Received: 18 December 2021 | Revised: 30 May 2022 | Accepted: 3 June 2022

DOI: 10.1002/dev.22309

Developmental Psychobiology WILEY

RESEARCH ARTICLE

Early life experience and sex influence acoustic repertoire use in wild-born, but hand-reared, captive cheetahs (*Acinonyx jubatus*)

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Funding information
International Research Project VOCOM; University Bretagne-Loire; Beauval Nature pour la Conservation et la Recherche; University of Rennes 1 and the CNRS

Abstract

Early deprivation of adult influence is known to have long-lasting effects on social abilities, notably communication skills, as adults play a key role in guiding and regulating the behavior of youngsters, including acoustic repertoire use in species in which vocal production is not learned. Cheetahs grow up alongside their mother for 18 months, thus maternal influences on the development of social skills are likely to be crucial. Here, we investigated the impact of early maternal deprivation on vocal production and use in 12 wild-born cheetahs, rescued and subsequently hand-reared either at an early (less than 2 months) or a later stage of development. We could distinguish 16 sound types, produced mostly singly but sometimes in repeated or multitype sound sequences. The repertoire of these cheetahs did not differ fundamentally from that described in other studies on adult cheetahs, but statistical analyses revealed a concurrent effect of both early experience and sex on repertoire use. More specifically, early-reared males were characterized by a high proportion of *Purr*, *Meow*, and *Stutter*; early-reared females *Mew*, *Growl*, *Hoot*, *Sneeze*, and *Hiss*; late-reared males *Meow*, *Mew*, *Growl*, and *Howl*; and late-reared females mostly *Meow*. Our study demonstrates therefore the long-term effects of maternal deprivation on communication skills in a limited-vocal learner and its differential effect according to sex, in line with known social differences and potential differential maternal investment. More generally, it emphasizes the critical importance to consider the past history of the subjects (e.g., captive/wild-born, mother/hand-reared, early/late-mother-deprived, etc.) when studying social behavior, notably acoustic communication.

KEYWORDS
Acinonyx jubatus, acoustic communication, acoustic repertoire, cheetahs, early-life experience, hand-rearing, maternal deprivation, sex-differences

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Hélène Bouchet and Alban Lemasson contributed equally to this work.

Developmental Psychobiology. 2022;64:e22309.
https://doi.org/10.1002/dev.22309

1 INTRODUCTION

The extent to which the early stages of life, notably in the case of a maternal deprivation, impact the future skills of an individual, notably his capacities at communicating socially beyond the mere ability to produce the species-specific repertoire of sound types, remains a field of interest that requires further investigation. Communication skills underlie a wide array of social competencies throughout life, therefore degraded communicative abilities are likely to impact, among others, social, parental, or else emotional skills. In fact, early-life experience has been demonstrated to have both short- and long-term effects on social skill and emotional regulation in a wide range of species (Pryce et al., 2005). When raised in the absence of adult models, especially when maternally deprived at an early stage, individuals often have difficulties appropriately interacting with peers later in life, notably due to a reduced propensity to form social bonds and an increased level of aggressiveness. For instance, adult-deprived individuals may be less inclined to engage in allogrooming (e.g., chimpanzees: Kalcher-Sommersguter et al., 2015; macaques: Mason, 1960), to seek spatial proximity with conspecifics (e.g., giraffes: Siciliano-Martina & Martina, 2018; pullets: Perré et al., 2002; mice: Bouet et al., 2011; cichlids: Hesse & Thünken, 2014; honey bees: Hewlett et al., 2018), to signal their intention by threatening before physically attacking (e.g., rats: Tóth et al., 2008), or to be responsive to maternal calls (e.g., degus: Braun et al., 2003). In addition, the frequency and severity of their aggressive displays often exceed that of mother-reared individuals (e.g., cats: Ahola et al., 2017; chimpanzees: van Leeuwen et al., 2014; macaques: Mason, 1960; Suomi, 1997; elephants: Slotow et al., 2000; horses: Bourjade et al., 2009; rats: Tóth et al., 2008; cichlids: Arnold & Taborsky, 2010; Hesse & Thünken, 2014). Breeding behavior can also be affected by early maternal deprivation in captive animals, subsequently hand reared by human caretakers (e.g., felids: Hampson & Schwitzer, 2016; Mellen, 1992; gorillas: Ryan et al., 2002; macaques: Suomi, 1997). Furthermore, adult-deprived individuals, even when developing among age peers, show impaired social and emotional profiles, being highly reactive to novelty (i.e., anxious and shy) and more impulsive than their mother-reared counterparts as a result of insecure early attachments (e.g., macaques: Suomi, 1997; elephants: Slotow et al., 2000; horses: Bourjade et al., 2009; giant pandas: Snyder et al., 2003; mice: Ros-Simó & Valverde, 2012; degus: Braun et al., 2003; pullets: Perré et al., 2002; cichlids: Bannier et al., 2017). Conversely, growing up along additional adult models tends to enhance the development of appropriate bonding behaviors (e.g., mice: D'Andrea et al., 2007). Adults in general seem to play a key role in regulating the behavior of youngsters (Bourjade et al., 2009; Slotow et al., 2000; Suomi, 1997).

Communication skills, themselves, are also likely to be greatly influenced by early-life conditions (Kaplan, 2017; Snowdon & Hausberger, 1997). Deprivation of adult tutors is well known to result in disrupted communication patterns in vocal learners such as songbirds (e.g., starlings: Bertin et al., 2007, 2009; Cousillas et al., 2006; Poirier et al., 2004; canaries: Lehongre et al., 2006; for reviews, see Nieder & Mooney, 2020; Woolley, 2012). However, it is only recently that, in some so-called nonvocal learners, parental feedback was found to play a key role in vocal development too. Thus, parentally deprived marmosets exhibit persisting infantile acoustic features ("babbling," larger diversity of sounds) until adulthood as compared to parent-raised individuals (Gultekin & Hage, 2017, 2018). Also, increasing experimentally the amounts of contingent parental vocal feedback led to an earlier transition in development from immature to mature contact calls in juvenile marmosets (Takahashi et al., 2017). Moreover, although it is generally admitted that most terrestrial mammals are able to produce their species-specific calls from birth (Hammerschmidt & Fischer, 2008; Tyack, 2020), when shifting the focus from vocal production learning (i.e., modification of the acoustic structure of the signal as a result of experience with peers) to contextual learning (i.e., modification of call use as a result of social experience), quite a few limited-vocal learners have been found to demonstrate remarkable socially guided abilities for flexible call use (Cheney & Seyfarth, 2018). For example, social experience is necessary for young vervet monkeys to refine the context of production of alarm calls to specific predators (Seyfarth & Cheney, 1986), while it is also likely to play a role in the acquisition of conversational rules such as turn-taking in monkeys (Bouchet et al., 2017; Chow et al., 2015; Lemasson et al., 2011) as it is the case in songbirds (e.g., starlings: Henry et al., 2015). Finally, the social status of an individual, determined notably by its sex, age, and hierarchical rank, can translate into the preferential use of specific call types at different stages in life (e.g., monkeys: Bouchet et al., 2010, 2012; apes: Mitani & Nishida, 1993).

Cheetahs (*Acinonyx jubatus*) stand out from the Felidae family with regard to sociality. While most felid species are solitary, with the exception of lions (*Panthera leo*) and feral domestic cats (*Felis silvestris catus*) (Bradshaw, 2016), cheetahs display a unique social organization. Females are solitary, unless accompanied by their dependent offspring, whereas males are facultatively social, living either alone or forming long-term alliances within pairs or trios (rarely quartets) (Caro, 1994; Sunquist & Sunquist, 2002; Wachter et al., 2018). Male coalitions typically consist of brothers from the same litter, but groups larger than two frequently include a nonrelative (Caro, 1993; Marker et al., 2010). Males in coalitions are more likely than single males to take and retain small territories (Caro, 1990; Caro & Collins, 1987). Other males are "floaters" roaming in large, overlapping, undefended home ranges (Wachter et al., 2018). Solitary females are not territorial either; they occupy large home ranges encompassing these of several males (Gottelli et al., 2007) and overlapping with those of related females, which suggests some degree of female philopatry as well as a certain level of tolerance toward other females (Caro, 1994; Laver, 2005). Females give birth to their first litter around 2–3 years old (Sunquist & Sunquist, 2002; Wachter et al., 2018). Mothers hide their cubs in a den for the first 8 weeks of life (Laurenson, 1993). After emergence, cubs follow their mother around, start feeding on solid food, and gradually acquire hunting skills; weaning occurs around 4 months of age (Caro, 1994). During the period that offspring rely upon their mother for solid food, mothers have been found to favor their litters containing two or more sons compared to those including a single son in terms of food provisioning, whereas no such effect was found for daughters (Caro, 1990). Young cheetahs reach independence at 18 months old (Laurenson et al., 1992) and family dissolution is initiated by the mother, often already pregnant (Wachter et al., 2018). Siblings then roam with their littermates for a further 6 months, until females split from their brothers and go on to produce their first litter (Caro, 1994; Marker et al., 2010). While females remain close to their natal home range, males usually disperse and settle away from their natal area (Wachter et al., 2018). Given that cubs grow alongside their mother and siblings for an extended period of time, social influences are expected to play a key role in the acquisition of social skills by young cheetahs.

While vocal development in cheetah cubs has received very little attention (Volodina, 1998), adults are known to rely on both acoustic and olfactory signals to communicate. While calling opens the possibility of communicating over long distances, scent marking enables indirect information transfer with a time delay (Wachter et al., 2018). Cheetahs' acoustic signals have been subject to several studies, but no consensus has been reached in the literature yet regarding call terminology, or even classification in some cases (Nagorzanski, 2018; Wachter et al., 2018) (see Appendix A). The cheetah's acoustic repertoire, that is, the list of species-specific types of sounds structurally and functionally distinguishable, thus deserves reassessment and clarification. Reports of vocal behavior from the wild give some contextual information about call emission, but often lack a detailed description of the acoustic structures, which prevents comparison (Caro, 1994; Peters, 1991; Sunquist & Sunquist, 2002). Studies in captivity have often focused on a limited number of call types and contexts, for instance "purring" (Eklund et al., 2010, 2012a; Eklund & Peters, 2013), agonistic calls (Eklund et al., 2012b), feeding calls (Stoeger-Horwath & Schwammer, 2003), and separation–reunion calls (Ruiz-Miranda et al., 1998). The most comprehensive studies of the cheetah acoustic repertoire so far have been conducted in captivity and report eight call types in adults and seven in juveniles (Smirnova et al., 2016; Volodina, 1998, 2000). In addition, the cheetah's vocal repertoire displays a certain level of gradation, in the form of intermediate sounds (i.e., displaying features characteristic of different call types) as well as transitional sounds (i.e., gradually morphing from one call type into another) (Eklund et al., 2012b; Volodina, 2000), although these have not been properly quantified yet. So far, these complex calls have been either disregarded or counted up separately (i.e., multiple parts of transitions counted as distinct calls) (Smirnova et al., 2016), preventing the analysis of additional acoustic variability at higher levels.

The main limitations of the current cheetah literature are, on the one hand, the lack of quantitative information regarding individual use of the different sound types in wild-born animals (in other words, a reference point to compare captive-born animals with) and, on the other hand, the insufficient details regarding the social/developmental background of the captive subjects whose acoustic repertoire has been investigated (see Appendix B). Whether subjects have been housed singly or within same sex or mixed groups is often unspecified (e.g., Smirnova et al., 2016; Volodina, 2000), despite the known impact of social background on physiology and behavior (e.g., in females: Wielebnowski et al., 2002; in males: Chadwick et al., 2013; Koester et al., 2015) and its likely influence on communicative patterns. Besides, captivity itself has been shown to cause chronic stress in cheetahs and to be associated with lower levels of testosterone in males (Terio et al., 2004). More importantly, most captive cheetahs that have been studied were captive born and are susceptible to have been hand reared by human caretakers instead of mother reared, as it is a quite common practice (Bell et al., 2012; Bircher & Noble, 1997; Woc Colburn et al., 2018).

