP in the calls of multiple species can evoke alarm in a context of interspecific vocal communication.

In human listeners, there is some evidence that auditory roughness found in screams and artificial alarm signals activates subcortical structures involved in assessing danger, possibly

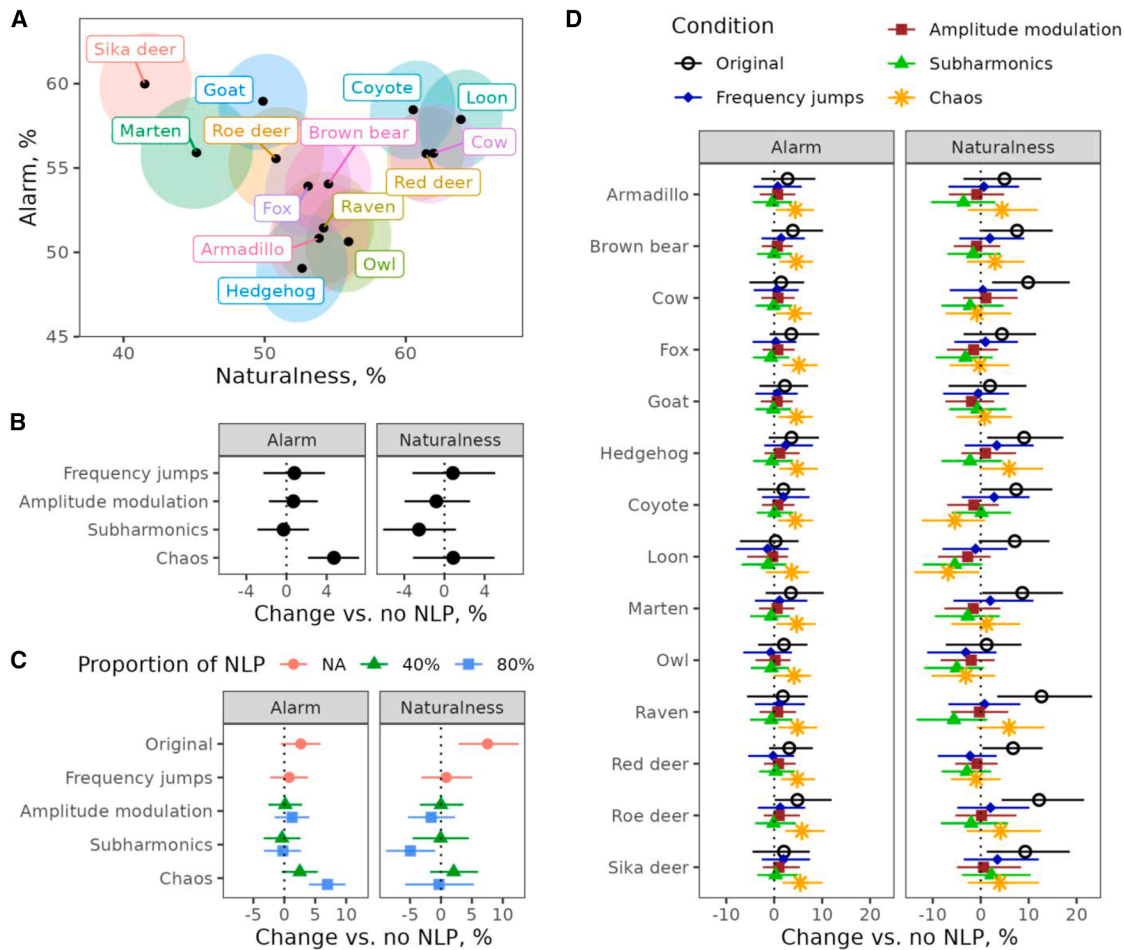


Figure 2. The ratings of the original and resynthesized vocalizations in a perceptual experiment

(A) The alarm and naturalness ratings of calls vary across the tested animal species. The points are the most credible values per species averaging over all conditions, and ellipses are 50% credible intervals (CIs).

