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

3
4 **Running title:** Acoustic repertoire use in cheetahs

5
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16
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26
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29
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31
32 **Abstract:** Early deprivation of adult influence is known to have long-lasting effects on social
33 abilities, notably communication skills, as adults play a key-role in guiding and regulating the
34 behaviour of youngsters, including acoustic repertoire use in species in which vocal production
35 is not learned. Cheetahs grow up alongside their mother for 18 months, thus maternal
36 influences on the development of social skills are likely to be crucial. Here, we investigated
37 the impact of early maternal deprivation on vocal production and use in 12 wild-born cheetahs,
38 rescued and subsequently hand-reared either at an early (less than 2 months) or a later stage
39 of development. We could distinguish 16 sound types, produced mostly singly but sometimes
40 in repeated or multi-type sound sequences. The repertoire of these cheetahs did not differ
41 fundamentally from that described in other studies on adult cheetahs, but statistical analyses
42 revealed a concurrent effect of both early experience and sex on repertoire use. More
43 specifically, early-reared males were characterized by a high proportion of *Purr*, *Meow*, and

44 *Stutter*; early-reared females *Mew*, *Growl*, *Hoot*, *Sneeze*, and *Hiss*; late-reared males *Meow*,
45 *Mew*, *Growl*, and *Howl*; late-reared females mostly *Meow*. Our study demonstrates therefore
46 the long-term effects of maternal deprivation on communication skills in a limited-vocal
47 learner and its differential effect according to sex, in line with known social differences and
48 potential differential maternal investment. More generally, it emphasizes the critical
49 importance to consider the past history of the subjects (e.g. captive/wild-born, mother/hand-
50 reared, early/late-mother-deprived...) when studying social behaviour, notably acoustic
51 communication.

52

53 **Keywords:** early-life experience, maternal deprivation, hand-rearing, sex-differences, acoustic
54 communication, acoustic repertoire, cheetahs, *Acinonyx jubatus*.

55 **INTRODUCTION**

56

57 The extent to which the early stages of life, notably in the case of a maternal deprivation,
58 impact the future skills of an individual, notably his capacities at communicating socially
59 beyond the mere ability to produce the species-specific repertoire of sound types, remains a
60 field of interest that requires further investigation. Communication skills underlie a wide array
61 of social competencies throughout life, therefore degraded communicative abilities are likely
62 to impact, among others, social, parental or else emotional skills. In fact, early-life experience
63 has been demonstrated to have both short- and long-term effects on social skill and emotional
64 regulation in a wide range of species (Pryce et al., 2005). When raised in the absence of adult
65 models, especially when maternally-deprived at an early stage, individuals often have
66 difficulties appropriately interacting with peers later in life, notably due to a reduced
67 propensity to form social bonds and an increased level of aggressiveness. For instance, adult-
68 deprived individuals may be less inclined to engage in allogrooming (e.g. chimpanzees:
69 Kalcher-Sommersguter et al., 2015; macaques: Mason, 1960), to seek spatial proximity with
70 conspecifics (e.g. giraffes: Siciliano-Martina & Martina, 2018; pullets: Perré et al., 2002; mice:
71 Bouet et al., 2011; cichlids: Hesse & Thünken, 2014; honey bees: Hewlett et al., 2018), to signal
72 their intention by threatening before physically attacking (e.g. rats: Tóth et al., 2008), or to be
73 responsive to maternal calls (e.g. degus: Braun et al., 2003). In addition, the frequency and
74 severity of their aggressive displays often exceed that of mother-reared individuals (e.g. cats:
75 Ahola et al., 2017; chimpanzees: van Leeuwen et al., 2014; macaques: Mason, 1960; Suomi,
76 1997; elephants: Slotow et al., 2000; horses: Bourjade et al., 2009; rats: Tóth et al., 2008;
77 cichlids: Arnold & Taborsky, 2010; Hesse & Thünken, 2014). Breeding behaviour can also be
78 affected by early-maternal deprivation in captive animals, subsequently hand-reared by
79 human caretakers (e.g. felids: Hampson & Schwitzer, 2016; Mellen, 1992; gorillas: Ryan et al.,
80 2002; macaques: Suomi, 1997). Furthermore, adult-deprived individuals, even when
81 developing among age-peers, show impaired social and emotional profiles, being highly-
82 reactive to novelty (i.e. anxious and shy) and more impulsive than their mother-reared
83 counterparts as a result of insecure early attachments (e.g. macaques: Suomi, 1997;
84 elephants: Slotow et al., 2000; horses: Bourjade et al., 2009; giant pandas: Snyder et al., 2003;
85 mice: Ros-Simó & Valverde, 2012; degus: Braun et al., 2003; pullets: Perré et al., 2002; cichlids:
86 Bannier et al., 2017). Conversely, growing up along additional adult models tends to enhance
87 the development of appropriate bonding behaviours (e.g. mice: D'Andrea et al., 2007). Adults
88 in general seem to play a key-role in regulating the behaviour of youngsters (Bourjade et al.,
89 2009; Slotow et al., 2000; Suomi, 1997).

