

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/364161535>

Vocal expression of emotions in farmed spotted paca (*Cuniculus paca*)

Article in *Applied Animal Behaviour Science* · October 2022

DOI: 10.1016/j.applanim.2022.105753

CITATIONS

0

READS

42

7 authors, including:



Stella G. C. Lima

Universidade Estadual de Santa Cruz

10 PUBLICATIONS 94 CITATIONS

[SEE PROFILE](#)



Sergio Nogueira-Filho

Universidade Estadual de Santa Cruz

107 PUBLICATIONS 1,162 CITATIONS

[SEE PROFILE](#)



Suzanne Held

University of Bristol

46 PUBLICATIONS 1,972 CITATIONS

[SEE PROFILE](#)



Michael Mendl

University of Bristol

251 PUBLICATIONS 12,183 CITATIONS

[SEE PROFILE](#)

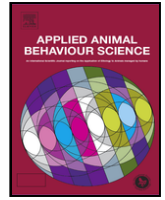
Some of the authors of this publication are also working on these related projects:



Neotropical mammals nutrition [View project](#)



Wildlife management: pest control [View project](#)



Vocal expression of emotions in farmed spotted paca (*Cuniculus paca*)

Allison F. Lima^{a, 1}, Stella G.C. Lima^{a, 1}, Sérgio L.G. Nogueira-Filho^a, Suzanne Held^b,
Elizabeth Paul^b, Michael Mendl^b, Selene S.C. Nogueira^{b, *}

^a Laboratório de Etologia Aplicada, Universidade Estadual Santa Cruz, Rodovia Jorge Amado km 16, Ilhéus, BA 45662-900, Brazil

^b Bristol Veterinary School, University of Bristol, Langford House, Langford, Bristol BS40 5DU, UK

ARTICLE INFO

Keywords:

Acoustic parameters
Animal communication
Animal emotion
Animal welfare
Bioacoustics

ABSTRACT

Vocal emissions in non-human mammals can be used as non-invasive indicators of animal emotion and welfare. Therefore, we aimed to validate the use of acoustic parameters as indicators of affective states and welfare in farmed spotted paca (*Cuniculus paca*). We recorded the vocalizations of 36 pacas, living in 12 groups (two females and one male/group), during four distinct experiences that were assumed to generate different affective states (negative, positive, ambiguous, and highly positive). Spotted pacas emitted more snorts, either as single elements or phrases, when experiencing a negative affective state. Four acoustic parameters of snorts, roars, and barks, which were recorded during all experiences, differed according to the affective valence assumed to be experienced by the spotted pacas. During the negative condition – morning cleaning routine spotted pacas emitted many more snort calls, which are characterized by a shift in the mean amplitude towards a higher level of intensity and as well as by a shift in the energy distribution (Q75) towards a higher frequency than those emitted in the positive condition compared to those emitted in the assumed positive valence condition – feeding time with the regular diet. These call-characteristics, along with the increase in the mean amplitude of snort calls from the lowest to the highest arousal levels, may thus reflect negative affective state and arousal in spotted paca. Therefore, the increase in the overall emission of snorts together with changes in their acoustic parameters may be valuable as indicators of negative emotions of *C. paca*, and thus have potential as an automated and non-invasive tool for welfare assessment in this species.

1. Introduction

A major challenge in animal welfare science is to identify indicators that allow us to assess animal emotions (Mendl and Paul, 2017). Emotion is a multi-component phenomenon (Désiré et al., 2002; Mendl et al., 2010) which can be conceptualized in simple terms as a bi-dimensional space with axes of affective valence (positivity vs negativity) and affective arousal (high or low activation) (Russell, 1980, 2003; Mendl et al., 2010). Thus, in a threatening situation likely to generate a fear-like emotion, an animal's affective state is considered to be negatively valenced and highly aroused, whilst in a positive social context generating an excitement-like emotion, its affective state is considered to be positively valenced and highly aroused (Briefer, 2012).

In a comprehensive review, Briefer (2012); updated in 2020) showed that acoustic parameters in vocalizations of non-human mammals can be used as a tool to access animal emotions and thus as a non-invasive indicator of animal welfare. To date, authors have found asso-

ciations between acoustic parameters and emotions in several species and situations (e.g. *Equus przewalskii*: Maigrot et al., 2018; *Sus scrofa domestica*: Briefer et al., 2019; *Capra hircus*: Baciadonna et al., 2020; Briefer et al., 2022). According to Morton's motivational rules (Morton, 1977; August and Anderson, 1987), acoustic parameters in vocalizations differ depending on the motivational context in which they were produced. The source-filter theory states that speech is produced through breathing, phonation, resonance and articulation processes (Fant, 1960; Titze, 1994). Vocalization is generated when the air from lungs passes through the vocal cords, which vibrate, producing the frequency spectra, energy distribution, and formants, which are determined by the anatomy and physiology of the sub-pharyngeal vocal tract (Fant, 1960; Titze, 1994; Taylor and Reby, 2010). For instance, the formants, amplitude, and duration of the vocalizations emitted by wild boar (*Sus scrofa*) vary according to the caller's assumed emotional state when facing different stimuli (Maigrot et al., 2018). In hostile contexts, vocalizations are usually louder, longer-lasting and with lower fre-

* Corresponding author.

E-mail address: selene@uesc.br (S.S.C. Nogueira).

¹ Both authors contributed equally to this work.

quency, while during non-hostile contexts the vocalizations are shorter and with higher frequency (August and Anderson, 1987). To test the link between emotion and acoustic parameters in vocalizations, it is necessary to record calls given by animals in conditions assumed to trigger different affective states.

At present, more evidence has been reported that emotions in a certain conditions can be translated from vocalizations. During positive conditions, for instance, pigs (*Sus scrofa domesticus*) usually emit grunts with specific features (higher formants, narrower range of the third formant, a shorter duration, a lower fundamental frequency and lower harmonicity) than during negative conditions (Briefer et al., 2019). In a study analyzing pig calls produced from early age up to slaughter under several conditions and emotional valences, the authors conclude that acoustic parameters of calls are affected by emotional valences (positive and negative) and context (Briefer et al., 2022). Recently, Baciadonna et al. (2020) used the anticipatory response paradigm to investigate the affective state in goats (*Capra hircus*) and found changes during positive condition, such as an increase in activity time, rapid head movements and vocalization rate, assuming that positive condition is the best situation in which to evaluate goats' emotions. In turn, a study comparing the vocal expression of emotions between domestic horses (*Equus caballus*) and wild Przewalski horses (*Equus przewalskii*) found that some calls (nickers) were emitted during positive contexts (e.g. food reward), while others (whinnies and squeals) occurred during negative situations (e.g. agonistic), concluding that some call parameters can be useful to investigate Przewalski horses emotions (Maigrot et al., 2018). Studies involving validation of species-specific acoustic behaviour and emotional valences (positive and negative) can improve welfare monitoring and the development of automated vocalization recognition, as was recently proposed for domestic pigs (Briefer et al., 2022).

Studies addressed to animal welfare and emotions in rodents have increased, and recently authors have progressed in their evaluation of animals' affective states (positive and negative), helping to improve rodents' facilities (for review see Jirkof et al., 2019; Simola and Granon, 2019). In rats, for example, calls with 50 Hz are associated with pleasurable contexts, while calls with 22 Hz are associated with negative emotional valences (Burman et al., 2007; Burgdorf et al., 2020; Hinchcliffe et al., 2020). Vocalizations in rodents vary among species and contexts (for review see Fernández-Vargas et al., 2021), and except for rats and mice, few rodent species have been studied regarding vocalization parameters and affective states (Zaytseva et al., 2019). Therefore, we followed this approach, aiming to validate the use of acoustic parameters in spotted paca (*Cuniculus paca*) vocalizations as non-invasive tools for welfare assessment in this species.

The spotted paca is a Neotropical rodent, classified as being of least concern by the International Union for Conservation (IUCN) (Pérez, 1992; Emmons, 2016), which ranges from southeastern Mexico to northern Argentina, and which was also introduced into Cuba and Algeria (Eisenberg and Redford, 1989). Among Neotropical mammals, people most appreciate the meat of spotted paca and, for this reason, farming of this species is increasing in Neotropical countries such as Brazil, Ecuador, Panama, Mexico and Colombia (Barquero and Barquero, 2008; Aldrigui et al., 2018; Hosken et al., 2021). Development of production systems has increased productivity and thus promotes the economic viability of spotted paca farming (Aldrigui et al., 2018). However, little is known about welfare recommendations for this species (Nogueira et al., 2021), and farmers adopt different production systems, breeding them in couples or groups composed of one male and two to five females (Hosken et al., 2021). In this context, it is essential to determine welfare indicators to properly evaluate spotted paca production systems and husbandry practices.