Cheetahs are listed as vulnerable within the IUCN red list (Durant et al., 2010, 2017; Marker et al., 2010). In situ conservation centers are committed to rescuing victims of human–wildlife conflict where adult individuals are frequently killed, leaving their offspring orphaned at various stages of development. Depending on the age young cheetahs are rescued, hand-rearing is sometimes necessary. Hand-rearing is known to have a significant impact on cheetahs' subsequent mating behavior and parental skills (Hampson & Schwitzer, 2016), and an unpublished master's study suggests that it may also impact their social behavior with hand-reared males engaging more frequently in allogrooming and physical contact, but vocalizing less often than their mother-reared counterparts (Rose, 2012). In this study, we aimed at investigating more closely the possible impact of maternal deprivation and subsequent hand-rearing on the acoustic repertoire size (i.e., number of different sound types produced) and use (i.e., sound types produced preferentially) of adult cheetahs. We hypothesized that, because cheetahs are considered, like most terrestrial mammals, as non- or limited-vocal learners, repertoire composition and size would vary little, whereas the development of repertoire use would be under adult influence. We expected therefore to find differences in repertoire use according to age at maternal deprivation and possibly according to sex, as mothers show a differential care according to their offspring's sex and as social dispositions vary according to sex. Twelve captive hand-reared adult cheetahs of both sexes were studied. In an attempt to also clarify the classification of sounds produced by this species, we started with establishing the acoustic repertoire of our study population based on distinctive acoustic features. We then investigated whether the relative use of the different sound types varied according to sex and early-life experience ("early" vs. "later" deprivation and hand-rearing), in terms of quantity or quality.

2 | METHODS

2.1 | Study subjects and housing conditions

This study was conducted at the Cheetah Conservation Fund (CCF), a center dedicated to the conservation of cheetahs founded in 1990 and located near Otjiwarongo, Namibia. The CCF center hosts around 30 wild-born cheetahs rescued as cubs or juveniles after their mother had been killed or disappeared. In Namibia, it is considered that individuals orphaned before the age of 6 months have not learned the necessary skills from their mother to ensure successful release back into the wild and therefore remain in captivity (Walker et al., 2022). At the CCF center, captive cheetah cubs are hand reared by the staff of wildlife professionals until they reach maturity. Whenever possible, orphaned cubs are kept in groups of siblings or paired with same-sex, same-age peers. As there are large differences in the developmental stages at which the CCF cubs were rescued, the center distinguishes between "early" versus "late" hand-rearing depending on whether they were rescued before or after the age of 2 months. Early-reared individuals require hand-feeding and sometimes even bottle-feeding every couple of hours; these individuals are kept in a nursery enclosure at the center. If there is only a single cub, they are kept with a human keeper nearly 24 h a day, to compensate to some extent for the absence of attention and nurturing a mother cheetah would normally provide. If the cubs come in as a social group or could be bonded to other cubs, they still require a lot of attention from keepers, but less so, as they are able to provide social stimulation to each other between feedings. Keepers encourage vocal production in cubs by responding to their spontaneous vocalizations with mimicking sounds whenever possible. Late-reared individuals are already independent in terms of food consumption and require less human intervention. They are not kept in a nursery but are put out in a slightly larger enclosure. When they first arrive, the cubs still have regular contact with keepers and vocalizations are still encouraged, but to a lesser extent as the time spent with cubs is less than that for early reared. Also, it appears that these young cheetahs tend to respond less to human stimulations than the very young cubs (personal observation). All young cheetahs live in enclosures surrounded by other groups of hand-reared cheetahs that provide additional acoustic stimulations.

For this study, we selected hand-reared individuals that had reached adulthood, were living in stable same-sex groups, and were housed away from the headquarters, thus with human contact limited to daily visits for feeding and checking.

The study subjects were 12 cheetahs, four females and eight males: seven of them (two females, five males) were rescued as cubs (a few days up to 2 months of age), thus "early-reared," while the other five (two females, three males) were rescued as juveniles (between 2 and 6 months of age), therefore "late-reared." At the time of the study, they were all adults, aged between 5 and 15 years (Table 1). All but one male (NAAJU1473) were sexually intact. These cheetahs lived in four same-sex groups of two to four individuals, including related pairs as well as unrelated individuals (Table 1). They were housed in large outdoor enclosures (2–5 ha) with natural shelter in the form of trees, and a three-sided artificial shelter. They were in visual and auditory, but not physical, contact with other neighboring cheetah groups. Cheetahs were fed once a day (apart from 1 day fasting per week to mimic eating habits in the wild for this species) with donkey or horse meat. They had ad libitum access to clean water.

2.2 | Data collection

Observations were carried out on the four study groups between August and November 2019. Cheetah groups were observed in a random order, with sessions spread throughout daytime between 6:00 a.m. and 7:00 p.m. A special focus was given to early mornings 6:00 a.m. to 12:00 p.m. (71.4%) and, to a lesser extent, to late afternoons 4:30 p.m. to 7:00 p.m. (21.4%) known to be the most active periods for cheetahs (Sunquist & Sunquist, 2002). For each group, four or five sessions were conducted prior to and throughout feeding, whereas all other sessions were conducted out of feeding context. In total, 70 observation sessions (16–19 per group) were conducted, lasting on average 3 h each (3 h 7 min ± 1 h 29 min), summing up to 218 h 44 min of recordings (Table 1).

During these observation sessions, cheetah acoustic signals were recorded following the all-occurrences sampling procedure (Altmann, 1974) using a directional microphone Sennheiser K6/ME66 attached to a portable stereo digital recorder Marantz PMD661 MKII (sampling frequency: 44,100 Hz, resolution: 16 bits). We collected a total of 3297 sounds in the four study groups. The identity of the caller was recorded whenever possible (i.e., for 2656 sounds).

2.3 | Data analysis

Spectrograms of the calls were generated for auditory and visual inspection using Ocenaudio audio editor (256-pt FFT Hanning window, sampling rate for inspection: 22,050 Hz). A dichotomous classification key was established based on distinctive frequency, pulse, and temporal features, an approach commonly used to describe the acoustic repertoire of mammal and bird species (Adret-Hausberger, 1989; André et al., 2020; Fournet et al., 2015; Hausberger & Guyomarc'h, 1981; Lemasson & Hausberger, 2011). We distinguished between vocal and nonvocal sounds: the former are sounds involving vibrations of the vocal cords, either through phonation or by contraction of the vocalis muscle (Frazer Sissom et al., 1991; Herbst et al., 2012; Weissengruber et al., 2008), whereas the latter are unvoiced sounds produced by the airflow being forced through a vocal tract constriction (e.g., snort, snore, and blow in horses: Stomp et al., 2018; sneeze in African wild dogs: Walker et al., 2017).

We observed both single- and multiunit sounds in our dataset consisting of 2656 sounds; thus, we coded all sounds at the unit level, in terms of unit types and number of units. As transitions between expiratory and inspiratory phases have been estimated to be quite short in cheetahs, with durations in the range of 50–200 ms in purrs for example (Eklund et al., 2010), we set up the threshold for two units (of any type) to be considered as parts of the same sound to $\Delta = 200$ ms. This way, we could code for single-type sounds, including either one (Single) or several (Repeated, in series) units of the same type, as well as multitype sounds made of a mix of several units of different types, either produced joined (Transitions, with $\Delta = 0$ ms) or juxtaposed (Combinations, with $0 < \Delta \leq 200$ ms). The level of agreement between two raters (HB, KC) at classifying the single-type sounds was 90.28% (2164 sounds similarly labeled out of 2397).

TABLE 1 Characteristics of the study subjects

Group[a]	Individual	NAAJU identifier	Sex	Rearing condition[b]	Estimated age (years)[c]	Relatedness (siblings)[d]	Observation time (N sessions)
G1	Harry	1474	F	Early	14.4	a	52 h 32 min ($N = 19$)
G1	Hermione	1475	F	Early	14.4	a	52 h 32 min ($N = 19$)
G1	Aurora	1641	F	Late	7.1	–	52 h 32 min ($N = 19$)
G1	Rainbow	1640	F	Late	7.1	–	52 h 32 min ($N = 19$)
G2	Shunga	1549	M	Early	11.8	b	55 h 58 min ($N = 18$)
G2	N'Dunge	1548	M	Early	11.8	b	55 h 58 min ($N = 18$)
G2	LittleC	1532	M	Early	12.5	–	55 h 58 min ($N = 18$)
G2	Ron	1473	M	Early	14.4	a	55 h 58 min ($N = 18$)
G3	Phoenix	1565	M	Early	11.3	–	56 h 36 min ($N = 17$)
G3	B2	1646	M	Late	5.8	–	56 h 36 min ($N = 17$)
G4	Mischief	1581	M	Late	10.7	c	53 h 38 min ($N = 16$)
G4	Phil	1583	M	Late	10.7	c	53 h 38 min ($N = 16$)

[a] Physical contacts between subjects were limited to individuals belonging to the same group (either G1, G2, G3, or G4), but visual and auditory contacts were possible across groups (both study groups and unobserved ones within the CCF center).

[b] Rescued before ("Early-reared") or after ("Late-reared") 2 months old.

[c] Age at the end of the study (December 2019), based on first estimation at the time of rescue.

[d] Individuals with the same letter in that column are siblings.

2.4 | Statistical analysis

Statistical analysis was performed using R Studio 1.1.463 (R version 3.5.0) (R Core Team, 2016; RStudio Team, 2016), except for Chi-squared tests conducted using Microsoft Excel.

We first assessed whether sex and/or rearing conditions had an impact on calling rates (i.e., average number of sounds produced per hour per individual) and repertoire size (i.e., number of different sound types produced within single-type sounds by each individual) using Mann–Whitney or Kruskal–Wallis tests (for $N = 2$ or $N > 2$ categories of individuals included in the comparison, respectively) ("wilcox.test" and "kruskal.test" in R *stats* package).

We aimed at evaluating the relative use of the different sound types by cheetahs with different sex and early-life experiences. More specifically, we tested whether the different types of single-type sounds (i.e., Single or Repeated) occurred in the same or different proportions within the repertoire displayed by each category of individuals (females vs. males, early vs. late-reared). A $\text{GLMM}_{\text{binomial–logit}}$ model was built using the "glmer" function (in R *lme4* package), the response variable being the proportion of a given single-type sound type out of the whole sample of sound (both single- and multitype) recorded for a given individual on a given day. All explanatory variables (sound type, subjects' sex, and early-life experience) were fitted in the model as fixed factors, alongside the corresponding two- and three-way interactions. Subjects' identity and the day of observation (from Day-01, first day of recording, onward) were included in the model as random factors. We verified that the model met the assumption of independence between the values of the residuals and the values estimated by the model, and checked for overdispersion with an acceptable ratio of residual deviance on degrees of freedom set to be <2 (using "plotresid" and "overdisp.glmer" functions in R *RVAideMemoire* package, respectively). To test for the significance of the fixed factors and their interactions, we applied a type III ANOVA to the model (using "Anova" function in R *car* package). We additionally verified the goodness of fit of the model (using "r.squaredGLMM" in R *MuMIn* package that computes the pseudo-*R*-squared for GLMM) and conducted comparisons with null models including either a constant value or including only sound type as a fixed factor (using "anova" function in R *stats* package). Then, we conducted post hoc pairwise comparisons between the different categories of individuals (females vs. males, early vs. late-reared) within each sound type (using "lsmeans" function in R *lsmeans* package), with *p*-values adjusted for multiple comparisons (Sidak method). We further confirmed these general results by comparing the frequency of use, out of the whole sample of sounds recorded, of the four most frequently produced types of single-type sounds in the different individuals using Chi-squared tests.

All tests were two tailed and we set the significance threshold at $\alpha = .05$.