90

91 Communication skills, themselves, are also likely to be greatly influenced by early-life
92 conditions (Kaplan, 2017; Snowdon & Hausberger, 1997). Deprivation of adult tutors is well
93 known to result in disrupted communication patterns in vocal learners such as songbirds (e.g.
94 starlings: Bertin et al., 2007, 2009; Cousillas et al., 2006; Poirier et al., 2004; canaries: Lehongre
95 et al., 2006; for reviews see Nieder & Mooney, 2020; Woolley, 2012). However, it is only

96 recently that, in some so-called non-vocal learners, parental feedback was found to play a key
97 role in vocal development too. Thus, parentally-deprived marmosets exhibit persisting
98 infantile acoustic features (“babbling”, larger diversity of sounds) until adulthood as compared
99 to parent-raised individuals (Gultekin & Hage, 2017, 2018). Also, increasing experimentally the
100 amounts of contingent parental vocal feedback led to an earlier transition in development
101 from immature to mature contact calls in juvenile marmosets (Takahashi et al., 2017).
102 Moreover, although it is generally admitted that most terrestrial mammals are able to
103 produce their species-specific calls from birth (Hammerschmidt & Fischer, 2008; Tyack, 2020),
104 when shifting the focus from vocal production learning (i.e. modification of the acoustic
105 structure of the signal as a result of experience with peers) to contextual learning (i.e.
106 modification of call use as a result of social experience), quite a few limited-vocal learners
107 have been found to demonstrate remarkable socially-guided abilities for flexible call use
108 (Cheney & Seyfarth, 2018). For example, social experience is necessary for young vervet
109 monkeys to refine the context of production of alarm calls to specific predators (Seyfarth &
110 Cheney, 1986), while it is also likely to play a role in the acquisition of conversational rules
111 such as turn-taking in monkeys (Bouchet et al., 2017; Chow et al., 2015; Lemasson et al., 2011)
112 as it is the case in songbirds (e.g. starlings: Henry et al., 2015). Finally, the social status of an
113 individual, determined notably by its sex, age and hierarchical rank, can translate into the
114 preferential use of specific call types at different stages in life (e.g. monkeys: Bouchet et al.,
115 2010, 2012; apes: Mitani & Nishida, 1993).