The vocal repertoire of captive spotted paca was described as composed of eight types of calls (seven vocal types and one mechanical-tooth chattering) (Lima et al., 2018). These calls are emitted in specific

contexts (agonistic: bark, roar, snort, groan, growl and tooth chattering and alarm: bark, roar, and snort; and contact: click and cry). Spotted paca vocalize most during agonistic contexts (Lima et al., 2018) and it is plausible that acoustic parameters of agonistic calls may vary according to the animal's situation and reflect the affective state of the caller. We propose that the acoustic parameters of *C. paca* calls vary according to context and the affective state (positive or negative affect) it is assumed to induce. We aimed here to identify the acoustic parameters of the spotted pacas' calls that can be used as indicators of emotional state and context. We hypothesized that the daily cleaning routine was a threatening event that generated a negative affective state, while the daily feeding event generated a positive state, which, in turn, was more or less positive depending on the palatability of the food provided. Feeding time was chosen as a reward based on Nogueira et al. (2021), who reported that *C. paca*, even when experiencing threatening conditions, continues to search for fruits, its preferred food type (Beck-King et al., 1999). Consequently, we assumed that feeding time, which triggered approach behaviour, induced a positively valenced affective state. Thus, it is reasonable to expect that variations in the feeding routine can lead to different intensities of positive emotion according to the value of the reward offered (Mendl and Paul, 2020).

In negative/fearful situations, such as during cleaning routine, spotted pacas usually emit alarm calls (Lima et al., 2018). On the other hand, spotted pacas usually eat together, usually sharing the same feeder, when consuming feeds such as corn bran and vegetables. However, they often pick and carry fruits such as banana and mango to eat separately from each other (Lima, personal observation). Thus, we expected a higher level of arousal according to the degree of food preference and, consequently, changes in the acoustic parameters of the emitted calls. Therefore, following theoretical concepts, which state that the motivational-structural rules can be better understood by following the emotional state of the caller during positive or negative scenarios (August and Anderson, 1987; Briefer, 2012, 2020), we predicted a higher emission of alarm calls in the negative valence condition compared to the positive conditions. Additionally, it is reasonable to assume a gradual decrease in the emission of these calls as the reward received increases. Following the same theoretical concepts (see Briefer, 2012; Briefer, 2020), we expected that in the negative affective state the calls of a distressed animal would be characterized by low-frequency sounds of longer duration and at a higher rate (elements produced per time unit) than those emitted in positive conditions (pleased animal). We also predicted that, along with an increased arousal level, spotted pacas would emit calls with an increase in call duration, rate (number of elements/duration), formant contour, fundamental (F0) frequency contour, amplitude contour, energy distribution, and peak frequency.

2. Material and methods

2.1. Ethics approval

This work followed Brazilian laws and was approved by the Animal Use Ethics Committee (CEUA) of the Universidade Estadual de Santa Cruz (protocol # 029/18).

2.2. Subjects and housing conditions

This study was carried out on a commercial farm located near the town of Soledade de Minas, state of Minas Gerais, Brazil. We recorded the vocalizations of 36 adult spotted pacas (24 females and 12 males), born and raised in captivity, and aged from one to four years. The animals were not individually marked; however, it was possible to identify them by natural characteristics, such as scars and fur colour.

The spotted pacas lived in 12 groups, composed of two females and one male each, which were maintained in 4 m² pens. The pens resemble

small horse stalls, located isolated from other buildings on the farm, with a cement floor and a roof of ceramic tiles. They were surrounded by a 2.0 m-high wire mesh above 0.5 m-high brick wall, which allowed natural day/night cycle, and relatively constant temperature around 20°C throughout the data collection. In each pen, there was a wooden shelter (1.5 m long x 1.5 m wide x 1.0 m high), a water tank (0.6 m long x 0.3 m wide x 0.3 m high) and three feeders (0.4 m long x 0.3 m wide x 0.3 m high). The study was carried out following the farm routine as much as possible, except for the additional positive food conditions that extended the feeding time (see below), while feeding (ambiguous and positive valences-detailed below) and cleaning (negative valence-detailed below) periods were not much modified. The keeper delivered food to the three feeders (one feeder per animal) around 1600 h each day. The meal was composed of corn bran (150 g per animal) as well as seasonal fruits, which only occasionally included mango due to its high cost, and vegetables *ad libitum*. Water was available *ad libitum* in the water tank. The keeper cleaned the pens daily in the morning at 0700 h, when the floor and the shelter were swept, and the feeders and drinkers washed.

2.3. Data collection

Only one observer simultaneously recorded the behaviour and vocalizations of the spotted pacas using the *ad libitum* observational approach (Altmann, 1974). The observer remained outside of the pens (~2.0 m far from the animals) and recorded the vocalizations using a Sennheiser ME-66 directional microphone (Wedemark, Germany) and a Tascam digital recorder (model: DR-100 MK II, with recorder settings: WAV format, mono mode, 48 kHz sampling rate and 16-bit resolution). Additionally, a camcorder (HDR-CX240 Sony, Manaus, Brazil) was used to record the spotted pacas' behaviours. The animals were habituated to the observer's presence during a period of seven consecutive days before the data collection. Following this habituation period, the observer started to record both vocalizations and behaviours when the animals in the selected pen began to vocalize and maintained the recording until the end of any sound emission, following Lima et al. (2018).

As explained above, the food was routinely provided only once a day at 1600 h. This procedure would not have allowed all the tested treatments to be distributed to all the groups. Therefore, we extended the feeding time, and consequently our observation sessions to between 1400 h and 1700 h (the negative condition was not included here – see below), when the spotted pacas were more active. Although spotted pacas in the wild show a nocturnal habit (Emmons, 2016), farmers modify their day/night cycle behaviour, making the animals more active during the day in response to handling and human interaction (Smythe and Brown Guanti, 1995; Nogueira Filho and Nogueira, 1999). The groups were observed in a randomized order for 18 consecutive days, to record behaviours and vocalizations in the emotion-inducing conditions (described below). The order in which groups and animals were observed daily was drawn by lot. Each group was observed for 10 min per day, during feeding time, for three consecutive days for all but the negative condition. For this condition, each group was observed between 0700 h and 0800 h for two minutes per day, because this was the time and duration of the cleaning of each pen.

2.4. Emotional valence of the conditions

We recorded vocalizations during four presumed different emotional conditions: positive (routine food, except mango), ambiguous (just corn bran), highly positive (just mango), and negative (cleaning). We created different feeding contexts by changing the composition of the animals' diet, which, we hypothesized, would lead to three different degrees of positive valence. During the 'positive' condition (positive valence), spotted pacas were fed routine food, *i.e.* a selection of corn bran, vegetables and seasonal fruits, except mango (explanation

below). We considered that feeding the spotted pacas only corn bran would induce a less intense state ('ambiguous' valence). In turn, following Laska et al. (2003), who determined that the mango is the preferred fruit for the spotted paca, we then assumed that a more intense positive state condition would be generated when only this fruit was offered ('highly positive' valence). Because daily cleaning procedures generated an increase in avoidance behaviour, as most of the animals remained inside the wooden shelter while the keeper cleaned the pen (Lima et al., 2018), we assumed that this was perceived by spotted paca as a threatening situation and induced a negatively valenced affective state (negative valence). We subjected the animals to each one of these four conditions three times.

Body movements can also affect vocal parameters through changes in breathing patterns (Maigrot et al., 2018). Moreover, body movements are considered to be good indicators of arousal among species (Forkman et al., 2007). Thus, we used the spotted paca's body movements to evaluate the emotional arousal the individual was experiencing during its vocal production, and used it as a control factor in our statistical model, following Maigrot et al. (2018). To this end, an independent observer, blind to the hypothesis, the conditions (*i.e.* assumed valence) and the identity of spotted pacas, analyzed video footage using the software CowLog 3.0.2 (Hänninen and Pastell, 2009). To perform this analysis, the observer previously received a list of the analyzed calls and the moment when they occurred in the video footages. To this end, these calls were identified by alphanumeric code. The observer could easily identify the caller because the groups were composed of only three individuals each (two females and one male) as well as due to their natural characteristics, as explained above. Analysis of the video footage began when the animal emitted each call, and lasted for 20 s during the emission of vocalizations. Following Maigrot et al. (2018), the observer used the proportion of time the individual spent in five categorical excitation levels: standing upright with head down (SHD: lowest arousal); standing upright with head facing forward (SFF: 2nd lowest arousal); standing upright with head up (SHU: intermediary arousal); walking (WAL: 2nd highest arousal) or running (RUN: highest arousal) during these 20 s, to score the animal's emotional arousal.