2.5 | Ethical note

All applicable international, national, and institutional guidelines for the care and use of animals were followed. This study was conducted in accordance with the current laws in France and Namibia. It complies with the 2010/63/UE directive on the protection of animals used for scientific purposes. Data collection was evaluated as noninvasive observations and respecting the ethical rules by the "Comité Rennais d'Ethique en matière d'Expérimentation Animale" (i.e., Rennes Ethical Comity for Experiments using Animals; CREEA

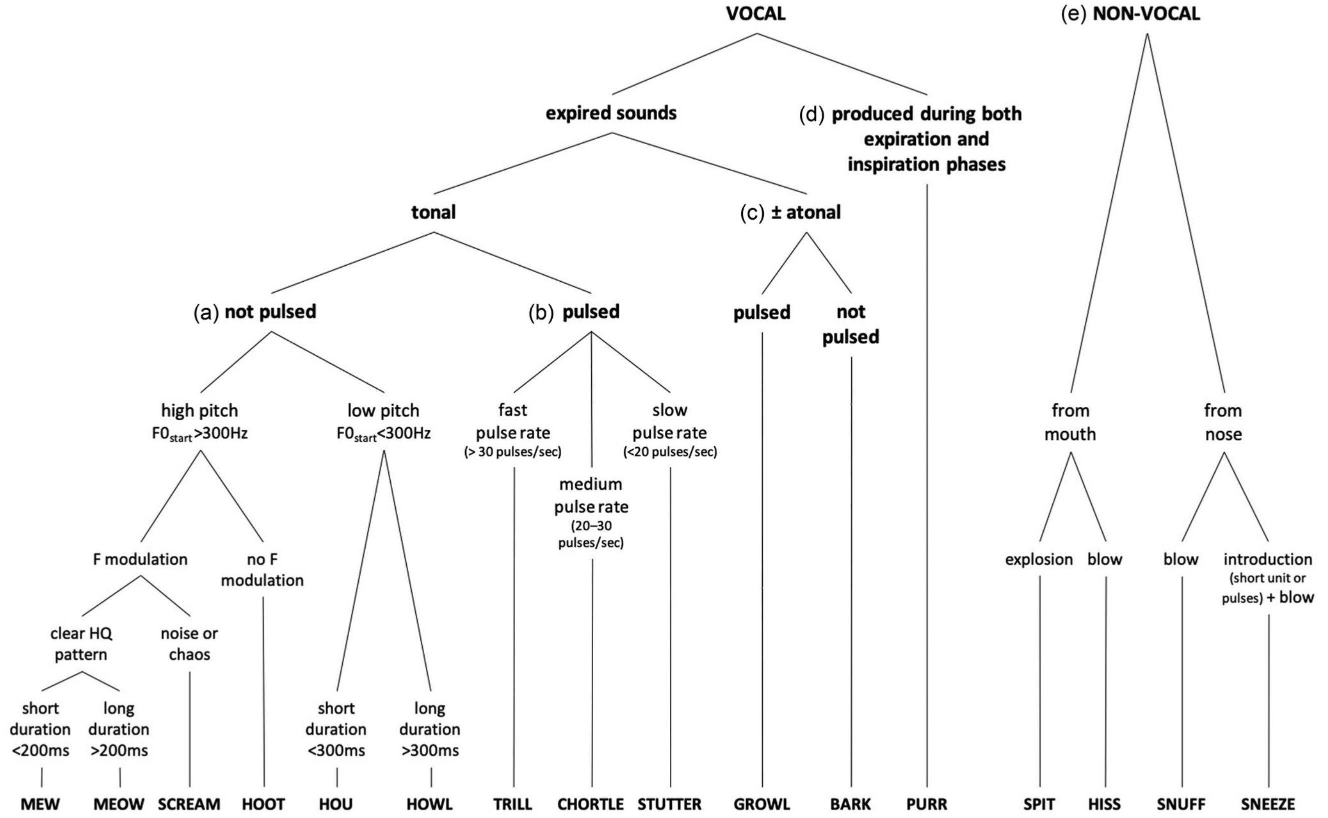

FIGURE 1 Classification key established for cheetah acoustic signals. The letters, from (a) to (e), refer to the associated group of spectrograms in Figure 2

approval #201806081359001). The staff of the CCF center was responsible for all animal husbandry and care. Research at CCF was conducted under the authorization #201805701 awarded by the Namibian National Commission on Research, Science and Technology.

3 | RESULTS

3.1 | Cheetahs' acoustic repertoire

A total of 2656 sounds from identified callers could be analyzed. Most of them (90.2%, $N = 2397$) were single-type sounds (i.e., made of either one or several units of the same type): we identified 16 different single-type sound types including 12 vocal and four nonvocal types (Figure 1).

3.1.1 | Definition of the sound types

A. *Vocal sound types*

Among the 12 vocal types, all but one (*Purr*) were produced during the expiration phase of the breathing cycle only.

A.1. *Tonal types.* Nine of the expired vocal types were clearly tonal (with visible harmonics).

A.1.1. *Unpulsed*. Six of them displayed frequency bands with a continuous tracing (Figure 2a). Of the six unpulsed calls, four were high-pitched calls, of which three (*Mews*, *Meows*, and *Screams*) were characterized by a modulated fundamental frequency: *Mews* were shorter than *Meows* (≈100–200 ms and ≈200–700 ms, respectively), *Screams* were slightly higher pitched ($F0_{mean} > 500$ Hz) and much noisier; and one, *Hoots*, had a slightly lower nonmodulated fundamental frequency ($F0_{mean} \approx 300–500$ Hz) and a short duration (≈100–200 ms). Two calls were lower pitched calls: *Hous* were shorter (≈100–300 ms) than *Howls*, which could even exceed 2 s, sometimes developing into a slow wave-like modulation pattern.

A.1.2. *Pulsed*. The other three tonal call types had a pulsed structure and were distinguishable based on their pulse rate (Figure 2b), respectively, fast (range: 30–45 pulses/s) for *Trills* (also higher pitched with $F0_{mean} > 400$ Hz), medium (20–30) for *Chortles*, and slow (10–20) for *Stutters*.

A.2. *Atonal types.* Two expired vocal types were atonal, with more or less visible formants (Figure 2c). *Growls* were low-pitched, fast-pulsed calls (>30 pulses/s) and could exceed 2 s, whereas *Barks* were relatively short and noisy units corresponding to an abrupt exhalation.

A.3. *Expired/inspired type.* The remaining vocal type, *Purr*, had a pulsed structure and the specificity to be produced continuously during both

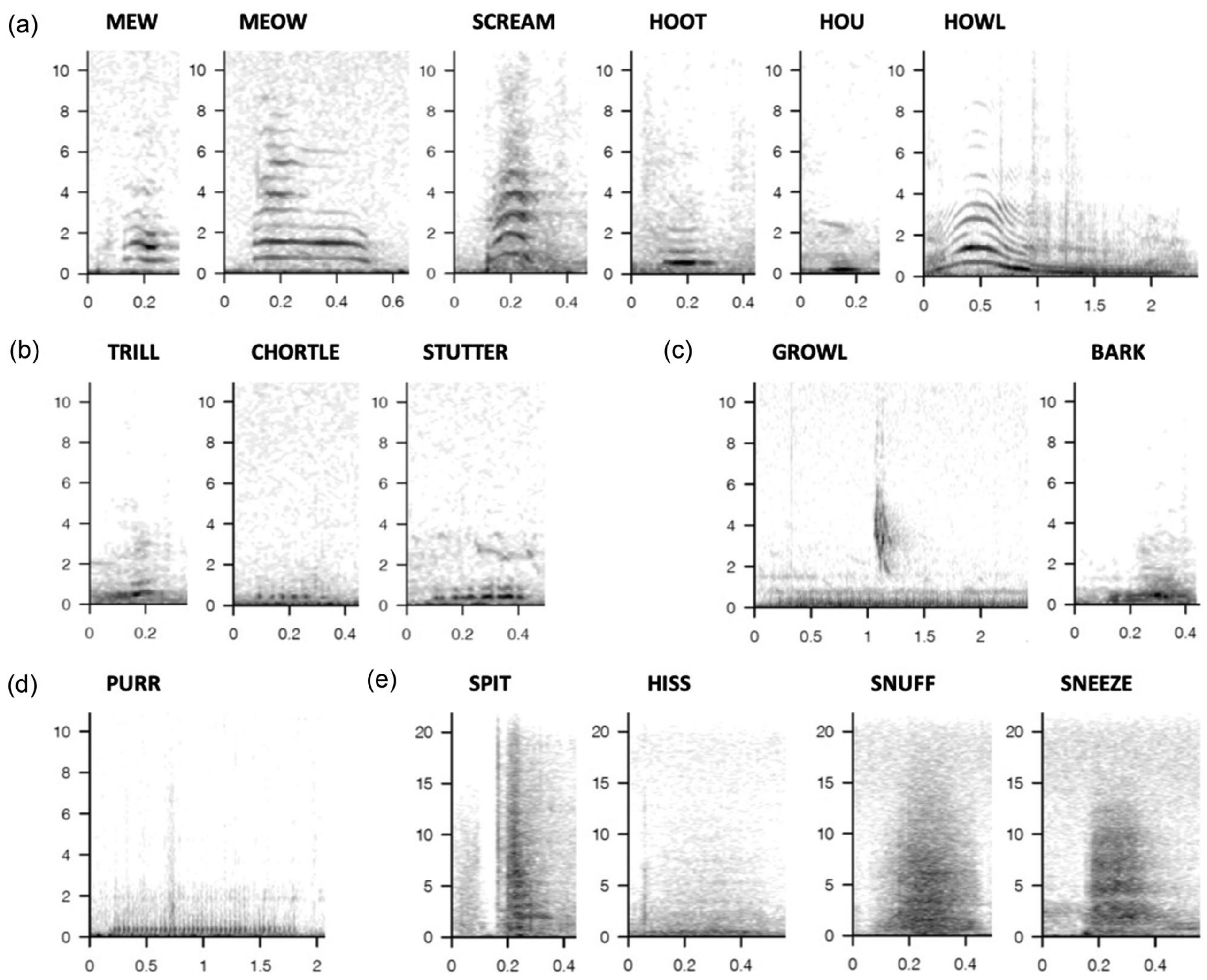

FIGURE 2 Cheetah single-type sounds can be divided into (a) vocal tonal unpulsed, (b) vocal tonal pulsed, (c) vocal atonal, (d) purring, and (e) nonvocal sounds. Spectrograms were drawn using "spectro" function in R seewave package (512-pt FFT Hanning window, sampling rate: 44,100 Hz, *y*-axis range: 0–11 kHz for vocal sounds, 0–22 kHz for nonvocal sounds). Corresponding audio files are available as ESM (+hyperlink)

exhalation and inspiration phases (Figure 2d). *Purrs* could cover one to over a hundred of respiration cycles and last several minutes.

B. *Nonvocal sound types*

The four nonvocal (unvoiced) sounds could be distinguished based on their production source: the airflow was being forced through either the mouth or the nose (Figure 2e).

B.1. *From the mouth.* *Spits* were explosive sounds, whereas *Hisses* were aperiodic sounds corresponding to a harsh blow with the mouth open.

B.2. *From the nose.* *Snuffs* and *Sneezes* were abrupt blowing nasal sounds, *Sneeze* being characterized by an additional introductory unit (either a short tonal unit or a short series of pulses).

3.1.2 | Single-type sounds: Single and repeated

Although they were mostly produced as isolated utterances (Single = 79.4% of the dataset, *N* = 2108), sounds could also be made of a series of units of the same type (Repeated = 10.9%, *N* = 289). *Purrs* were the most frequent Repeated pattern, as they were produced mostly as long series of expired units (94.6% of *N* = 203; Figure 3), alternating with audible inspired units in two thirds of the cases, although isolated single expired units were produced occasionally (5.4%). Some other sound types could be produced as series of same-type units: *Hous* (85.7% of N = 7; Figure 3), *Hoots* (37.1% of N = 35), *Chortles* (34.8% of N = 23), *Barks* (33.3% of N = 3), *Screams* (20% of N = 30), *Trills* (14.3% of N = 21), and to a lesser extent, *Mews* (5.2% of N = 461; Figure 3), *Stutters* (3.9% of N = 541), *Growls* (3.9% of N = 178), and *Meows* (1.1%

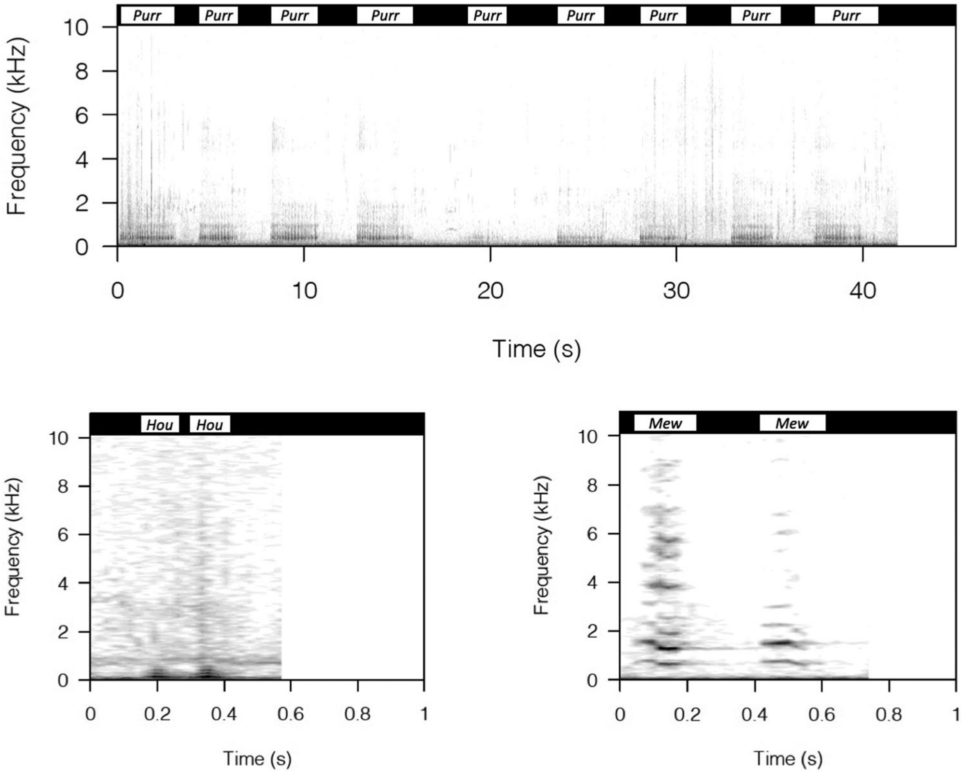

FIGURE 3 Examples of single-type cheetah sounds produced in series ("Repeated"). Top: 9-expired units *Purr*; bottom left: 2-units *Hou*; bottom right: 2-units *Mew*. Spectrograms were drawn using "spectro" function in R seewave package (512-pt FFT Hanning window, sampling rate: 22,050 Hz). Corresponding audio files are available as ESM (+hyperlink)

of $N = 703$). On the contrary, *Howl* ($N = 30$) and the unvoiced *Snuff* ($N = 79$), *Sneeze* ($N = 67$), *Hiss* ($N = 12$), and *Spit* ($N = 4$) were never produced in series.