(B and C) Only chaos enhances the alarming nature of the tested calls. Change in ratings relative to no NLP, overall (B) and as a function of the relative duration of NLP (C).

(D) The alarming nature of chaos is remarkably consistent across the species. All points correspond to medians of posterior distributions, and error bars to 95% CIs. $N = 8981$ ratings of 882 vocalizations by 90 listeners.

even during sleep, which could indicate adaptive reactions for survival.^{28,29} Vocalizations also become perceptually rougher in the presence of NLP, particularly chaos.²² One interpretation of our observations is therefore that human listeners generalize this rule to a large range of animal vocalizations, associating auditory roughness with alarming or threatening stimuli. On the other hand, rough-sounding amplitude modulation in our study did not enhance the perception of alarm, which means that roughness alone is unlikely to explain why chaos is so alarming.

A second possible mechanism is that NLP signal high arousal and distress. Because high arousal is likely to occur in life-threatening situations,¹⁴ it should be adaptive for receivers to associate the presence of NLP with negatively valenced and alarming contexts, not only in the vocalizations of their own species but also in those of other animals. Indeed, this generalization may be largely justified given that harsh vocalizations rich in NLP are often produced by highly distressed or aggressive animals.^{5,7,10,12,13} In

mammals, the vocal configuration of emitters in intense emotional states is typically associated with strong muscular tension and subglottal pressure, leading to irregularities in the vibration of the vocal folds,³⁰ and thus to the production of calls containing NLP. In birds, on the other hand, the mechanisms of vocal production depend on the species,³¹ and no study has made a direct link between emitter's emotions and the appearance of NLP, even though some species tend to emit sounds with more NLP in aversive contexts.⁵ More specifically, chaos is the form of NLP produced with the strongest subglottal pressure,³² and it is particularly common in the calls of highly aroused animals in contexts associated with distress and aggression.³ A recent study of interspecific vocal communication also showed that experimentally adding chaos to puppy whines increased perceived distress in humans.²¹ These observations do not imply that the only function of NLP is to signal distress and cause alarm. Indeed, the production—or avoidance—of NLP has been shown or

hypothesized to contribute to such diverse social functions as individual recognition,³³ fitness displays,³⁴ signal localization,³⁵ and body size exaggeration.^{3,36,37}

As expected, the ratings of alarm and naturalness varied strongly across species (Figure 2A). The calls of small animals, such as hedgehogs, armadillos, and owls, were often perceived as less alarming than those of larger ones, but with interesting exceptions: for example, listeners found the calls of martens more alarming than those of bears. Presumably, loudness normalization removes an important cue to body size, so that a relatively feeble squeak by a small animal is no longer easy to distinguish from the scream of a much larger, dangerous creature. Long-distance calls of sika deer were rated as least natural and most alarming, perhaps because they were unfamiliar to listeners and because of their inherent eerie quality. Overall, there was no obvious correlation between alarm and naturalness ratings across species, and the effect of chaos on listeners' sensation of alarm was consistent across species. Since NLP manipulations had no effect on naturalness ratings, the observed effect of chaos on perceived alarm is unlikely to be caused by any artifacts of our resynthesis but represents a genuine and general perceptual association.

Because assessing alarm in heterospecific alarm or distress calls is likely to affect survival in sympatric species sharing predation pressures,^{38–40} further playback experiments using the parametric approach reported here are now needed to establish whether non-human mammal receivers are also sensitive to NLP as a cue to alarm in heterospecific calls. This would allow us to determine whether this alarming function of NLP is universal. Finally, from an applied perspective, identifying a cross-species alarming functionality of NLP, combined with their assumed effect of limiting habituation in receivers,^{23,41} could help manage human-animal conflicts, such as controlling pests or reducing wildlife-vehicle collisions, by developing universal acoustic deterrents that are effective against multiple species.