2.5. Acoustic analysis

We analyzed the acoustic parameters of both elements and phrases of calls emitted by the spotted pacas. Elements are the smallest vocal units of the calls, defined as a continuous sound without interruption (*sensu* Feng et al., 2009; Barros et al., 2011). We considered a phrase to be a sequence of at least two elements separated from other similar groups by a longer interval of time (twice the duration) than any interval between notes within a phrase, following Barros et al. (2011). For the acoustic analysis, we selected only the calls with high quality, without background noise and/or overlapping. Therefore, from a recorded total of 1804 elements and 247 phrases, we selected 1605 elements and 244 phrases of the best quality for the analysis of acoustic parameters. However, to compare the occurrence of call types in negative and positive emotional conditions (see below), we considered all emitted calls regardless of their acoustic quality (Table 1). Thereafter, we used Raven Pro software version 1.5 (Cornell Lab of Ornithology, Ithaca NY) to perform the visual and aural inspection of spectrograms and oscillograms using the following settings: Hanning window length of 1460, 90 % overlap and DFT size (FFT) of 4096.

An observer classified the recorded calls following Lima et al. (2018) as: snort (low vocalization produced alone or in sequences of three to seven elements); roar (loud and harsh sound emitted as a single element or in sequences of two to five elements); bark (produced alone or in sequences of two to ten short elements); growl (a harsh sound produced as a single element or in sequences of two to five elements); tooth chattering (a mechanical sound produced by the clash of upper and lower incisors); or cry (loud sound with broadband noise that presents

Table 1

Total number of barks, cries, growls, roars, snorts, and tooth chattering emitted whether as a single element or in phrases and mean (\pm standard deviation) number of elements per phrase (NElem/P) by spotted pacas (N = 36) according to the emotional valence conditions.

Emotional valence	Negative			Ambiguous			Positive			High Positive		
	Elements	Phrases	NElem/P	Elements	Phrases	NElem/P	Elements	Phrases	NElem/P	Elements	Phrases	NElem/P
Snort	726	139	4.5 \pm 0.9	22	3	4.0 \pm 0.8	37	8	3.1 \pm 1.0	3	0	0
Roar	583	44	2.5 \pm 0.6	18	2	2.0 \pm 0.0	58	7	2.1 \pm 0.3	4	0	0
Bark	202	25	2.3 \pm 0.5	26	2	2.5 \pm 0.0	60	14	2.6 \pm 0.7	17	0	0
Growl	1	0	0	3	0	0	28	0	0	0	0	0
Tooth chattering	12	3	3.0 \pm 0.0	0	0	0	0	0	0	0	0	0
Cry	0	0	–	0	0	–	2	0	–	0	0	–
Total	1524	211	–	69	7	–	185	29	–	24	0	–

harmonic structures emitted singly or in a sequence of two to four elements).

Thereafter, we also used the Raven Pro software version 1.5 (Cornell Lab of Ornithology, Ithaca NY) to measure six acoustic parameters of roar and bark calls – which were the only calls emitted by spotted pacas during all emotional valence conditions (Table 1) – emitted by the spotted pacas as single elements or as phrases: low frequency (Hz) (lower frequency threshold), high frequency (Hz) (upper frequency limit of the selection), peak frequency (Hz) (frequency that corresponds to the maximum occurrence of power in the selection of elements or phrases), energy quartiles: 1st quartile frequency (Hz) (Q25: frequency value at the upper threshold of the first energy quartile), 3rd quartile frequency (Hz) (Q75: frequency value at the upper threshold of the third energy quartile), and duration (total duration in seconds) (Charif et al., 2010). Additionally, using the same software we measured the duration of phrases (duration of the total sequence of elements in seconds), number of elements, and rhythm (number of elements/total duration of the phrase).

We also examined spectrograms to measure 10 more acoustic parameters including the presence of vocal complexity through structural variability, such as formants (vocal tract resonance frequencies) (Riede and Fitch, 1999). For this supplementary analysis we used Praat software version 5.3.06 (Boersma and Weenink, 2022), with the following settings: time step: FFT method, window length: 0.01; time step: 1000; frequency step: 250; Hanning window shape; dynamic range: 60 dB. In this analysis we determined the formants (Hz) (first formant, second formant, and third formant – F1, F2, and F3, respectively) of roar and bark calls emitted as single elements or as phrases (see Fig. 1 for more

information on how the acoustic parameters were measured) as well as the amplitude contour (dB) (sequence of amplitude values across the vocalization, which include: mean amplitude; minimum amplitude; and maximum amplitude) (Briefer, 2012) of snort, roar and bark calls emitted as single elements, which occurred in all valence emotional conditions (Table 1). We also used the Praat software to measure the fundamental (F0) contour (Hz) (sequence of the lowest frequency across the vocalization, including: mean F0; minimum F0; maximum F0; and F0 range – difference between maximum F0 and minimum F0) (Briefer, 2012) of snort, roar and bark calls emitted as single elements. However, the Praat software did not automatically recognize the fundamental parameters of snort and bark calls, which are very noisy and have no visible harmonics. These characteristics prevented us from making these measurements manually as well.

2.6. Statistical analysis

As we had a different observation time in each trial (negative condition – morning cleaning routine: 1.8 h; ambiguous and positive valence conditions: 9.0 h each), we determined the percentage of each type of call emitted in each condition. Thereafter, we used Chi-square tests and *post hoc* partitioning to verify which call types are more prevalent in each emotional valence experienced by spotted pacas. For this analysis, to satisfy assumptions, we compared only the emissions of snort, roar, and bark calls emitted as single elements or as phrases (one Chi-square test for calls emitted as single elements and another one for calls emitted as phrases).

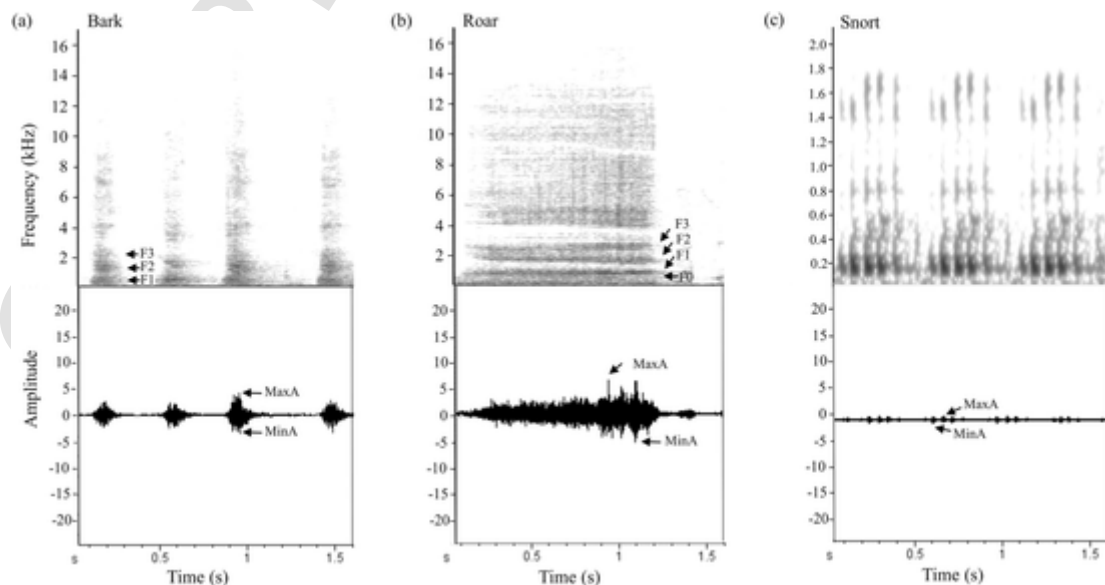


Fig. 1. Oscillograms (below) and spectrograms (above) of the most usual calls emitted by farmed spotted pacas: (a) bark (emitted as phrase with four elements), (b) roar (emitted as single element), and (c) snort (emitted as phrase with three elements).