3.1.3 | Multitype sounds

Sounds made of units of different types (Multitype sounds = 9.7% of the dataset, $N = 259$) were more frequently produced as Transitions (i.e., joined units at $\Delta = 0$ ms, 6.8%, $N = 181$) than as Combinations (i.e., juxtaposed units at $0 < \Delta < 200$ ms, 2.5%, $N = 66$). Some sounds (made of three units or more) displayed an intermediate pattern with joined as well as juxtaposed units (Mixed = 0.4%, $N = 12$).

Multitype sounds consisted in two or three different types of units produced concurrently, with up to seven units produced in a row (Figure 4). It is noteworthy that some unit types appeared more frequently within multitype sounds rather than within single-type ones: *Bark* and *Trill* units were associated to other units in over 80% of cases, mainly within transitional sounds. Other units frequently involved in multitype sounds are *Howl*, *Growl*, and *Scream* (involved in such associative patterns in 28%–40% of cases) and, to a lesser extent, *Meow*, *Hou*, *Hoot*, and *Stutter* (15%–20% of cases). *Chortle*, *Mew*, *Purr*, and *Sneeze* were rarely involved in multitype sounds (<6% of cases), whereas the nonvocal *Snuff*, *Hiss*, and *Spit* were never produced concurrently with other types of units.

3.2 | Repertoire use at the population level

Out of 3297 sounds recorded in the four study groups, caller's identity could be recorded for a total of 2656 sounds (i.e., 80.6%). The number of sounds recorded per subject varied greatly (range: 0.21–13.73 sounds per hour), with an average of 4.02 ± 3.98 sounds per hour per individual (mean ± *SD* across individuals). Early-reared animals tended to produce less sounds (i.e., be less vocal) than late-reared individuals (Table 2; Mann–Whitney on hourly call rates of early- vs. late-reared individuals: $W = 7$, $p = .1061$). Individual repertoire sizes (for single-type sounds) did not differ according to sex or rearing condition (Kruskal–Wallis on the four "sex × rearing" categories individuals: $H = 5.3181$, $df = 3$, $p = .1499$), although the two early-reared females had the smallest repertoire with only seven and four different types of single-type sounds (nine to 12 for all other individuals) (see Appendix C: repertoire of single-type sounds).

Single-type sounds ($N = 2397$) were largely predominant as they accounted for 90.5% ± 6.6% of the total sound production at the individual level (mean ± *SD* across individuals), with 76.0% ± 14.6% produced singly (Single) and 14.5% ± 15.6% as a sequence of the same repeated unit (Repeated). Multitype sounds ($N = 259$) represented only 9.5% ± 6.6% of sound production within individual repertoires, including 2.1% ± 1.9% of Combinations, 6.9% ± 5.8% of Transitions, and 0.6% ± 1.1% of Mixed pattern (Table 2).

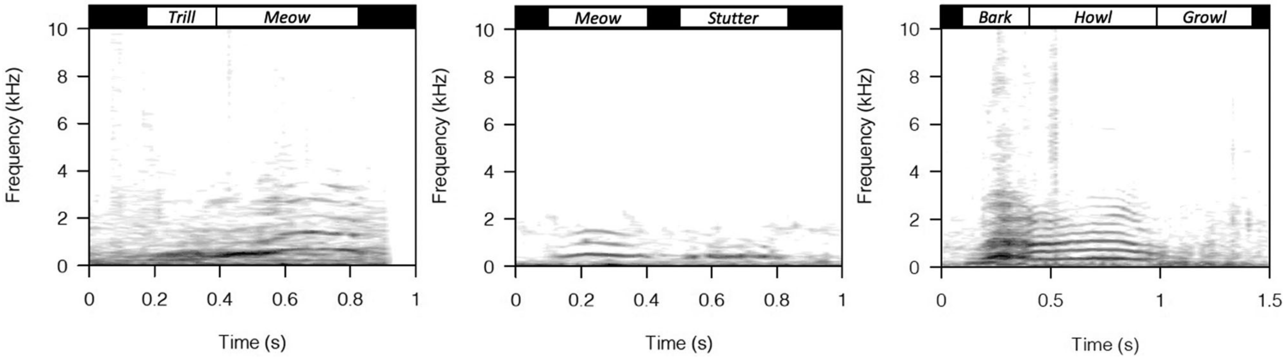

FIGURE 4 Examples of multitype cheetah sounds. From left to right: Trill-Meow (transition), Meow-Stutter (combination), and Bark-Howl-Growl (transition). Spectrograms were drawn using “spectro” function in R seewave package (512-pt FFT Hanning window, sampling rate: 22,050 Hz). Corresponding audio files are available as ESM (+hyperlink)

TABLE 2 Proportion of sounds (percentage of total production) within each category (single, repeated, combined, transitional) for the 12 study subjects

			Single-type		Multitype			
Sex[a]	Rearing[b]	Subject (NAAJU)	Single (%)	Repeated (%)	Combination (%)	Transition (%)	Mixed[c] (%)	*N* total
F	Early	1474	73.6	9.4	5.7	7.5	3.8	53
F	Early	1475	90.9	0.0	0.0	9.1	0.0	11
F	Late	1641	69.4	4.5	2.3	23.0	0.9	222
F	Late	1640	86.0	3.5	0.0	8.8	1.8	114
M	Early	1549	70.5	23.0	5.0	1.4	0.0	139
M	Early	1548	73.6	21.5	2.1	2.8	0.0	144
M	Early	1532	74.5	19.1	0.0	6.4	0.0	47
M	Early	1473	36.4	58.2	1.8	3.6	0.0	55
M	Early	1565	76.6	9.5	4.1	9.1	0.6	777
M	Late	1646	85.1	11.3	1.6	2.0	0.0	443
M	Late	1581	84.9	7.8	1.3	6.0	0.0	232
M	Late	1583	90.5	5.7	1.2	2.4	0.2	419

[a] Sex: F, female; M, male.
[b] Rearing: “Early” = rescued before 2 months old; “Late” = rescued between 2 and 6 months old.
[c] “Mixed” are multitype sounds of three units or more, some being produced juxtaposed (alike combinations) and other joined (alike transitions).

Overall, success rate at identifying the caller was 81.3% for single-type sounds (2397 identified out of the 2947 single-type sounds recorded in the four study groups). However, some sound types were more difficult to assign to a given individual because of high levels of sound overlap and excitation during the associated contexts of production, potentially leading to being under-evaluated. This is the case for *Hoots*, *Howls*, *Hous*, *Growls*, *Trills*, and *Barks* (in decreasing order of success rate for caller identification of single-type sounds, range: 71.4%–42.8%).

Among these 2397 single-type sounds, the most frequently produced single-type sounds were *Meows*, *Mews*, *Purrs*, *Growls*, *Stutters*, *Sneezes*, and *Snuffs* (Figure 5). *Mews*, *Growls*, and *Sneezes* were emitted by all 12 study subjects (see Appendix C: repertoire of single-type sounds). *Meows*, *Purrs*, and *Hisses* were not given by all subjects but were nevertheless recorded in individuals of all four classes (early- and late-reared of both sexes). More precisely, most sounds (*N* = 2108) were produced singly, and consisted then mostly in *Meows* and *Mews* (28.2% ± 21.4% and 23.3% ± 12.6% of Single production), whereas a smaller number of them (*N* = 289, produced by 11 out of 12 individuals; Table 2) were produced in repeated series, consisting mostly in *Purrs* (54.6% ± 33.4% of Repeated).

Although more anecdotal (*N* = 259), multitype sounds were emitted by all 12 study subjects, with a predominance of the units *Meow*, *Stutter*, *Trill*, *Growl*, *Bark*, and *Mew*, followed by *Howl*, *Scream*, *Hoot*, and *Hou* (see also Appendix C: repertoire used within multitype sounds). On rare occasions, *Purr* units were combined or interspersed with *Chortle* or *Sneeze*. The unit types *Meow*, *Trill*, and *Growl* could be produced concurrently to almost all other unit types, but the

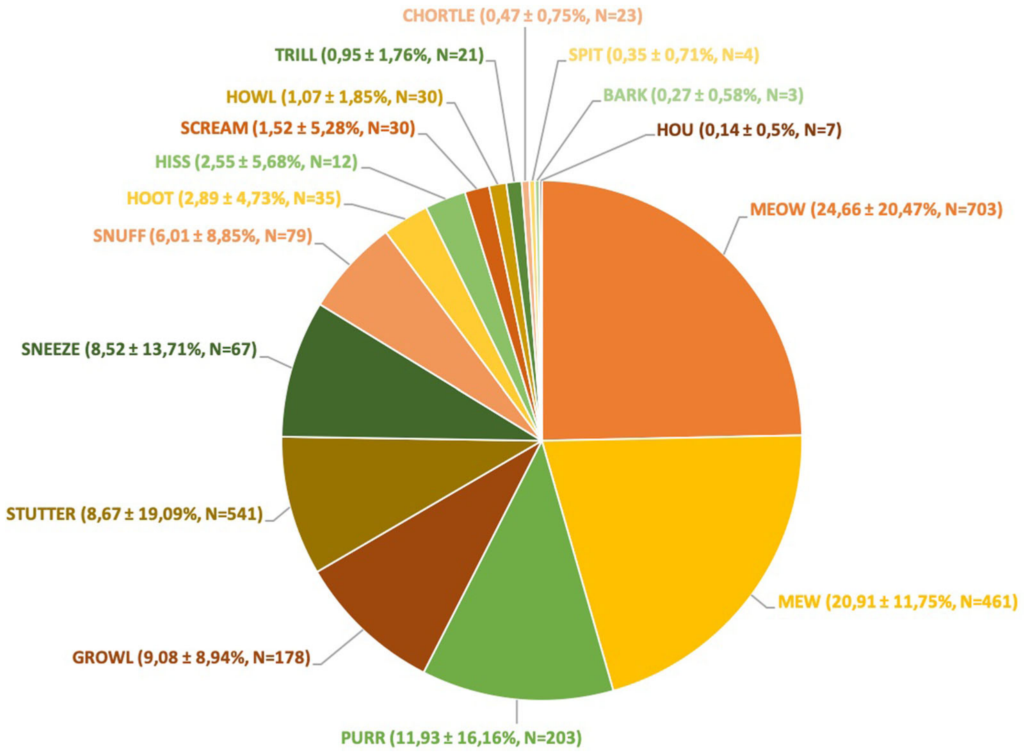

FIGURE 5 Average proportion of each sound type in individual repertoires for single-type sounds only (for each sound type: mean value across individuals ± *SD*, *N* = total number of sounds recorded in the population)

most frequently observed associations were *Stutter+Meow* (mainly transitional, $N = 82$), *Trill+Meow* (almost always transitional, $N = 62$), and *Bark+Growl* (mainly transitional, $N = 33$), followed by the more rarely observed associations *Meow+Mew* (always combined, $N = 12$), *Howl+Growl* (almost always transitional, $N = 12$), *Stutter+Mew* (mainly combined, $N = 9$), and *Trill+Scream* (almost always transitional, $N = 5$) (Figure 4). Within these multitype sound patterns, units could be ordered both ways: for instance, *Stutter+Meow* can be produced as either *Stutter–Meow* or *Meow–Stutter*.