Limitations of the study

While the results of this study are based on a pool of human listeners living in the United Kingdom and the United States, additional playback cross-cultural studies using a similar parametric approach should be conducted to determine whether these findings hold across diverse human cultures. Most importantly, to establish the universality of the alarming function of NLP, further studies should be carried out on a wider number of species, both to create stimuli and to study their perception.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Anna Terrade (anna.terrade@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All audio and datasets for data analysis are provided as electronic supplements (<https://osf.io/s84gt>).

- R scripts for data analysis are provided as electronic supplements (<https://osf.io/s84gt>).
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

A.T., A.A., M.M., and D.R. conceived the idea. A.T., A.A., and L.P. designed online experiments. A.T. and A.A. created stimuli. A.A. analyzed the data. A.T., A.A., M.M., and D.R. wrote the original draft of the paper and led the revisions, and N.M. critically reviewed several versions of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS
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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Original recordings, datasets, and analysis scripts	Repository	https://osf.io/s84gt/
Experimental models: Organisms/strains		
Human subjects	Recruiting platform <i>Prolific</i> (Palan and Schitter. ⁴²)	https://www.prolific.co/
Software and algorithms		
R version 4.0.3	(Team RC. ⁴³)	https://www.R-project.org/
R package <i>soundgen</i> (version 2.7.1)	(Anikin, A. ²⁵)	https://cran.r-project.org/package=soundgen
R package <i>brms</i>	(Bürkner, P. ⁴⁴)	https://CRAN.R-project.org/package=brms

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants were recruited on Prolific (<http://www.prolific.com>)⁴² and self-reported having normal hearing. Eighteen participants were excluded because their responses poorly correlated with the average responses of all participants (Pearson's $r < 0.2$), suggesting random responses or technical problems. The remaining quality sample consisted of 90 participants living in the United Kingdom or the United States, including 44 women, 44 men, and 2 individuals of unknown gender, aged 18 to 64. With this sample size, each of 882 stimuli was rated on average 5.1 times on each response scale. A robustness analysis confirmed that the main reported outcomes also hold in the full sample of 108 participants (Figure S1 in electronic supplements: <https://osf.io/s84gt/>).

METHOD DETAILS

Acoustic stimuli

To investigate the effect of the presence and type of NLP in animal calls on human listeners' perceptual ratings of alarm and naturalness, we used parametric sound synthesis to resynthesize natural mammalian calls. We selected 98 calls (duration $M \pm SD = 1.9 \pm 1.3$ s, range [0.5, 7.2]) produced by 18 species of terrestrial mammals and birds: loons (*Gavia Immer*), owls (*Tyto* sp., *Strix aluco*), *Asio flammeus*, *Asio otus*, *Athene noctua*), ravens (*Corvus corax*, slowed down without changing their frequency), martens (*Martes martes*), hedgehogs (*Erinaceus europaeus*), armadillos (*Dasypus novemcinctus*), foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), goats (*Capra hircus*), sika deer (*Cervus nippon*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), cows (*Bos taurus*) and bears (*Ursus arctos*). The recordings were either freely shared on social media (<https://www.youtube.com/>) or taken from our own collections. None of the recordings were performed specifically for this study, and roe deer distress calls were recorded during captures as part of population monitoring (capture, marking and release) in the 1990's.⁴⁵ We extracted very accurate f_0 contours of these recordings using the *pitch_app* interactive environment in the R package *soundgen* (version 2.7.1).^{6,43} When the original calls were highly chaotic and did not have a clear f_0 contour, a plausible smoothed contour was drawn by hand to be able to resynthesize tonal version of these calls. Using NLP-rich recordings as prototypes is not a drawback but a desirable feature that improves the quality of resynthesis. Indeed, the original recordings were particularly selected to be rich in NLP because it is more natural to remove NLP episodes or change their type rather than to create irregular phonation in a call that originally contained no NLP at all.⁴⁶ Using the function *soundgen()* (*soundgen* R package), a fully synthetic acoustic source corresponding to the extracted f_0 contours was then combined with smoothed spectro-temporal envelopes of the original recordings, resulting in highly naturalistic and fully controlled resynthesized exemplars. The source was created in eight NLP conditions: *no NLP*, *frequency jumps* (a single jump, 3-12 semitones in magnitude, timing and direction chosen stochastically), *amplitude modulation* (AM, frequency 25-120 Hz, depth 30-60%, 40% or 80% of the call's duration), *subharmonics* (frequency $f_0/2$, $f_0/3$, or $f_0/4$, depth 30-60%, 40% or 80% of the call's duration), or *chaos* (jitter depth 1-3 semitones, 40% or 80% of the call's duration). Amplitude modulation, subharmonics, and chaos were added in one to three episodes, with stochastically determined onset time(s). Some reverberation was added to the resynthesized calls to make them sound more like field recordings, with identical reverberation settings used for all eight versions of a particular prototype. The original unmanipulated recordings were tested as the ninth, *original* condition (Figure 1). For each of 98 original recording, there were thus eight resynthesized variants, resulting in a total of 892 stimuli. R codes used for the acoustic synthesis are available at <https://osf.io/s84gt/>.