As the 16 acoustic parameters of the calls were likely to be inter-correlated, we first carried out two principal component analyses (PCA) – one PCA for calls emitted as single elements and another PCA for calls emitted as phrases – to select a set of non-redundant parameters, following Briefer et al. (2022). This procedure resulted in the following parameters to be included in subsequent tests: mean amplitude, Q75, F0 range, duration, minimum F0, and formant F1 of snort, roar, and bark calls emitted as single elements and the duration and rhythm of snort, roar, and bark calls emitted as phrases (see S1 for more information on the PCAs).

We applied linear mixed-effect models (LMMs) to test the hypothesis that the calls' acoustic parameters vary according to the emotional condition experienced by spotted pacas. We included in the models (one model per parameter: mean amplitude, Q75, F0 range, duration, minimum F0, and formant F1 of snort, roar, and bark calls emitted as single elements as well as one model per parameter: duration and rhythm of snort, roar, and bark calls emitted as phrases), as fixed factors, the type of call (snort, roar, and bark (Fig. 1; see supplementary audio files S2, S3, and S4) – which were the only calls emitted by spotted pacas during all emotional valence conditions (Table 1), the valence condition (negative, ambiguous, positive, or highly positive), physical arousal level (standing upright with head down; standing upright with head facing forward; standing upright with head up; walking or running) and the interaction between types of calls and valence conditions. We could not estimate all other possible interactions due to the lack of occurrences. We used the same model to compare the F0 range of roars emitted as single elements – excluding the types of calls and their possible interactions from the model. Additionally, for this analysis we could not estimate the interaction between valence and arousal due to the lack of occurrences. In all models, the identity of spotted pacas nested within their group was included in the models as a random factor. This allowed us to control for repeated measurements and dependencies. When the interaction was significant, we performed further *post hoc* Tukey tests. We graphically checked the residuals of every model for normal distribution and homoscedasticity, and we used logarithmic transformations for all but the mean amplitude parameter to satisfy these assumptions. We used Minitab 19.1 software (Minitab Inc., State College, PA) and set the significance level at $\alpha = 0.05$ for all analyses. All means are given with standard deviations (SD).

3. Results

3.1. Call type emission and emotional valence conditions

Most snorts, roars, and barks, emitted as single elements or in phrases, occurred in the negative condition (Table 1). The tooth chattering call, emitted by just one individual, either as a single element or as phrases, occurred only in the negative condition and when the animal was running (highest arousal level) (Table 1). Only one individual emitted the cry call twice, and just as a single element, during the positive condition and when it was standing upright with head up (intermediary arousal level) (Table 1). The growl call was emitted only as a single element by five individuals when they were walking (2nd highest arousal level), and most occurrences of this call (28 out of 32) were recorded during the positive condition, while three growls occurred in the ambiguous condition and remaining one occurred in the negative condition (Table 1).

Regarding snort, roar, and bark calls emitted as single elements, the independence chi-square test indicates association between call types and emotional valence condition (Chi-square = 76.50, DF = 6; $P < 0.001$) (Fig. 2). The *post hoc* partitioning showed that in the negative valence condition spotted pacas similarly emitted more snorts and roars (Chi-square = 0.10, DF = 1; $P = 0.753$) than barks (Chi-square = 13.69, DF = 1; $P < 0.001$) (Fig. 2a). In the ambiguous condition, they emitted similar numbers of snort, roar and bark calls (Chi-square =

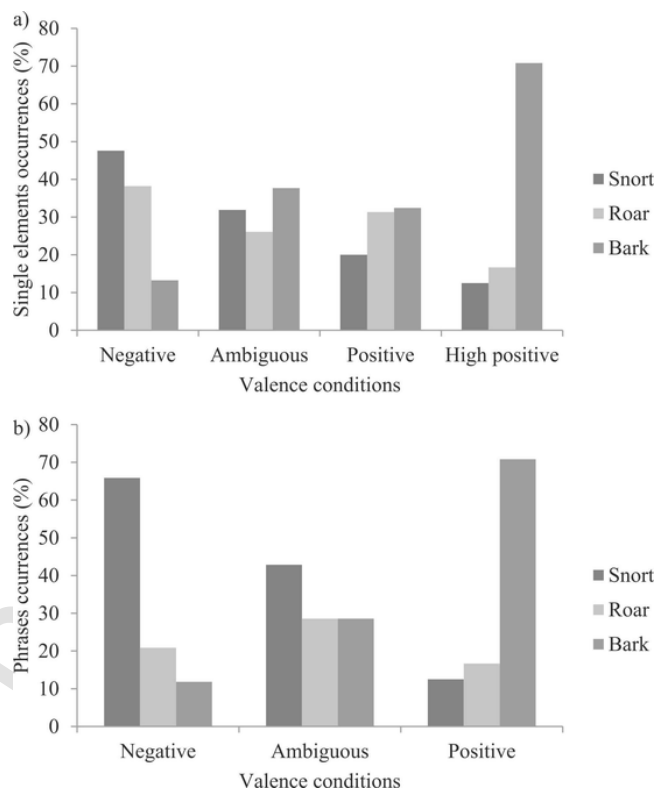


Fig. 2. Occurrences (%) of snort, roar and bark calls emitted by spotted pacas as single elements (a) or as phrases (b) according to the emotional valence condition. Valence conditions: Negative – morning cleaning of the pens; Ambiguous – feeding time with only corn bran; Positive – feeding time with the regular diet; Highly positive – feeding time with mango, its favorite fruit.

3.80, DF = 1; $P = 0.051$) (Fig. 2a). In the positive condition, they similarly emitted more snorts and barks (Chi-square = 0.39, DF = 1; $P = 0.530$) than roars (Chi-square = 4.54, DF = 1; $P = 0.033$) (Fig. 2a). In the highly positive valence condition the spotted pacas emitted more barks than snorts and roars (Chi-square = 50.97, DF = 1; $P < 0.001$) (Fig. 2a).

Concerning calls emitted as phrases, the independence chi-square test indicates association between call types and valences as well (Chi-square = 87.55, DF = 4; $P < 0.001$). The *post hoc* partitioning showed that in the negative valence condition spotted pacas emitted more snorts than roars (Chi-square = 6.23, DF = 1; $P = 0.013$) than barks (Chi-square = 5.89, DF = 1; $P = 0.015$) (Fig. 2b). In the ambiguous condition, they emitted more snorts than roars and barks (Chi-square = 4.20, DF = 1; $P = 0.040$) (Fig. 2a). In the positive condition the spotted pacas emitted more barks than snort and roar calls (Chi-square = 71.23, DF = 1; $P < 0.001$) (Fig. 2b).

3.2. Emotional conditions and acoustic analysis of calls

The statistical model (see S5 for complete statistical analysis, including differences in acoustic parameters among call types) showed a significant interaction between assumed emotional valence conditions and types of calls for the mean amplitude of snorts, roars and barks emitted as single elements ($F_{6, 1537.23} = 12.24$, $P < 0.001$). The *post hoc* tests showed that the mean amplitude of bark and roar calls in the negative valence condition was higher than that recorded in the positive, highly positive and ambiguous valence conditions (Fig. 3a). The mean amplitude of snort calls in the negative valence was higher than those recorded in the positive and ambiguous valences. However, the mean amplitude of these calls did not differ between the negative and highly positive valences (Fig. 3a). Nevertheless, this result may have been bi-