3.3 | Influence of sex and early-life experience on individual repertoire use

Repertoire use varied across individuals depending on their sex and early-life experience. A few single-type sounds were only produced by individuals of a given sex (see Appendix C: repertoire of single-type sounds). *Howls* and *Stutters* were produced by males only, and *Hous* were emitted by one single late-reared male. *Screams* were produced by one single late-reared female only (but note that another late-reared female and an early-reared male also produced *Scream* units as part of transitional sounds). Moreover, only males produced series of *Mews* (recorded in three early- and three late-reared subjects), *Stutters* (one early- and two late-reared males), *Hous* (a single late-reared male), *Chortles* (one early- and two late-reared subjects), and *Trills* (two early-reared males). *Barks* and *Screams* were produced in series by one single late-reared female. Lastly, only late-reared individuals produced *Meows* in series (recorded in one late-reared female and three late-reared males).

Overall, the relative frequency of use (i.e., proportion of total acoustic production) of the 16 single-type sound types (i.e., Single or Repeated) appeared to differ across individuals depending concurrently on their sex and early-life experience (ANOVA on $\mathrm{GLMM}_{\mathrm{binomial-logit}}$, significant three-way interaction "SoundType × Sex × EarlyLife": Table 3; post hoc pairwise comparisons: see Sidak-adjusted *p*-values in the text below).

Thus, each category of individuals had a specific predominant use of some sound types in particular (Figure 6). Males used high proportions of *Meows* and *Stutters*, as well as *Mews* for the late-reared males (>20% of the total number of sounds produced, based on GLMM model estimates). Early reared females were characterized by a predominance of *Mews* and *Growls* (>20%), and late-reared females by a predominance of *Meows* (38%). More specifically, post hoc statistical comparisons revealed that

- early-reared males used a higher proportion of *Purr* (compared with late-reared males: $p < .0001$, and late-reared females: $p < .0001$), *Meow* (than early-reared females: $p = .0098$), and *Stutter* and *Sneeze* (than late-reared males: $p = .0030$ and $p = .0111$, respectively) (Figure 6a);
- late-reared males used a greater proportion of *Meow* (than early-reared females: $p = .0043$), *Mew* and *Growl* (compared with early-reared males: $p < .0001$ for both, and late-reared females: $p = .0035$ and $p < .0001$, respectively), *Purr* (than late-reared

TABLE 3 Factors influencing individual use of the acoustic repertoire (GLMM$_{\text{binomial–logit}}$: Analysis of deviance table, Type III Wald Chi-square tests)

		χ^2		*df*		*p*-value
Intercept		0.0000		1		.9954
SoundType		33.1925		15		**.0044**
Sex		0.0000		1		.9968
EarlyLife		0.0000		1		.9967
SoundType × Sex		58.4729		15		**<.0001**
SoundType × EarlyLife		42.0043		15		**.0002**
Sex × EarlyLife		0.0001		1		.9939
SoundType × Sex × EarlyLife		83.3293		15		**<.0001**
Pairwise comparisons with null models	*df*	AIC	Deviance	χ^2	*df*	*p*-value
Null model 1	3	11,378.0	11,372.0			
Model	66	6350.9	6218.9	5153.1	63	<.0001
	df	AIC	Deviance	χ^2	*df*	*p*-value
Null model 2	18	7146.9	7110.9			
Model	66	6350.9	6218.9	892	48	<.0001

Note: Response variable: *N* of single-type sounds of a given type/*N* total. SoundType: sound type among the 16 described in Figure 1. Sex: "female" versus "male". EarlyLife: "early" versus "late" rearing, as shown in Table 1.
Subjects' identity (ID) and the day of observation (Day) were included in the model as random factors.
Model: glmer(cbind(N, N_{total}–N) ~ SoundType × Sex × EarlyLife + (1|Day) + (1|ID), family = binomial(link = logit)).
Goodness of fit: conditional pseudo-*R*-squared for GLMM (delta method) = .7749.
Pairwise comparisons with null models: Akaike's information criterion (AIC) and between-models comparisons (Chi^2 difference tests).
1) Null model 1 including a constant value: glmer(cbind(N, N_{total}–N) ~ 1 + (1|Day) + (1|ID), family = binomial(link = logit)).
2) Null model 2 including only sound type as a fixed factor: glmer(cbind(N, N_{total}–N) ~ SoundType + (1|Day) + (1|ID), family = binomial(link = logit)).

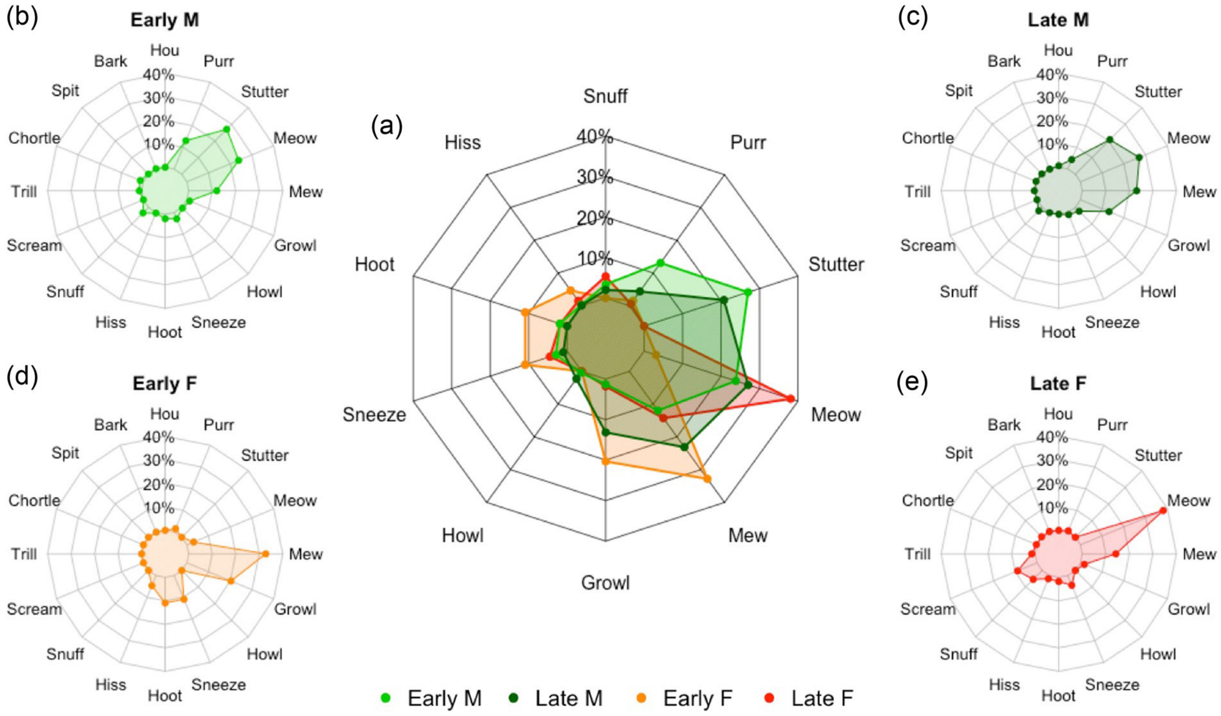

FIGURE 6 Relative frequency of use (GLMM model estimates, percentage of total acoustic production) of the 16 different single-type sound types according to sex and early-life experience. (a) The central chart represents only the 10 call types for which statistically significant differences were found across classes (post hoc pairwise comparisons following the GLMM). (b–e) To illustrate repertoire use within each sex/rearing category, one chart is drawn per class: F = females, M = males, Early = early-reared, Late = late-reared

females: $p = .0293$), and *Howl* (than early-reared males: $p = .0036$) (Figure 6b);
- early-reared females used a higher proportion of *Mew*, *Growl*, and *Hoot* (compared with late-reared females: $p = .0030$, $p < .0001$, and $p = .0053$, respectively, and early-reared males: $p < .0001$, $p < .0001$, and $p = .0003$, respectively), as well as *Sneeze* and *Hiss* (compared with early-reared males: $p = .0078$ and $p = .0022$, respectively, and late-reared males: $p < .0001$ and $p = .0036$, respectively) (Figure 6c);
- late-reared females used a greater proportion of *Meow* (compared with early-reared females: $p = .0003$, early-reared males: $p < .0001$, and late-reared males: $p = .0007$) and *Snuff* and *Sneeze* (than late-reared males: $p = .0105$ and $p = .0009$, respectively) (Figure 6d).

No difference across categories of individuals could be found for the rare (N emitters ≤ 6; see Appendix C: repertoire of single-type sounds) *Scream*, *Trill*, *Chortle*, *Spit*, *Bark*, and *Hou* (Figure 6), possibly due to the limited sample size for these sound types.

Apart from the post hoc pairwise comparisons reported above and illustrated in Figure 6a, all others were statistically nonsignificant.

These results were further confirmed when testing the relative use of the four most frequently produced single-type sound types (*Meows*, *Mews*, *Purrs*, and *Growls*) at the individual level using nonparametric Chi-squared tests (Figure 7): the general patterns highlighted by the GLMM are repeatedly found at the individual level in most subjects within any given sex/rearing class.

Finally, some differences appeared also in the production of multitype sounds (see Appendix C: repertoire used within multitype sounds). Although the *Trill+Meow*, *Bark+Growl*, and *Meow+Mew* were produced by both sexes ($N_{\text{ind}} = 7$, 11, and 6 individuals, respectively, for a total of $N = 62$, 33, and 12 recorded exemplars), some patterns were produced only by males (with both types of early-life experience), namely, *Stutter+Meow*, *Howl+Growl*, and *Stutter+Mew* ($N_{\text{ind}} = 3$, 5, and 2 individuals, respectively, for $N = 82$, 12, and 9 exemplars), whereas the *Trill+Scream* were recorded only in females ($N_{\text{ind}} = 2$ late-reared subjects, $N = 5$ exemplars). Besides, some multitype sounds were occasionally recorded in just a few individuals (often a single one), with some patterns limited to males: *Growl+Mew*, *Stutter+Growl*, *Purr+Sneeze*, *Chortle+Purr*, *Hoot+Growl*, *Hoot+Meow*, *Hou+Growl*, *Hou+Howl*, *Howl+Bark*, *Howl+Meow*, *Trill+Bark*, *Trill+Growl*, *Trill+Stutter*, *Bark+Howl+Growl*, *Growl+Trill+Hoot*, *Stutter+Trill+Meow*, *Trill+Bark+Growl*, and *Trill+Meow+Growl* (recorded in seven different subjects with both types of early-life experience; $N_{\text{ind}} \leq 3$ and $N \leq 3$ exemplars each); and others to females: *Trill+Mew*, *Trill+Hoot*, *Scream+Trill+Growl*, *Meow+Scream+Trill*, and *Hoot+Growl+Bark* (recorded in three different subjects with both types of early-life experience; $N_{\text{ind}} \leq 2$ and $N \leq 4$ exemplars each). Other rare patterns, *Meow+Growl* and *Scream+Growl*, were produced by individuals of both sexes ($N_{\text{ind}} = 3$ and 2, respectively; $N \leq 4$ exemplars).

4 | DISCUSSION

In this study, based on recordings of 12 hand-reared adult cheetahs, we described an acoustic repertoire comprising 16 different sound types and distinguished between 12 vocal and four nonvocal types. Cheetahs produced mostly single-type sounds (either singly or repeated, i.e., series of units of the same type) but also some multitype sounds (i.e., sounds made of units of different types, either as transitions or combinations). Our study population included individuals of both sexes whose early-life experience differed to some extent: all were wild-born and had been subsequently hand reared, but some had been deprived of their mother earlier in life (thus “early-reared” by humans) than others (“late-reared”). Interestingly, although repertoire size was rather homogeneous, we found high levels of interindividual variability in the use of the acoustic repertoire that appeared to be related to both sex and early-life experience.

4.1 | The cheetah acoustic repertoire: Universal features?