116
117 Cheetahs (*Acinonyx jubatus*) stand out from the Felidae family with regards to sociality.
118 While most felid species are solitary, with the exception of lions (*Panthera leo*) and feral
119 domestic cats (*Felis silvestris catus*) (Bradshaw, 2016), cheetahs display a unique social
120 organisation. Females are solitary, unless accompanied by their dependant offspring, whereas
121 males are facultatively social, living either alone or forming long-term alliances within pairs or
122 trios (rarely quartets) (Caro, 1994; Sunquist & Sunquist, 2002; Wachter et al., 2018). Male
123 coalitions typically consist of brothers from the same litter, but groups larger than two
124 frequently include a non-relative (Caro, 1993; Marker et al., 2010). Males in coalitions are
125 more likely than single males to take and retain small territories (Caro, 1990; Caro & Collins,
126 1987). Other males are “floaters” roaming in large, overlapping, undefended home ranges
127 (Wachter et al., 2018). Solitary females are not territorial either, they occupy large home
128 ranges encompassing those of several males (Gottelli et al., 2007) and overlapping with those
129 of related females, which suggests some degree of female philopatry as well as a certain level
130 of tolerance towards other females (Caro, 1994; Laver, 2005). Females give birth to their first
131 litter around 2-3 years old (Sunquist & Sunquist, 2002; Wachter et al., 2018). Mothers hide
132 their cubs in a den for the first 8 weeks of life (Laurenson, 1993). After emergence, cubs follow
133 their mother around, start feeding on solid food and gradually acquire hunting skills; weaning
134 occurs around 4 months of age (Caro, 1994). During the period that offspring rely upon their
135 mother for solid food, mothers have been found to favour their litters containing two or more
136 sons compared to those including a single son in terms of food provisioning, whereas no such

137 effect was found for daughters (Caro, 1990). Young cheetahs reach independence at 18
138 months old (Laurenson et al., 1992) and family dissolution is initiated by the mother, often
139 already pregnant (Wachter et al., 2018). Siblings then roam with their littermates for a further
140 6 months, until females split from their brothers and go on to produce their first litter (Caro,
141 1994; Marker et al., 2010). While females remain close to their natal home range, males
142 usually disperse and settle away from their natal area (Wachter et al., 2018). Given that cubs
143 grow alongside their mother and siblings for an extended period of time, social influences are
144 expected to play a key-role in the acquisition of social skills by young cheetahs.

145

146 While vocal development in cheetah cubs has received very little attention (Volodina, 1998),
147 adults are known to rely on both acoustic and olfactory signals to communicate. While calling
148 opens the possibility of communicating over long distances, scent marking enables indirect
149 information transfer with a time delay (Wachter et al., 2018). Cheetahs' acoustic signals have
150 been subject to several studies, but no consensus has been reached in the literature yet
151 regarding call terminology, or even classification in some cases (Nagorzanski, 2018; Wachter
152 et al., 2018) (see Appendix 1). The cheetah's acoustic repertoire, i.e. the list of species-specific
153 types of sounds structurally and functionally distinguishable, thus deserves reassessment and
154 clarification. Reports of vocal behaviour from the wild give some contextual information about
155 call emission, but often lack a detailed description of the acoustic structures which prevents
156 comparison (Caro, 1994; Peters, 1991; Sunquist & Sunquist, 2002). Studies in captivity have
157 often focused on a limited number of call types and contexts, for instance 'purring' (Eklund et
158 al., 2010, 2012a; Eklund & Peters, 2013), agonistic calls (Eklund et al., 2012b), feeding calls
159 (Stoeger-Horwath & Schwammer, 2003), and separation-reunion calls (Ruiz-Miranda et al.,
160 1998). The most comprehensive studies of the cheetah acoustic repertoire so far have been
161 conducted in captivity and report eight call types in adults and seven in juveniles (Smirnova et
162 al., 2016; Volodina, 1998, 2000). In addition, the cheetah's vocal repertoire displays a certain
163 level of gradation, in the form of intermediate sounds (i.e. displaying features characteristic
164 of different call types) as well as transitional sounds (i.e. gradually morphing from one call
165 type into another) (Eklund et al., 2012b; Volodina, 2000), although these have not been
166 properly quantified yet. So far, these complex calls have been either disregarded or counted
167 up separately (i.e. multiple parts of transitions counted as distinct calls) (Smirnova et al., 2016),
168 preventing the analysis of additional acoustic variability at higher levels.