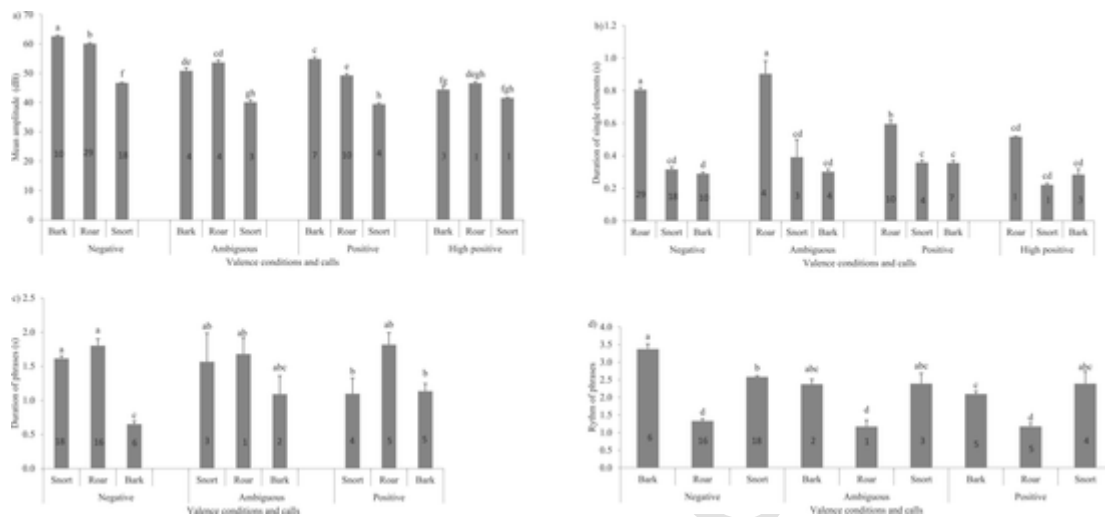


Fig. 3. Means (+SE) of the acoustic parameters: (a) mean amplitude and (b) duration of snort, roar, and bark calls emitted by spotted pacas as single elements; (c) duration and (d) rhythm (number of elements/total duration of the phrase) of snort, roar, and bark calls emitted as phrases according to the emotional valence conditions. Valence conditions: Negative – morning cleaning of the pens; Ambiguous – feeding time with only corn bran; Positive – feeding time with the regular diet; Highly positive – feeding time with mango, its favorite fruit. Different letters above bars indicate difference between means by Tukey tests ($P < 0.05$). The numbers within the bars indicate the number of individuals that emitted each call at the different arousal levels.

ased due to the fact that only a single individual emitted snort calls in the high positive valence (Fig. 3a).

There was also a significant interaction between assumed emotional valence conditions and types of calls for the duration of snorts, roars, and barks emitted as single elements ($F_{6, 1370.02} = 8.99, P < 0.001$). The *post hoc* tests showed that the duration of roar calls in the negative and ambiguous conditions was higher than that recorded in the positive and high positive valence conditions (Fig. 3b). In contrast, the duration of bark calls in the positive valence was higher than that recorded in the negative valence condition (Fig. 3b); while the duration of bark calls did not differ between the negative, ambiguous and highly positive valences (Fig. 3b). On the other hand, the duration of snort calls did not differ among all emotional valence conditions (Fig. 3b). Additionally, there were also significant interactions between assumed emotional valence conditions and types of calls for the duration ($F_{4, 212.24} = 9.91, P < 0.001$) and rhythm ($F_{4, 208.32} = 13.97, P < 0.001$) of snorts, roars, and barks emitted as phrases. The *post hoc* tests showed that the duration of snorts emitted as phrases in the negative condition was higher than that recorded in the positive valence condition (Fig. 3c). In contrast, the duration of bark calls emitted as phrases in the positive valence was higher than that recorded in the negative valence condition (Fig. 3c); while the duration of roar calls emitted as phrases did not differ between the negative, ambiguous and highly positive valences (Fig. 3c). In turn, the rhythm of bark calls in the negative condition was higher than that recorded in the positive valence condition (Fig. 3d). In contrast, the rhythm of snort and roar calls did not differ among the negative, ambiguous and positive valences (Fig. 3c).

The assumed emotional valence conditions, as a single factor, affected the 3rd quartile frequency (Q75) of snort, roar and bark calls emitted as single elements ($F_{3, 1402.79} = 27.48, P = 0.003$) and the F0 range of roar calls emitted as single elements ($F_{3, 290.27} = 15.29, P < 0.001$). The *post hoc* tests showed that the Q75 of bark, roar, and snort calls in the negative valence was higher than those recorded in positive, highly positive and ambiguous valence conditions (Fig. 4a). The F0 range of roar calls recorded in the negative valence was the highest, while the F0 range of this call recorded in the highly positive condition was the lowest (Fig. 4b).

The arousal, as a single factor, affected four acoustic parameters of only the calls emitted as single elements, as follows: the mean amplitude ($F_{4, 1542.14} = 9.81, P < 0.001$) and the Q75 ($F_{4, 1488.92} = 4.08, P = 0.003$) of snort, roar and bark calls; as well as the minimum F0 of

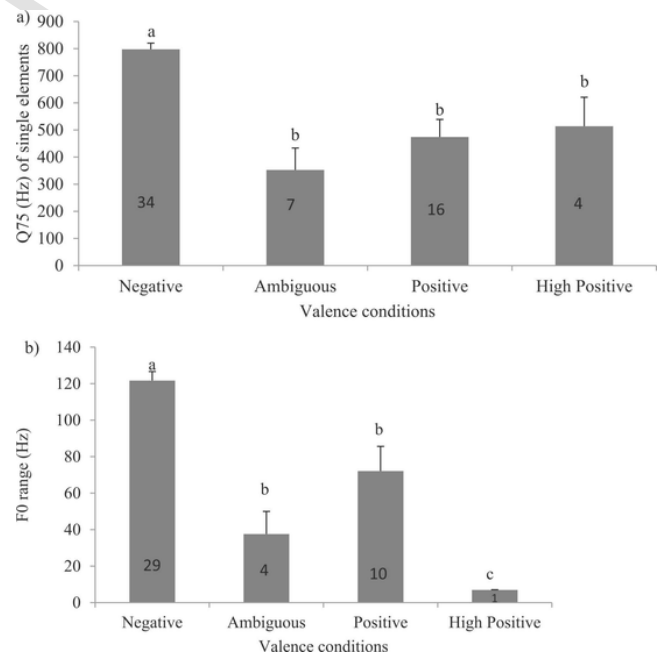


Fig. 4. Mean (+SE) of the acoustic parameters: (a) the 3rd quartile frequency (Hz) (Q75) of snort, roar, and bark calls and (b) the F0 range of roar calls emitted by spotted pacas according to the assumed affective valence conditions. Valence conditions: Negative – morning cleaning of the pens; Ambiguous – feeding time with only corn bran; Positive – feeding time with the regular diet; Highly positive – feeding time with mango, its favorite fruit. Different letters above bars indicate difference between means by Tukey tests ($P < 0.05$). The numbers within the bars indicate the number of individuals that emitted each call at the different arousal levels.

roar calls ($F_{4, 467.03} = 3.45, P = 0.009$). The *post hoc* tests showed that the mean amplitude of snort, roar, and bark calls was higher when spotted pacas were running and walking (highest arousal levels) than when they were standing upright with head down or facing forward (lowest arousal levels) (Fig. 5a). The Q75 of roar, bark, and snort calls as well as the minimum F0 of roar calls were higher when spotted pacas were walking (2nd highest arousal level) than when they were standing upright with head down (lowest arousal level) (Fig. 5b and c). However,