In our classification, based on acoustic structures, we identified 16 sound types, all but one (*Hou*) emitted by at least three subjects. Repertoire size varied little between individuals and, besides the *Hou* that was recorded here in a single male individual, the other two male-specific call types in our study (*Howl* and *Stutter*) have been previously recorded in wild as well as captive females, in contexts that we may have missed the chance to observe (i.e., stranger intrusion for “howls,” and during male–female or mother–cubs interactions for “stutters”) (Caro, 1993; Eklund et al., 2012b; Sunquist & Sunquist, 2002; Volodina, 2000).

The repertoire we have established is twice larger (in terms of number of different sound types identified) than what has been reported by Volodina (2000) and Smirnova et al. (2016) for captive cheetahs. However, among the sounds that we added in the repertoire, some types match what has been described, under the same or a different label, in other studies on adult cheetahs (e.g., *Spit*: Eklund et al., 2012b and Peters, 1991; *Mew*: labeled “Yelp” in Stoeger-Horwath & Schwammer, 2003 and Nagorzanski, 2018) (see Appendix A). It is noteworthy that several of the sound types described here in cheetahs have also been found in other felids (Bradshaw & Cameron-Beaumont, 2000; Stanton et al., 2015), notably in the domestic cat (Schötz et al., 2017; Tavernier et al., 2020): *Mew/Meow*, *Trill*, *Stutter*, *Purr*, *Growl*, *Howl*, *Scream* (“pain shriek”), *Hiss*, and *Spit* for instance.

On the one hand, several sound types were easy to match with earlier published descriptions of cheetahs’ communicative behavior due to their distinctive and unambiguous acoustic pattern. This was the case for the extensively studied *Purr* (Eklund et al., 2010, 2012a; Eklund & Peters, 2013; Frazer Sissom et al., 1991; Peters, 2002), the frequently

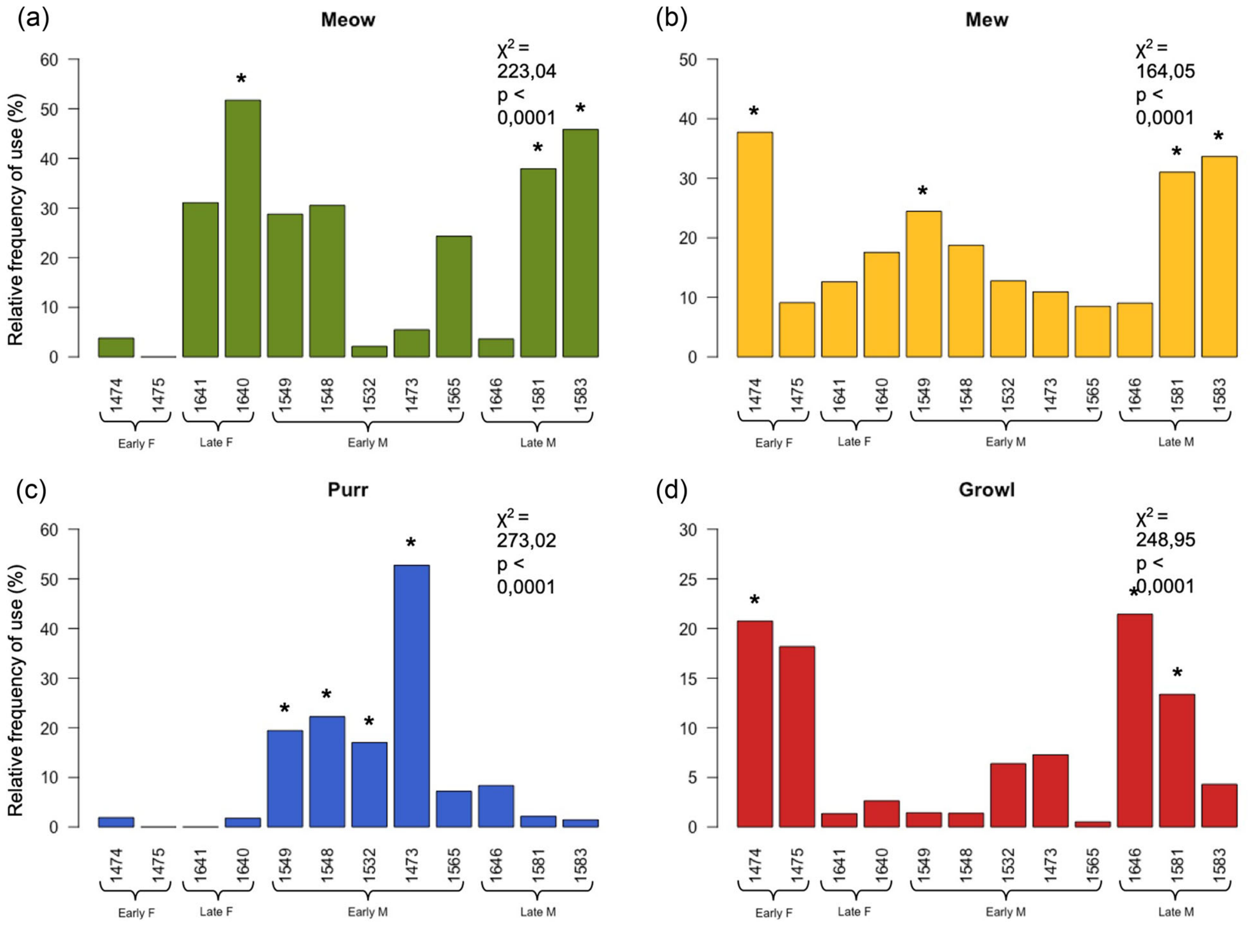

FIGURE 7 Comparison of individual relative frequencies of use (percentage of total acoustic production) for the four most frequently produced call types: *Meow* (a), *Mew* (b), *Purr* (c), and *Growl* (d). Individuals are grouped by class: F = females, M = males, Early = early-reared, Late = late-reared. Significance: Asterisk (*) is used when standardized Chi-squared residuals are >2 (see Agresti, 2002, p.81)

reported *Howl*, *Stutter*, *Growl*, and *Hiss* (Eklund et al., 2012b; Peters, 1991; Smirnova et al., 2016; Sunquist & Sunquist, 2002; Volodina, 2000), and the occasionally reported *Spit* (Eklund et al., 2012b; Peters, 1991) (see Appendix A). On the other hand, discrepancies between our classification and published ones likely originate from our attempt to clarify the cheetah vocal repertoire regarding ambiguous structures not matching the commonly reported acoustic templates. For instance, we divided high-pitched tonal calls into four types (*Mew*, *Meow*, *Scream*, and *Hoot*), and we added one low-pitched tonal (*Hou*), two tonal pulsed (*Trill* and *Chortle*), and one atonal (*Bark*) types never reported so far (see Appendix A). Unlike most previous studies, however, and despite extensive recordings, there is one call type (the "chirp") that we could not identify in our recordings. Rather than a specificity of our maternally deprived subjects, we suspect that it could have more to do with their age (>5 years old, well beyond the juvenile stage) as compared with previously studied populations that included young adults just 2–3 years old (see Appendix A). It could otherwise be due to methodological discrepancies in terms of classification criteria (see Appendix A).

Another novelty in our approach is to integrate more nonvocal sounds within the acoustic repertoire in addition to *Hiss* and *Spit*, such as *Snuff* and *Sneeze*. Although included in the repertoire for the first time here, they certainly do not constitute a peculiarity of our subjects (see "snort/snuffle" mentioned in Wachter et al., 2018). Recent studies revealed that "sneezes" play a role in group movement coordination in the African wild dog (Walker et al., 2017) and that "snorts" reflect positive emotions in horses (Stomp et al., 2018) and possibly rhinos (Policht et al., 2008), suggesting that such nonvocal sounds deserve more attention. Also, nasal sounds used as friendly close-range calls ("prusten" and "puffing") have been identified in lions, leopards, jaguars, and tigers (Peters & Tonkin-Leyhausen, 1999). For this reason, although their context of emission requires further clarification, we recommend that *Snuff* and *Sneeze* be included in the description of the cheetah acoustic repertoire.

It does not seem that the particular ontogenetic status of our subjects has influenced repertoire size and composition, as their repertoire does not differ drastically from those described in other studies (see Appendix A). This supports the hypothesis of the cheetah as a non- or limited-vocal learner, like many other terrestrial mammals, but still leaves open the possibility for vocal production in a very broad sense (refinement of repertoire via parental reinforcement) and/or use learning (Gultekin & Hage, 2018; Nieder & Mooney, 2020).

Unfortunately, the status (mother-reared vs. hand-reared) of individuals is not always mentioned in studies of captive cheetahs (e.g., Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Volodina, 2000) (see Appendix B), although hand-rearing in both zoos and conservation centers is a common necessity (Bell et al., 2012; Bircher & Noble, 1997; Woc Colburn et al., 2018). Thus, most literature on cheetahs' acoustic behavior is susceptible to be, for a large part, based on hand-reared subjects. Interestingly, Eklund et al.'s extensive studies on "purrs" were conducted in captive, generally hand-reared individuals in the context of cheetah–human interactions (Eklund et al., 2010, 2012a; Eklund & Peters, 2013), whereas their study on agonistic calls was conducted in wild-caught, only semi-habituated individuals awaiting relocation and managed under minimum human contact conditions (Eklund et al., 2012b) (see Appendices A and B). That choice of focus individuals may in fact explain the predominance of either type of sounds in these populations with contrasting early-life backgrounds and subsequent behaviors toward humans. It is also noteworthy that while most studies in captivity have mentioned the "meow" call type, this is not the case for studies conducted in the wild (Peters, 1991; Sunquist & Sunquist, 2002). This may be either because this call type is unusual in wild populations, or it may be that this soft call is harder to observe in natural conditions. To get a better understanding of the factors driving variability in cheetahs' acoustic communication patterns, future studies should make a practice of providing all relevant background information for their study subjects (i.e., wild- vs. captive-born, mother- vs. hand-reared, semi- vs. fully-habituated to humans, housed singly or within a mixed- or same-sex social group, etc.). This would ease comparisons across populations, and also help disentangle the influence of early-life experience and current social environment on cheetahs' communicative behavior.

Another aspect that remains poorly described in the literature is the existence of repeated and multitype calls (combinations or transitions). Repeated calls have not been mentioned in the cheetah literature thus far (and were probably counted as distinct single utterances), except for *Purrs* known to be produced in long series, unlimited in duration (Eklund et al., 2012a; Volodina, 2000). Here, we found that 11 out of the 16 sound types could be produced in series (i.e., all but *Howl* and the unvoiced *Snuff*, *Sneeze*, *Hiss*, and *Spit*). Multitype calls, on the other hand, have already been described in cheetahs. Smirnova et al. (2016) reported the most frequent transitional calls as being "purr-meow," "growl-howl," and "growl-meow" calls. Volodina (2000) reported transitional calls made of tonal sounds ("miaowing" or "chirping") alternating with pulsed sounds ("churtling," "growling," or "gurgling") as well as intermediate sounds between "churtling–miaowing," "howling–growling," "howling–miaowing," and "miaowing–chirping." Eklund et al. (2012b) also reported intermediate patterns between "moan–growl." In addition, we can find direct equivalents of cheetah multitype calls in the domestic cat vocal repertoire: Schötz et al. (2019) listed, for example, "trill–meow," "growl–howl," "meow–howl," and "meow–purr" (see also "broadband hybrid units" in Owens et al., 2017). These earlier findings are quite in accordance with our observations, where the most frequently observed patterns were *Stutter+Meow*, *Trill+Meow*, and *Bark+Growl*, followed by the less frequent *Meow+Mew* and *Howl+Growl*. These complex associative patterns definitely deserve further investigation in cheetahs in order to determine whether or not they convey messages that differ in some ways from those of single calls, as found in different mammal species (Blumstein & Armitage, 1997; Manser, 2001; Ouattara et al., 2009; Schel et al., 2010), or whether it may be a by-product of other factors such as adult deprivation and a lack of canalization of acoustic patterns (Nelson, 1997).