Procedure

The experiment was performed online and designed to mimic camping in a forest at night with a corresponding background image (Figure S2 available at <https://osf.io/s84gt/>) and a background night-time soundscape with continuous sounds of crickets, crackling fire, thunder, wind, etc. Before starting an experiment, participants were informed that they would listen to animal calls. They were asked to use headphones and to complete the experiment in a quiet environment. They also listened to three natural vocalisations comparable to the test sounds in order to familiarize themselves with the acoustic range of upcoming calls and to adjust the sound level to a comfortable volume, which was then kept constant during the whole experiment.

During the experiment, participants were instructed to rate alarm (“How alarmed or scared would you be?”) and naturalness (“Does this sound natural, like something you might hear on a real hike?”) perceived in each stimulus using a sliding scale ranging from 0 (alarm: calm; naturalness: not natural) to 100 (alarm: extremely alarmed; naturalness: very natural). Each participant completed 100 trials in two blocks: 50 trials of rating animal calls on the alarm scale and 50 on the naturalness scale. The order of blocks and calls within block was randomized, and the same call was never repeated in multiple trials.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data from playback experiments were analyzed with Bayesian multilevel models using the *brms* R package.⁴⁴ Ratings of perceived alarm and naturalness were re-encoded to a range of (0, 1) and modeled as beta-distributed. The model syntax was as follows:

$$\text{respNorm} \sim \text{nlpProp} * \text{scale} + (\text{nlpProp} * \text{scale} | \text{species}) + (\text{scale} | \text{prototype} + \text{sound} + \text{subject}),$$

$$\text{phi} \sim (1 | \text{subject})$$

where *nlpProp* corresponds to NLP condition and relative duration (a factor with 9 levels: original, no NLP, frequency jump, subharmonics 40%, subharmonics 80%, AM 40%, AM 80%, chaos 40%, and chaos 80%), *scale* to the response scales (two levels: alarm and naturalness), *species* = animal taxon (14 levels – all five owl species are treated as one group as they are acoustically similar), *prototype* to the original recording (98 levels), *sound* to the manipulated version (98 prototypes x 9 conditions = 882 levels) and *subject* to the participant. We let the effects of NLP condition per scale vary across species and assigned a random intercept to each participant, sound, and prototype on each scale. An additional random intercept per subject was assigned to the dispersion (*phi*) parameter to account for individual differences in using the response scale (some listeners used the entire scale, whereas the responses of others clustered in a small portion of the scale). Mildly informative conservative priors were assigned to all regression coefficients to improve model convergence (see supplementary materials on <https://osf.io/s84gt/> for convergence checks). Posterior distributions of models’ parameters were summarized by the median and 95% credible intervals. All reported main effects, contrasts between conditions, and plots were obtained from the posterior distribution of the same model.