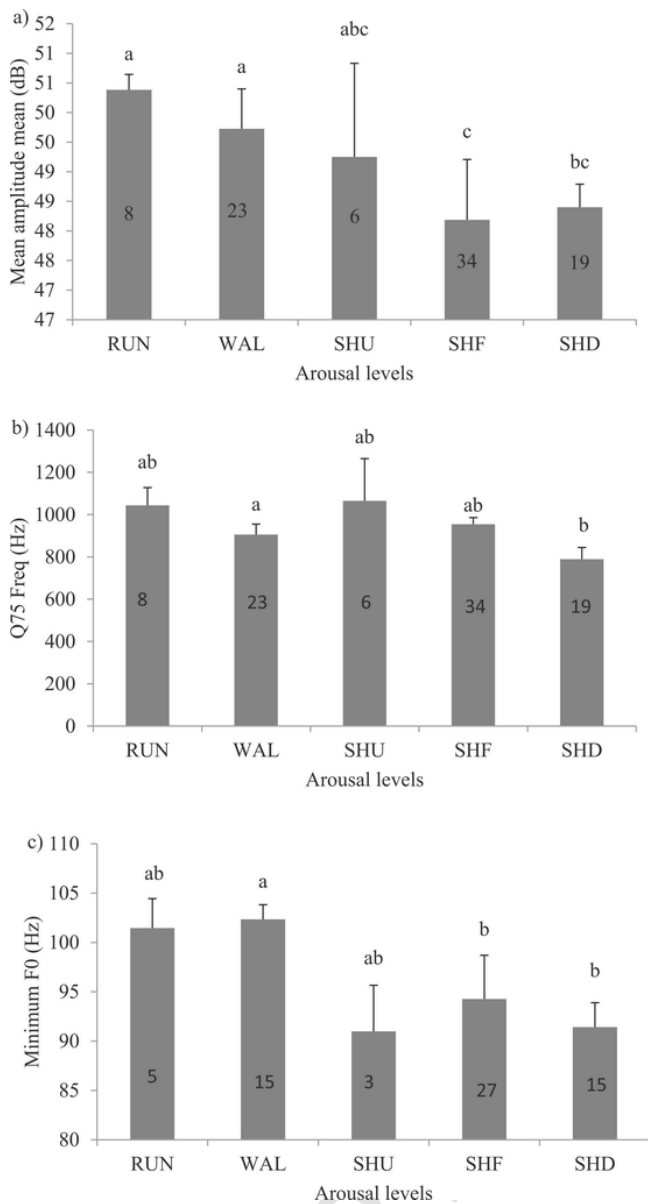


Fig. 5. Mean (+ SE) of the acoustic parameters: (a) amplitude mean and (b) 3rd quartile frequency (Q3 freq) of snort, roar, and bark calls; and (c) the minimum F0 of roar calls emitted by spotted pacas according to the arousal levels (body movement). RUN: running; WAL: walking; SHU: stand up with head up; SHF: stand up with head facing forward; SHD: stand up with head down. Different letters above bars indicate difference between means by Tukey tests ($P < 0.05$). The numbers within the bars indicate the number of individuals that emitted each call at the different arousal levels.

the Q75 of roar, bark, and snort calls as well as the minimum F0 of roar calls did not differ between when spotted pacas were running (highest arousal level) and standing upright with head down (lowest arousal) (Fig. 5b and c). Therefore, these results suggest that the energy distribution and fundamental frequency are not good indicators of arousal for this species. Additionally, the formants F1 of the bark and roar calls were not affected by valence ($F_{3, 467.74} = 2.17, P = 0.091$ and neither by arousal ($F_{4, 462.70} = 1.55, P = 0.187$) (see S5 for complete statistical analysis).

4. Discussion

The results support our hypothesis that the daily cleaning routine is a threatening event for spotted paca and thus generates a negative af-

fective state. As we expected, most of the alarm calls, snorts, roars and barks, emitted either as a single element or as phrases, occurred at this time. The alarm calls were triggered by the keeper entering the pen and sweeping the floor, thus waking up spotted pacas that were sleeping in their shelter. Previously, snorts have been recorded among captive spotted pacas during cleaning of the pen activities as well (Lima et al., 2018). Although most of the roars emitted either as single elements or as phrases occurred in the negative valence condition, this call was prevalent in the positive affective valence condition as well. Therefore, the overall number of roars is not a useful indicator of emotional valence for this species. Although the high overall number of barks recorded in the negative valence, this call was more prevalent in the assumed positive and highly positive valences (see below).

The tooth chattering call also occurred only in the negative condition, and previously this call was also associated with stressful events, such as keeper proximity, weaning, and agonistic encounters (Lima et al., 2018). One can argue that keeper proximity is not a true threat, because the keeper usually brings the food, which could be associated with positive valence. However, tooth chattering is present in other caviomorph species and occurs in similar negative valences, such as agonistic, threatening and presence of human (*Kerodon rupestris*: Lacher, 1981; *Hydrochoerus hydrochaeris*: Barros et al., 2011; *Cavia aperea*, Monticelli and Ades, 2013). In any case, further behavioural studies along with physiological measures are still necessary to confirm that the daily cleaning routine is negative for *C. paca*. Additionally, although the tooth chattering calls were emitted while running, indicating arousal, this occurred for a only single individual. Therefore, whether the emission of tooth chattering can be useful indicator of emotional valence or arousal needs to be confirmed in further studies.

Our results partially support the assumption that feeding time induces a positively valued affective state for spotted pacas, as they emitted far fewer snorts at this time. Additionally, spotted paca seems to experience different emotions while the reward received increases. The animals emitted, either as single elements or as phrases, similar numbers of snort, roar and bark calls when fed only with corn bran – the assumed ambiguous valence condition. However, the emission of snorts gradually decreased, while bark calls became progressively more prevalent when fed regular diet, which includes seasonal fruits such as banana and guava, as well as when they were fed only mango, the species' favourite food (Laska et al., 2003). Thus, the overall emission of barks by spotted pacas could be perceived as a positive valence indicator (see below).

On the other hand, the emission of barks can also be related to agonistic interactions. Besides the alarm context, the emission of barks by spotted pacas was also related to agonistic encounters (Lima et al., 2018). Therefore, it would be reasonable to assume that, rather than a positive valence indicator, the emission of barks seems to be related to competition for a limited and preferred food resource (mango and other fruits). We observed that when animals were fed a regular diet, the three spotted pacas in each group usually ate the mix of corn bran and vegetables together, even though these foods were distributed in three separate feeders. However, they often picked and carried the seasonal fruits that comprised the regular diet, as well as the mango, to eat separately from one other, as also previously observed (Lima, personal observation). In this case, the feeding time could be considered as a negative valence condition due to competition for favourite items in the diet. Meanwhile, some acoustic parameters of barks suggest that this call is indeed related to positive emotional valences for the spotted paca. For instance, the rhythm of barks in the negative valence was much higher than in the positive valence condition (Fig. 3c). If the bark call was related to food disputes and therefore a negative valence indicator, the emission rate in the positive valence should be at least similar to the one recorded in the negative valence condition.

Beyond differences in the overall number of alarm calls, the acoustic parameters of snorts, roars and barks differed according to the assumed

affective valence experienced by spotted pacas as well as by their arousal levels, as follows. The rhythm of barks follows the predicted pattern of higher emission rate by distressed animals in the negative valence compared to the positive valence (pleased animal) (Briefer, 2012, 2020). As we also predicted the roars and barks emitted as single elements as well as snorts and barks emitted as phrases were longer in the negative valence than in the positive condition. However, the duration of barks did not differ between the negative and highly positive valence conditions, while the duration of snort calls emitted as single elements and roars emitted as phrases did not differ among the emotional valence conditions. Therefore, the duration of these calls seems not to be useful as an indicator of emotional valence for this species.

On the other hand, during the negative valenced condition – the morning cleaning routine – the snort, roar and bark calls are characterized by a shift in the mean amplitude towards a higher level of intensity compared to the ambiguous and positive valence conditions. One can argue that to measure the intensity (amplitude contour) it would be necessary to control the distance of the animal during the audio recording. This option was not possible under our conditions, as the animals are of a relatively small size and move freely in their enclosures. However, during the audio recording, this situation occurred in all conditions tested. It is thus reasonable to suppose that this lack of accuracy was similar in all conditions and did not interfere with the results. Furthermore, as these results have potential to be used as an automated, non-invasive tool for welfare assessment in this species, it would not be possible to make adjustments during recordings.

Besides the increase in the mean amplitude, snort, roar and bark calls emitted in the negative valence condition are also characterized by a shift in the energy distribution (Q75) towards a higher frequency. In turn, the fundamental range (F0 range) of roars emitted in the positive valence conditions is characterized by a shift towards narrower F0 range than those produced in the negative valence. These results were not expected, as changes in amplitude contour, energy distribution and fundamental range are usually good indicators of arousal (Briefer, 2012, 2020). However, changes in intensity (amplitude) and energy distribution (Q75) can also be found in human voice, which reflect changes in emotional valences – higher in the positive than negative situation (e.g. Hammerschmidt and Jürgens, 2007; Goudbeek and Scherer, 2010) – as verified here for the spotted paca. Furthermore, African elephant (*Loxodonta africana*) emit rumbles with narrower F0 range in positive social contexts (affiliative interactions) than those produced in negative social contexts (dominance interactions), despite such differences were more related to emotional arousal (Soltis et al., 2011). Therefore, changes in the amplitude, energy distribution, and fundamental range of snort, roar and bark calls, together with the also expected increase in the amplitude from the lowest to the highest arousal levels, as previews suggested (Briefer, 2012, 2020), point to the possibility of using changes in these acoustic parameters, especially those of snort calls, as indicators of negative affective state and for welfare assessment in farmed spotted paca. These differences in acoustic parameters may be explained by the animals' physical reactions to a stimulus, which directly influence breathing and muscle tension and thus affect phonation, resonance and articulation of vocalizations (Briefer, 2020). In mammals, the larynx transforms airflow into sound waves (Laurijs et al., 2021). These sound waves are then filtered by the supralaryngeal vocal tract (pharynx, vocal, oral and nasal cavities, nostrils, lips, tongue, teeth and jaw of the animal), which is responsible for the vocal sounds of animals (Laurijs et al., 2021). One can argue that the circadian rhythm could affect our results, because the negative condition always occurred in the morning, while the food supply (all positive valence conditions) occurred in the afternoon. Indeed, the expression of different behavioural patterns, such as exploratory, agonistic and reproductive activities in spotted pacas, is influenced by the time of day (Hosken et al., 2021). Thus, the circadian rhythm may have affected our results, which must be verified in further studies. However, it

is important to note that the data collection in our study followed the farm's regular routine (cleaning and feeding schedule), which, in turn, represents how the farmers proceed with breeding these animals.