4.2 | Long-term impact of early-life experience on repertoire use varies according to sex

In our study population of hand-reared adult cheetahs, we uncovered a concurrent effect of both early-life experience and sex in determining repertoire use at the individual level. Indeed, we detected both between- and within-sex differences in call use ascribable to the history of our subjects, namely, the stage at which they were maternally deprived: either before or after 2 months old, the latter group having gained a much more extensive experience alongside their mother outside of the den. More specifically, we found that early-reared females displayed a less varied acoustic repertoire (i.e., smaller repertoire size) than other individuals, that early-reared individuals of both sexes tended to vocalize less frequently (i.e., lower calling rates) than their late-reared counterparts, and finally that males with either type of early-life experience produced a greater diversity of repeated and multitype calling patterns (i.e., higher acoustic diversity) than females. Most importantly, our analyses on the use of the repertoire of single-type sounds revealed that the four sex/rearing classes of individuals produced 10, out of the 16, types of sounds in significantly different proportions (i.e., contrasting repertoire use). Either lack of adult canalization or sex-dependent increased social dispositions could explain the patterns that we observed in our study population

In most studies where parental/adult influence on vocal development was investigated, it appeared that adults played a role in "pruning" the repertoires of innate call types by canalizing varied immature production toward pertinent more restricted adult structures (e.g., marmosets: Gultekin & Hage, 2017, 2018; Australian magpies: Kaplan, 2017; European starlings: Bertin et al., 2007; cowbirds: West et al., 1997). Although the human caretakers here, at the CCF center, stimulated acoustic production in the early-reared animals, these actions did not lead to higher vocal production (higher calling rates) nor diversity (larger repertoire size and/or variety of associative acoustic patterns). It may be that the lack of appropriate contingency, a crucial aspect for acoustic maturation in marmosets, humans, and songbirds (Goldstein et al., 2003; Gultekin & Hage, 2017, 2018; Kuhl et al., 2003), and/or the different acoustic structure of the human imitations may have prevented any influence. When adopted, the cubs had already had experience with their mother's voice, which is likely to convey powerful emotional information as reported in degus (Ziabreva et al., 2003). In degus, parentally deprived animals vocalize less (Braun et al., 2003), which is also the case here for early-reared cheetahs (see also

Rose, 2012), revealing that age at separation may be an important feature for acoustic development.

Although both sexes are supposedly able to produce all the call types of the species repertoire as early as infancy (Volodina, 1998, 2000), we found that the acoustic repertoire of early-reared females was less varied overall than that of all other categories, while males' repertoire was enriched with a wide variety of associative acoustic patterns. This suggests opposite effects of early deprivation on males and females: lack of canalization in males (as in marmosets for instance: Gultekin & Hage, 2017) versus decreased acoustic production in females (as in degus for instance: Braun et al., 2003). The differential influence of maternal deprivation on the acoustic repertoire of male and female cheetahs that we report here could be in part attributable to differences in the maternal rearing of male and female cheetah cubs. For instance, mothers have been found to make greater efforts to provision litters containing two or more sons: not only do they spend increasing amounts of time hunting and thus providing a greater number of meals to brothers (compared with litters comprising a single son), but mothers also abstain from feeding on carcasses to favor their multiple sons (but not their single son or daughters) (Caro, 1990). This bias in food provisioning would reflect a preferential investment in favor of offspring of the cooperating sex (i.e., cheetah brothers prone to form a life-long coalition) (Caro, 1990), and it is likely to not only influence offspring's growth (as in, e.g., macaques: Hinde, 2007; red deer: Landete-Castillejos et al., 2005) but also to impact their social ontogeny (as in, e.g., horses: Cameron et al., 2008; gorillas: Robbins et al., 2007; mouse lemurs : Perret & Colas, 1997). The higher maternal investment may be associated with an increased dependency on mother's care and a tendency to an increased neotenic behavior of young males relative to young females. While data on differences in the impact of early social experience on vocal development according to sex are overall quite scarce, some examples are known from other species as well. The impact of early deprivation from adult contact differentially affects males and females in starlings (e.g., Cousillas et al., 2006, 2008; Henry et al., 2008). Also, in degus, the broadcast of the mother's voice led to opposite effects in young separated males and females, modulating the effects of separation in males, but increasing them in females (Ziabreva et al., 2003). It is possible that the mother's emotional buffering is more important for males, or that these gender-specific responses may be due to interactions of gonadal hormones.

An alternative cause for the observed differences between the repertoire use of males and females (i.e., differences in preferentially produced sound types and in their levels of acoustic diversity regarding associative patterns) could be related to their contrasting "social dispositions" (Mason, 1978). Male cheetahs have a greater propensity at interacting and bonding and, unlike females, are prone to form long-term coalitions (Caro, 1994; Sunquist & Sunquist, 2002; Wachter et al., 2018), which could lead to differential use of acoustic signals with different social values. Indeed, social organization and bonding propensities can translate into a differential expression of the vocal repertoire across classes of individuals (e.g., in primates: Bouchet et al., 2010, 2012; Hohmann, 1991). Also, these higher levels of variability in communicative patterns in males could be directly linked to the higher frequency of social interactions they experience, and the tighter bonds they maintain with their peers (Caro, 1993), compared with females whose social tolerance level remains low even when housed in a single-sex group in captivity (Wielebnowski et al., 2002).

Regarding the preferential usage of particular sound types at the individual level, we observed that, within the early-reared subjects of our study population, females were characterized by the preferential use of *Mews* and *Growls*, while males used a high proportion of *Meows* and *Stutters*. Most remarkable was the early-reared males' production of *Purrs* in far greater proportions than any other class of individuals. On the other hand, late-reared individuals of both sexes uttered *Meow* calls in series that their early-reared counterparts never used. Late-reared females stood out for using the highest proportion of *Meows* in this population, while late-reared males were further characterized by high proportions of *Meows*, *Mews*, *Stutters*, *Growls*, and *Howls*. It is quite remarkable to find such a persisting impact of "early versus late" maternal deprivation in adult subjects (>5 years old). The concomitant impact of sex on vocal repertoire use is of additional interest. The preferential use of certain sound types by one or several sex/rearing classes of individuals could in fact be dependent on the social communicative function of the sound types, and again be related to interindividual (interclass) differences in either dependency on mother or "social dispositions."

Several of the sounds expressed differentially by cheetahs based on early versus late maternal deprivation are related to positive intraspecific interactions. In cheetahs, *Purrs* are produced by wild and captive animals when resting, before or after a meal, and during friendly encounters or mutual grooming with conspecifics (Caro, 1993; Smirnova et al., 2016; Sunquist & Sunquist, 2002). In captivity, however, according to Eklund and Peters (2013) and Smirnova et al. (2016), cheetahs of all ages purr primarily in the context of physical contact with humans. But the early experience of these captive subjects, notably regarding hand-rearing, needs to be clarified (see Appendix B). Indeed, the redirection of purring toward humans may well be related to the amount of human contact and/or lack of contact to conspecifics experienced at earlier stages. Whether the increased purring in males is attributable to increased effects of maternal deprivation/persistence of neotenic behaviors or a greater propensity at interacting and bonding among male peers still remains to be understood. In domestic cats, purring is known to emerge almost from birth. Its production by kittens while suckling stimulating maternal care. Later in life, cats purring toward a familiar partner is viewed as a sign of contentment from an animal "feeling well" and "comfortable," or alternatively as a contact- and care-soliciting signal like in neonates (Bradshaw & Cameron-Beaumont, 2000; Little et al., 2014; Peters, 2002).

Stutters and *Mews* also relate to signals known to be used in the context of interactions between mother and cubs, among social partners, or during courting (Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Sunquist & Sunquist, 2002; Volodina, 1997, 2000; Volodina & Volodin, 1996) (see Appendix A for correspondence between call terminologies). In our maternally deprived hand-reared subjects, the increased production of *Stutters* in early-reared males and *Mews* in early-reared females relative to their late-reared counterparts may again be a redirection from intra- to interspecific communication toward humans, as for *Purrs*, similarly to the way domestic cats use "meows" (Bradshaw & Cameron-Beaumont, 2000; Nicastro, 2004).

Another sound associated with mother–cub interactions in cheetahs is the "meows." "Meows" are notably produced by juvenile cheetahs in an attempt to attract attention and care (Volodina, 1997). In adults, "meows" are emitted to call over a conspecific or when in contact with a social partner, as well as during courting (Ruiz-Miranda et al., 1998; Smirnova et al., 2016; Volodina & Volodin, 1996) (see Appendix A for correspondence between call terminologies). "Meows" are also produced by captive animals when calling to humans in the context of food anticipation, both by juveniles and adults (Smirnova et al., 2016; Stoeger-Horwath & Schwammer, 2003). In interspecific communication, the efficiency of "meows" at attracting human attention is suggested to have enhanced its production by domestic cats (Bradshaw & Cameron-Beaumont, 2000; Nicastro, 2004). Ongoing analyses of the context of production will help understand the increased proportion of *Meows* in late-reared cheetahs of both sexes, produced not only as single but also within repeated calls, with late-reared females using them in proportions significantly greater than any other class of individuals. The communicative value of *Meows* is expected to be either as a social signal (notably among male coalition partners) or as an interspecific communication signal (toward human caretakers who provision them). In addition, further investigation in naturalistic conditions would be needed to decipher the prevalence and contextual use of *Meow* calls, not explicitly reported in wild cheetah populations so far (see Appendix A). Of note, in other species, "meows" are rarely heard during felids' intraspecific interactions among adults (Bradshaw, 2016).

Other sounds are associated with aggressive interactions, which can be both intra- or interspecific. *Growls* and *Hisses*, which are produced more by early-reared females than any other categories of cheetahs, are considered to be agonistic signals (Eklund et al., 2012b; Volodina, 2000). Deprivation of adult influence at an early stage has been found to be associated with higher frequencies of aggressive behaviors in most species studied (e.g., cats: Ahola et al., 2017; chimpanzees: van Leeuwen et al., 2014; macaques: Mason, 1960; Suomi, 1997; elephants: Slotow et al., 2000; horses: Bourjade et al., 2009; rats: Tóth et al., 2008; cichlids: Arnold & Taborsky, 2010; Hesse & Thünken, 2014). It is probable that, like in other species, the cheetah mother plays a major role in regulating aggressive interactions within the litter once the youngsters have left the den. In cheetahs, females are the "asocial" sex, which means that they are more likely to develop aggressive behaviors toward conspecifics (Wielebnowski et al., 2002), as a result of their "social dispositions" (Mason, 1978). The absence of the canalizing influence of the mother when these behaviors develop may explain the higher frequency of these agonistic signals in the acoustic repertoire of the early-reared females.

Growls and *Howls* (or "moans"), which are produced in higher proportion by late-reared males than by their early-reared counterparts, have previously been reported to be produced in agonistic contexts by cheetahs, toward either conspecifics, predators, or humans (Eklund et al., 2012b; Smirnova et al., 2016; Sunquist & Sunquist, 2002; Volodina, 2000). Males living within a coalition, which is the case for all of our male subjects housed with same-sex peers, are more likely to become territorial (Caro, 1990; Caro & Collins, 1987). The more extensive experience gained alongside their mother by late-reared individuals, and possibly also along adult males encountered while away from the den (Hunter & Skinner, 2003), may have helped them acquire more advanced "typically male" social skills in terms of dominance and territoriality (Caro, 1993; Caro & Collins, 1987).

The functional value of the nonvocal sound *Sneeze* remains to be explored, as it is the case for *Snuff* (but see "snort/snuffle" mentioned in Wachter et al., 2018). Further studies are therefore needed to elucidate the reason for an increased production of *Sneezes* in females relative to males, irrespective of their early-life experience.

4.3 | Limitations, conclusion, and future directions

This description of cheetah acoustic repertoire provides a thorough view of the different sounds produced by adult hand-reared cheetahs, based on a large sample of recordings. This is, to our knowledge, the first study to provide a quantitative representation of the relative use of the different sound types at the individual level in cheetahs. Unfortunately, this precludes any direct comparison with previously published studies. Therefore, reporting quantitative data from other captive and wild cheetah populations, with various living conditions and developmental histories, should be the aim of future studies. The further finding that both early experience and sex strongly influence repertoire use opens important new lines of thought and raises methodological questions, notably regarding the lack of consideration for developmental history in studies using data from captive animals. However, we must acknowledge that the four classes of individuals (early/late-reared females vs. early/late-reared males) were represented by a low sample of subjects ($N = 2–5$) within our population, which is, however, rather usual for captive cheetah studies and other developmental studies in primates (e.g., Gultekin & Hage, 2017, 2018). In fact, one of the limitations in conducting such an investigation is that information about early-life experience of captive individuals is generally sparse and lacking details about when exactly they were separated from their mother and how they were subsequently taken care of by surrogates (e.g., hand-reared by wildlife professionals or any person, bottle-fed or directly meat-fed, kept in a social group with age peers or with adult conspecifics, isolated and raised by humans in the absence of conspecifics, etc.). The results obtained here emphasize how important it would be for future studies to access and report this information, and to consider all these individual factors of variations when investigating vocal behavior even in a so-called limited-vocal learner. This is especially critical in the context of captivity, in zoological parks and conservation centers, where animals are likely to have experienced early maternal/adult deprivation, or other disrupted social conditions of life that may have a long-lasting influence on not only their social but also their communicative skills.