Stressors can influence an individual's affective state, which in turn can affect its responses, including vocalizations, to environmental stimuli (Harding et al., 2004; Paul et al., 2005; Briefer, 2012). Emission of snort, roar, and tooth chattering calls during the daily cleaning routine thus likely reflects perception of threat by *C. paca* and may be associated with stress and motivation to defend their territory (Smythe, 1987; Emmons and Feer, 1997). Additionally, an overall increase in the emission of snorts from the positive to the negative condition indicates that monitoring this vocalization may be a feasible and practical way for farmers to evaluate the welfare of farmed *C. paca*. Routine cleaning procedures could also be altered to minimize associated negative affective states, using vocalizations as a marker for welfare improvements. For instance, having a connection aisle to manage animals while cleaning, or performing pen cleaning just before feeding time, when the animals are already awake and out of their shelters, may improve animal welfare, and this could be verified in future studies.

5. Conclusions

Changes in the acoustic parameters of *Cuniculus paca* vocalizations appear to be related to affective valence and arousal levels. In a negative valenced condition and higher arousal level, spotted pacas emit snorts with higher mean amplitude as well as by higher 3rd quartile frequency (Q75) than those emitted in the positive condition – feeding time with the regular diet. These results likely denote a negative affective state and thus offer promising new non-invasive indicators of spotted paca welfare. Farmers may be able to use the emission of snorts as a signal that allows them to monitor and improve husbandry practices adopted in spotted paca farming.

Uncited references

Acknowledgements

We thank Dr Andrey Anikin and two other anonymous reviewers for the valuable comments to the original manuscript. We are very grateful to Mr. Adilson Campos Pimenta for allowing us to study his pacas. This study was financed in part by the Bahia State Research Support Foundation (Fundação de Amparo à Pesquisa do Estado da Bahia, FAPESB #APP074/2016), Coordination for the Improvement of Higher Education Personnel (CAPES - Finance Code 001) and National Institute of Science and Technology in Interdisciplinary and Transdisciplinary Studies in Ecology and Evolution (IN-TREE – Process CNPq #465767/2014-1 and CAPES #23038.000776/2017-54), Bahia, Brazil. SSCN and SLGNF received a grant from the Council for Scientific and Technological Development (CNPq) (Processes # 303448/2019-9 and # 04226/2019-0, respectively). We are also grateful for a UK BBSRC Brazil Partnering Award (BB/R021112/1; PI: M. Mendl) for supporting the collaborative work described here.

CRedit authorship contribution statement

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Stella G. Callazans Lima and Allison Lima. The first draft of the manuscript was written by Allison Lima and Stella G. C. Lima, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflict of interest statement

Me and the co-authors of the ms 'Vocal expression of emotions in farmed spotted paca (*Cuniculus paca*)' have no actual or potential conflict of interest including any financial, personal or other relationships with other people or organizations within three years of beginning the submitted work that could inappropriately influence, or be perceived to influence, this work.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.applanim.2022.105753](https://doi.org/10.1016/j.applanim.2022.105753).

References

- Aldrigui, L.G., Nogueira-Filho, S.L.G., Altino, V.S., Mendes, A., Clauss, M., Nogueira, S.S.C., 2018. Direct and indirect caecotrophy behaviour in paca (*Cuniculus paca*). *J. Anim. Physiol. Anim. Nutr.* 102, 1774–1782. <https://doi.org/10.1111/jpn.12961>.
- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–266. <https://doi.org/10.1163/156853974x00534>.
- August, P.V., Anderson, J.G., 1987. Mammal sounds and motivation-structural rules: a test of the hypothesis. *J. Mammal.* 68, 1–9. <https://doi.org/10.2307/1381039>.
- Baciadonna, L., Briefer, E.F., McElligott, A.G., 2020. Investigation of reward quality-related behaviour as a tool to assess emotions. *Appl. Anim. Behav.* 225. <https://doi.org/10.1016/j.applanim.2020.104968>.
- Barquero, R., Barquero, A.M., 2008. Efecto de la dieta sobre la ganancia de peso en individuos de *Agouti paca* em cautiverio. *Rev. Mex. Mastozool.* 12, 6–16.
- Barros, K.S., Tokumaru, R.S., Pedroza, J.P., Nogueira, S.S.C., 2011. Vocal repertoire of captive capybara (*Hydrochoerus hydrochaeris*): structure, context and function. *Ethology* 116, 83–93. <https://doi.org/10.1111/j.1439-0310.2010.01853.x>.
- Beck-King, H., Von Helversen, O., Beck-King, R., 1999. Home Range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: a study using alternative methods. *Biotropica* 31, 675–685. <https://doi.org/10.1111/j.1744-7429.1999.tb00417.x>.
- Boersma, P., Weenink, D., 2022. Praat: Doing Phonetics By Computer (Version 5.3.06) [Computer software]. Institute of Phonetic Sciences, Amsterdam. (<http://www.praat.org>).
- Briefer, E.F., 2012. Vocal expression of emotions in mammals: mechanisms of production and evidence. *J. Zool.* 288, 1–20. <https://doi.org/10.1111/j.1469-7998.2012.00920.x>.
- Briefer, E.F., 2020. Coding for 'Dynamic' information: vocal expression of emotional arousal and valence in non-human animals. In: Aubin, T., Mathevon, N. (Eds.) *Coding Strategies in Vertebrate Acoustic Communication*. Animal Signals and Communication, vol 7. Springer, Cham. https://doi.org/10.1007/978-3-030-39200-0_6.
- Briefer, E.F., Vizier, E., Gyax, L., Hillmann, E., 2019. Expression of emotional valence in pig closed-mouth grunts: Involvement of both source-and filter-related parameters. *J. Acoust. Soc. Am.* 145, 2895–2908. <https://doi.org/10.1121/1.5100612>.
- Briefer, E.F., Sypherd, C.C.R., Linhart, P., Leliveld, L., Padilla de la Torre, M., Read, E.R., Tallet, C., 2022. Classification of pig calls produced from birth to slaughter according to their emotional valence and context of production. *Sci. Rep.* 12, 1–10. <https://doi.org/10.1038/s41598-022-07174-8>.
- Burgdorf, J., Brudzynski, S., Moskal, J., 2020. Using rat ultrasonic vocalization to study the neurobiology of emotion: from basic science to the development of novel therapeutics for affective disorders. *Curr. Opin. Neurobiol.* 60, 192–200. <https://doi.org/10.1016/j.conb.2019.12.008>.
- Burman, O.H., Ilyat, A., Jones, G., Mendl, M., 2007. Ultrasonic vocalizations as indicators of welfare for laboratory rats (*Rattus norvegicus*). *Appl. Anim. Behav.* 104, 116–129. <https://doi.org/10.1016/j.applanim.2006.04.028>.
- Charif, R.A., Waack, A.M., Strickman, L.M., 2010. Raven Pro 1.4 user's manual. Cornell Lab of Ornithology, Ithaca, New York, 25506974.
- Désiré, L., Boissy, A., Veissier, I., 2002. Emotions in farm animals: a new approach to animal welfare in applied ethology. *Behav. Process.* 60, 165–180. [https://doi.org/10.1016/S0376-6357\(02\)00081-5](https://doi.org/10.1016/S0376-6357(02)00081-5).
- Eisenberg, J.F., Redford, K.H., 1989. *Mammals of the Neotropics*. University of Chicago Press, Chicago, Illinois. Volume 3: Equador, Bolivia, Brazil.
- Emmons, L., 2016. *Cuniculus paca*. The IUCN Red List of Threatened Species 2016: e.T699A22197347. doi:10.2305/IUCN.UK.2016-2.RLTS.T699A22197347.en.
- Emmons, L., Feer, F., 1997. *Neotropical Rainforest Mammals: A Field Guide*, Second ed. University of Chicago Press, Chicago, Illinois.
- Fant, G., 1960. *Acoustic Theory of Speech Production*. The Hague. The Netherlands, Mouton.
- Feng, A.S., Riede, T., Arch, V.S., Yu, Z., Xu, Z.M., Yu, X.J., Shen, J.X., 2009. Diversity of the vocal signals of concave-eared torrent frogs (*Odorrana tormota*): evidence for individual signatures. *Ethology* 115, 1015–1028. <https://doi.org/10.1111/j.1439-0310.2009.01692.x>.
- Fernández-Vargas, M., Riede, T., Pasch, B., 2021. Mechanisms and constraints underlying acoustic variation in rodents. *Anim. Behav.* 184, 135–147. <https://doi.org/10.1016/j.anbehav.2021.07.011>.
- Forkman, B., Boissy, A., Meunier-Salaün, M.C., Canali, E., Jones, R.B., 2007. A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.* 92, 340–374. <https://doi.org/10.1016/j.physbeh.2007.03.016>.
- Goudbeek, M., Scherer, K.R., 2010. Beyond arousal: valence and potency/control cues in the vocal expression of emotion. *J. Acoust. Soc. Am.* 128, 1322–1336. <https://doi.org/10.1121/1.3466853>.
- Hammerschmidt, K., Jürgens, U., 2007. Acoustical correlates of affective prosody. *J. Voice* 21, 531–540. <https://doi.org/10.1016/j.jvoice.2006.03.002>.
- Hänninen, L., Pastell, M., 2009. CowLog: open-source software for coding behaviors from digital video. *Behav. Res. Methods* 41, 472–476. <https://doi.org/10.3758/BRM.41.2.472>.
- Harding, E.J., Paul, E.S., Mendl, M., 2004. Animal behavior: cognitive bias and affective state. *Nature* 427, 312–312. <https://doi.org/10.1038/427312a>.
- Hinchcliffe, J.K., Mendl, M., Robinson, E.S.J., 2020. Rat 50 kHz calls reflect graded tickling-induced positive emotion. *Curr. Biol.* 30, 1034–1035. <https://doi.org/10.1016/j.cub.2020.08.038>.
- Hosken, F.M., Oliveira, M.H.V., Malheiros, J.M., Martins, E.H., Ferreira, F.N.A., Ferreira, W.M., Lara, L.B., 2021. Experimental ethology of intensively reared lowland pacas (*Cuniculus paca*). *Trop. Anim. Health Prod.* 53, 1–8. <https://doi.org/10.1007/s1250-021-02801-4>.
- Jirkof, P., Rudeck, J., Levejohann, L., 2019. Assessing affective state in laboratory rodents to promote animal welfare-what is the progress in applied refinement research? *Animals* 9, 1026. <https://doi.org/10.3390/ani9121026>.
- Lacher, Jr, T.E., 1981. The comparative social behavior of *Kerodon rupestris* and *Galea spixii* and the evolution of behavior in the Caviidae. *Bull. Carne Mus. Nat. Hist.* 17, 1–71. https://agris.fao.org/agris-search/search.do?recor_dID=US201300338790.
- Laska, M., Baltazar, J.L., Luna, E.R., 2003. Food preferences and nutrient composition in captive pacas, *Agouti paca* (*Rodentia, Dasyproctidae*). *Mamm. Biol.* 68, 31–41. <https://doi.org/10.1078/1616-5047-00059>.
- Laurijs, K.A., Briefer, E.F., Reimert, I., Webb, L.E., 2021. Vocalisations in farm animals: a step towards positive welfare assessment. *Appl. Anim. Behav. Sci.* 236, 1–13. <https://doi.org/10.1016/j.applanim.2021.105264>.
- Lima, S.G., Sousa-Lima, R.S., Tokumaru, R.S., Nogueira-Filho, S.L.G., Nogueira, S.S.C., 2018. Vocal complexity and sociality in spotted paca (*Cuniculus paca*). *PLoS One* 13. <https://doi.org/10.1371/journal.pone.0190961>.
- Maigrot, A.L., Hillmann, E., Briefer, E.F., 2018. Encoding of emotional valence in wild boar (*Sus scrofa*) calls. *Animals* 8, 85. <https://doi.org/10.3390/ani8060085>.
- Mendl, M., Paul, E.S., 2017. Getting to the heart of animal welfare. The study of animal emotion. *Stichting Animales, Netherlands*.
- Mendl, M., Paul, E.S., 2020. Animal affect and decision-making. *Neurosci. Biobehav. Rev.* 112, 144–163. <https://doi.org/10.1016/j.neubiorev.2020.01.025>.
- Mendl, M., Burman, O.H., Paul, E.S., 2010. An integrative and functional framework for the study of animal emotion and mood. *Proc. R. Soc. B* 277, 2895–2904. <https://doi.org/10.1098/rspb.2010.0303>.
- Monticelli, P.F., Ades, C., 2013. The rich acoustic repertoire of a precocious rodent, the wild cavy *Cavia aperea*. *Bioacoustics* 22, 49–66. <https://doi.org/10.1080/09524622.2012.711516>.
- Morton, E.S., 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *Am. Nat.* 111, 855–869. <https://doi.org/10.1086/283219>.
- Nogueira, S.S.C., Nogueira-Filho, S.L.G., Duarte, J., Mendl, M., 2021. Temperament, plasticity, and emotions in defensive behaviour of paca (Mammalia, Hystricognatha). *Animals* 11, 293. <https://doi.org/10.3390/ani11020293>.
- Nogueira Filho, S.L.G., Nogueira, S.S.C., 1999. Criação de pacas (*Agouti paca*). FEALQ, Piracicaba, São Paulo, Brazil.
- Paul, E.S., Harding, E.J., Mendl, M., 2005. Measuring emotional processes in animals: the utility of a cognitive approach. *Neurosci. Biobehav. Rev.* 29, 469–491. <https://doi.org/10.1016/j.neubiorev.2005.01.002>.
- Pérez, E.M., 1992. *Agouti paca*. *Mamm. Species* 404, 1–7. <https://doi.org/10.2307/3504102>.
- Riede, T., Fitch, T., 1999. Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). *J. Exp. Biol.* 202, 2859–2867. <https://doi.org/10.1242/jeb.202.20.2859>.
- Russell, J.A., 1980. A circumplex model of affect. *J. Pers. Soc. Psychol.* 39, 1161. <https://doi.org/10.1037/h0077714>.
- Russell, J.A., 2003. Core affect and the psychological construction of emotion. *Psychol. Rev.* 110, 145. <https://doi.org/10.1037/0033-295X.110.1.145>.
- Simola, N., Granon, S., 2019. Ultrasonic vocalizations as a tool in studying emotional states in rodent models of social behavior and brain disease. *Neuropharmacology* 159, 107420. <https://doi.org/10.1016/j.neuropharm.2018.11.008>.
- Smythe, N., 1987. The paca (*Cuniculus paca*) domestic source of protein for the Neotropical humid lowlands. *Appl. Anim. Behav. Sci.* 17, 155–170. [https://doi.org/10.1016/0168-1591\(87\)90017-7](https://doi.org/10.1016/0168-1591(87)90017-7).
- Smythe, N., Brown Guanti, O.D., 1995. La domesticación y cría de la paca (*Agouti paca*) (No. L01/1667). FAO, Rome, Italy.
- Soltis, J., Blowers, T.E., Savage, A., 2011. Measuring positive and negative affect in the voiced sounds of African elephants (*Loxodonta africana*). *J. Acoust. Soc. Am.* 129, 1059–1066.
- Taylor, A.M., Reby, D., 2010. The contribution of source-filter theory to mammal vocal communication research. *J. Zool.* 280, 221–236. <https://doi.org/10.1111/j.1469-7998.2009.00661.x>.
- Titze, I.R., 1994. *Principles of Voice Production*. Prentice Hall, Englewood Cliffs, New Jersey.
- Zaytseva, A.S., Volodin, I.A., Ilchenko, O.G., Volodina, E.V., 2019. Ultrasonic vocalization of pup and adult fat-tailed gerbils (*Pachyuromys duprasi*). *PLoS One* 14. <https://doi.org/10.1371/journal.pone.0219749>.