ACKNOWLEDGMENTS

This project is part of the International Research Project VOCOM ("Evolution of Vocal Communication") coordinated by MH and supported by the CNRS (French National Center for Scientific Research). This work was funded by the International Research Project VOCOM, a Fyssen grant to KC, a grant from the University Bretagne-Loire granted to AL for hiring a postdoc, a grant from the Association "Beauval Nature pour la Conservation et la Recherche" (with our deepest thanks to Baptiste Mulot for his continued support), as well as financial support from the University of Rennes 1 and the CNRS. We thank Robyn Hetem for helpful discussions. We are grateful to Dr. Laurie Marker for permission to conduct research at the Cheetah Conservation Fund and to all cheetah keepers and staff of CCF for their help.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: Bouchet, H., Lemasson, A., Collier, K., Marker, L., Schmidt-Küntzel, A., Johnston, B., & Hausberger, M. (2022). Early life experience and sex influence acoustic repertoire use in wild-born, but hand-reared, captive cheetahs (*Acinonyx jubatus*). *Developmental Psychobiology*, *64*, e22309. https://doi.org/10.1002/dev.22309

APPENDIX A: SYNOPSIS OF THE CHEETAH'S VOCAL REPERTOIRE ESTABLISHED IN OUR STUDY AND PRESUMPTIVE EQUIVALENCES IN THE PREEXISTING LITERATURE

		Studies in captivity									Studies in the wild	
		Our team	Volodina's team			Ruiz-Miranda	Stoeger's team		Peters' team			Sunquist
		This study	Smirnova et al., 2016	Volodina, 2000[a]	Volodina, 1998	Ruiz-Miranda et al., 1998	Stoeger-Horwath & Schwammer, 2003	Nagorzanski, 2018	Eklund et al., 2010, 2012a; Eklund & Peters, 2013[b]	Eklund et al., 2012b[b]	Peters, 1991	Sunquist & Sunquist, 2002
Subjects		8 M 4 F	6 M 7 F	6 M 8 F	14 M/F + 1 M	4 M	4 cubs	26 M 28 F	5 M 5 F	1 M 5 F	M/F	M/F
Age		A: 5–15 years	A: >2 years	A: >3 years	J: 1.5–3 months + 1 N	A: 3–6 years	J: 14 months	A/J: 1–16 years	A/J: 0.5–13 years	A: 2–9 years	A/J	A/J
Vocal	Mew[c,d]	Meow [S+]	Miaowing [S]	Miaowing [S]		Yelp [S]	Yelp [S][d]				Yelp "yow" ?[d]
	Meow[c]				Eeaow [S]						
	Scream[c]									Bleating ?	
	Hoot[c]										
	Hou										
	Howl	✓ [S+]	✓ [S]	✓ [S]					Moaning [W]	Moaning	Moan
	Trill[e]										
	Chortle[f]	Gurgle ?	Gurgling [S] ?								Gurgle ?
	Stutter	Chirr [S+]	Churtling [S]	Churtling [S]	✓	Churr [S]				Churring	✓ or Churr
	Growl	✓ [S+]	✓ [S]	✓ [S]					✓ [W]	✓ and Snarling	✓
	Bark[g]										
	NA[h]	Chirp [S+]	Chirping [S] (explosive yelp)	Chirping [S]	Chirp [S]	Chirp [S]	Chirp [S]			Chirping or yelping	Yelp "yow" ?[d]
	Purr	✓ [S+]	✓ [S]	✓				✓ [W,S]		✓	✓

(Continues)

	Studies in captivity									Studies in the wild	
	Our team	Volodina's team			Ruiz-Miranda	Stoeger's team		Peters' team			Sunquist
	This study	Smirnova et al., 2016	Volodina, 2000[a]	Volodina, 1998	Ruiz-Miranda et al., 1998	Stoeger-Horwath & Schwammer, 2003	Nagorzanski, 2018	Eklund et al., 2010, 2012a; Eklund & Peters, 2013[b]	Eklund et al., 2012b[b]	Peters, 1991	Sunquist & Sunquist, 2002
Nonvocal	Spit								✓ [W]	✓	
	Hiss	✓ [S+]	✓ [S]	✓ [S]					✓ [S]	✓	
	Snuff										
	Sneeze										

Note: ✓ = already published using the same terminology as in this study; Abc = other terminology used for structurally similar sounds; ? = uncertain equivalence.

[S] = sonogram published; [S+] = sound exemplar provided along published sonogram; [W] = waveform published.

Subjects: M = male; F = female. Age class: A = adults; J = juveniles; N = newborn. Age in years or months when available.

[a] Sound exemplars from Volodina's studies available at http://www.bioacoustica.org/projects/acinonyx_eng.html.

[b] Sound exemplars from Eklund's studies available at https://www.youtube.com/user/DrJubatus/videos.

[c] Within high-pitched tonal calls, we could distinguish between four types (*Mew*, *Meow*, *Scream*, and *Hoot*), whereas only "meows" have been mentioned in most published studies as a global class (with high levels of variability in terms of both frequency patterns and duration; Volodina, 2000) for medium-pitched tonal calls, as opposed to the lower-pitched "howls" and the higher-pitched "chirps."

[d] In her unpublished master's thesis, Nagorzanski (2018) has suggested to set apart the "yelp" (following Stoeger-Horwath & Schwammer, 2003), defined as a call with a F0 modulation pattern resembling the "chirp" but as low in frequency as the "meow," which seems to correspond to our *Mew*. Also, the "yelp" mentioned by Sunquist and Sunquist (2002) may correspond to *Mew* or *Chirp* types (Nagorzanski, 2018).

[e] The acoustic pattern of *Trills*, not reported elsewhere, may have been mistaken for short *Purrs* in previous studies given that although Smirnova et al. (2016) reported the most frequent transitional call to be "purr–meow," we observed *Trill+Meow* quite frequently (also described in domestic cats by Schötz et al. [2017], where *Purr* and *Trill* are considered separately too).

[f] *Chortle* may correspond to the "gurgle" occasionally mentioned in the literature, although based on the couple of published spectrograms "gurgle" seems higher pitched than our *Chortle* (Peters & Tonkin-Leyhausen, 1999; Smirnova et al., 2016; Sunquist & Sunquist, 2002; Volodina, 2000).

[g] *Bark* has not been counted as a distinct type so far, although Volodina (2000) reported that *Growl* can occasionally fuse in a noisy vocalization.

[h] We did not identify "chirp" calls in our dataset. We see two plausible explanations to account for this discrepancy. First, this may be explained by the age range of our subjects, already well into adulthood. When recorded in juvenile cheetahs, "chirps" are very high-pitched calls with F0 > 2 kHz (Stoeger-Horwath & Schwammer, 2003). Now, when comparing the "chirps" recorded in 3- and 6-year-old cheetahs by Ruiz-Miranda et al. (1998), calls of the youngest are high pitched (F0 > 2 kHz), but those of the older individuals seem to match "meow" ("eeaow") in terms of frequency range. Therefore, it may be that juvenile's "chirp" calls morph into the lower pitched *Mew* at a later age. For clarification, this issue requires further investigation through longitudinal studies of vocal development in cheetahs. Otherwise, this may be explained by the fact that we did not rely on the fundamental frequency shape (but rather on duration) to classify *Meow* and *Mew* calls because we encountered a wide variety of patterns (U-inverted, V-inverted, descending, ascending, etc.) in both types. On the opposite, "chirps" were characterized by a descending frequency pattern in previous studies with adult subjects (Smirnova et al., 2016; Volodina, 2000), although its frequency range does not differ much from the modulated (typically U-inverted) "meow." So, the fact that we did not report "chirp" in our study may also be due to methodological discrepancies.

APPENDIX B: BACKGROUND INFORMATION GIVEN FOR THE SUBJECTS IN OUR STUDY AND IN PREVIOUSLY PUBLISHED STUDIES

	Studies in captivity									Studies in the wild	
	This study	Smirnova et al., 2016	Volodina, 2000	Volodina, 1998	Ruiz-Miranda et al., 1998	Stoeger-Horwath & Schwammer, 2003	Nagorzanski, 2018	Eklund et al., 2010, 2012a; Eklund & Peters, 2013	Eklund et al., 2012b	Peters, 1991	Sunquist & Sunquist, 2002
Number of subjects (*N*)	12	13	14	15	4	4	54	10	6	Number of subjects unspecified	Number of subjects unspecified
Sex	M + F	M + F	M + F	M + F (respective *N* not detailed)	M only	Sex unspecified	M + F	M + F	M + F	M + F	M + F
Age	A: 5–15 years	A: >2 years	A: >3 years	J: 1.5–3 months + 1 N	A: 3–6 years	J: 14 months	A/J: 1–16 years	A/J: 0.5–13 years	A: 2–9 years	A/J	A/J
Wild-born ↳ Parent-reared ↳ Hand-reared ↳ Early ↳ Late	✓ (all) ✓ orphaned ✓ (all) ✓ (*N* = 7) ✓ (*N* = 5)				?			✓ (3) ✓ orphaned ✓ (*N* = 3 “at a few weeks of age”)	✓ (all) ✓ (all)	✓ likely (all) ✓ likely (all)	✓ likely (all) ✓ likely (all)
Captive-born ↳ Parent-reared ↳ Hand-reared		✓ (all) ? rearing not specified	✓ (3) ? rearing not specified	✓ (all) ? rearing not specified	?	✓ (all) ✓ likely (all)	✓ (all) ✓ (some) ✓ (some)	✓ (1) ? rearing not specified			
Other comments			No information for the other 11 subjects coming from zoo commercial firms		No information except the Studbook #	Likely mother-reared as “currently living with their mother”	Respective number of parent- versus hand-reared subjects not detailed	No information for the other six subjects (2010 and 2013 studies)	Managed under minimum human contact conditions		

Note: Subjects: M = male; F = female. Age class: A = adults; J = juveniles; N = newborn. Age in years or months when available. Hand-reared: before (“Early”) or after (“Late”) 2 months old.

APPENDIX C: PRESENCE/ABSENCE OF THE 16 TYPES OF SOUNDS IN THE 12 STUDY SUBJECTS

Sex[a]	Rearing[b]	Subject (NAAJU)	*Mew*	*Growl*	*Sneeze*	*Meow*	*Purr*	*Snuff*	*Hiss*	*Hoot*	*Stutter*	*Trill*	*Chortle*	*Howl*	*Bark*	*Spit*	*Scream*	*Hou*	***N types within single-type sounds***	***N types within multi-type sounds***
F	Early	1474	☒	☒	■	☒	■		■	☒		×			×				***7***	***6***
F	Early	1475	■	■	■	×			■			×							***4***	***2***
F	Late	1641	☒	☒	■	☒		■	■	☒		☒	■		☒		☒		***11***	***7***
F	Late	1640	■	☒	■	☒	■	■	■	☒		×			×	■	×		***9***	***6***
M	Early	1549	☒	☒	■	☒	■	■		☒	☒	×	■		×				***9***	***7***
M	Early	1548	☒	☒	☒	☒	☒	■		■				☒	☒				***9***	***7***
M	Early	1532	■	☒	■	■	■	■	■			×		☒	×	■			***9***	***4***
M	Early	1473	☒	☒	■	■	■	■		■	■	☒			☒				***10***	***4***
M	Early	1565	☒	☒	☒	☒	☒	■	■	☒	☒	☒	☒	☒	×		×		***12***	***12***
M	Late	1646	☒	☒	■	☒	■	■	■		☒	☒		×	×				***9***	***7***
M	Late	1581	☒	☒	■	☒	■	■			■	☒	☒	☒	×	■			***11***	***7***
M	Late	1583	☒	☒	■	☒	■	■			☒	☒	☒	☒	×			☒	***11***	***9***
Number of emitting individuals within single-type sounds			*12*	*12*	*12*	*11*	*10*	*10*	*7*	*7*	*6*	*6*	*5*	*5*	*3*	*3*	*1*	*1*		
Number of emitting individuals within multi-type sounds			*9*	*11*	*2*	*10*	*2*	*0*	*0*	*5*	*4*	*11*	*3*	*6*	*11*	*0*	*3*	*1*		

(gray cell: recorded within single-type sounds, cell crossed out in black: recorded within multitype sounds, white cell: not recorded in this individual).

[a] Sex: F = female; M = male.

[b] Rearing: “Early” = rescued before 2 months old; “Late” = rescued between 2 and 6 months old.