169

170 The main limitations of the current cheetah literature are, on the one hand, the lack of
171 quantitative information regarding individual use of the different sound types in wild-born
172 animals (in other words, a reference point to compare captive-born animals with) and, on the
173 other hand, the insufficient details regarding the social/developmental background of the
174 captive subjects whose acoustic repertoire has been investigated (see Appendix 2). Whether
175 subjects have been housed singly, or within same-sex or mixed groups is often unspecified
176 (e.g. Smirnova et al., 2016; Volodina, 2000), despite the known impact of social background
177 on physiology and behaviour (e.g. in females: Wielebnowski et al., 2002; in males: Chadwick

178 et al., 2013; Koester et al., 2015) , and its likely influence on communicative patterns. Besides,
179 captivity itself has been shown to cause chronic stress in cheetahs and to be associated with
180 lower levels of testosterone in males (Terio et al., 2004). More importantly, most captive
181 cheetahs that have been studied were captive-born and are susceptible to have been hand-
182 reared by human caretakers instead of mother-reared, as it is a quite common practice (Bell
183 et al., 2012; Bircher & Noble, 1997; Woc Colburn et al., 2018).

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

207

208 **METHODS**

209

210 ***Study subjects and housing conditions***

211

212 This study was conducted at the Cheetah Conservation Fund (CCF), a centre dedicated to
213 the conservation of cheetahs founded in 1990 and located near Otjiwarongo, Namibia. The
214 CCF centre hosts around thirty wild-born cheetahs rescued as cubs or juveniles after their
215 mother had been killed or disappeared. In Namibia, it is considered that individuals orphaned
216 before the age of six months have not learned the necessary skills from their mother to ensure
217 successful release back into the wild and therefore remain in captivity (Walker et al., 2022).
218 At the CCF centre, captive cheetah cubs are hand-reared by the staff of wildlife professionals

219 until they reach maturity. Whenever possible, orphaned cubs are kept in groups of siblings or
220 paired with same-sex same-age peers. As there are large differences in the developmental
221 stages at which the CCF cubs were rescued, the centre distinguishes between ‘early’ versus
222 ‘late’ hand-rearing depending on whether they were rescued before or after the age of 2
223 months. Early-reared individuals require hand-feeding and sometimes even bottle-feeding
224 every couple of hours; these individuals are kept in a nursery enclosure at the centre. If there
225 is only a single cub, they are kept with a human keeper nearly 24 hours a day, to compensate
226 to some extent for the absence of attention and nurturing a mother cheetah would normally
227 provide. If the cubs come in as a social group or could be bonded to other cubs, they still
228 require a lot of attention from keepers, but less so, as they are able to provide social
229 stimulation to each other between feedings. Keepers encourage vocal production in cubs by
230 responding to their spontaneous vocalizations with mimicking sounds whenever possible.
231 Late-reared individuals are already independent in terms of food consumption and require
232 less human intervention. They are not kept in a nursery but are put out in a slightly larger
233 enclosure. When they first arrive, the cubs still have regular contact with keepers and
234 vocalizations are still encouraged, but to a lesser extent as the time spent with cubs is less
235 than for early-reared. Also, it appears that these young cheetahs tend to respond less to
236 human stimulations than the very young cubs (pers. obs.). All young cheetahs live in
237 enclosures surrounded by other groups of hand-reared cheetahs that provide additional
238 acoustic stimulations.

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

242 The study subjects were 12 cheetahs, four females and eight males: seven of them (2
243 females, 5 males) were rescued as cubs (a few days up to 2 months of age) thus ‘early-reared’,
244 while the other five (2 females, 3 males) were rescued as juveniles (between 2 and 6 months
245 of age) therefore ‘late-reared’. At the time of the study, they were all adults, aged between 5
246 and 15 years (Table 1). All but one male (NAAJU1473) were sexually intact. These cheetahs
247 lived in four same-sex groups of two to four individuals, including related pairs as well as
248 unrelated individuals (Table 1). They were housed in large outdoor enclosures (2–5 ha) with
249 natural shelter in the form of trees, and a three-sided artificial shelter. They were in visual and
250 auditory, but not physical, contact with other neighbouring cheetah groups. Cheetahs were
251 fed once a day (apart from one day fasting per week to mimic eating habits in the wild for this
252 species) with donkey or horse meat. They had *ad libitum* access to clean water.

253

254

-- Table 1 --

255

256 **Data collection**

257

258 Observations were carried out on the four study groups between August and November
259 2019. Cheetah groups were observed in a random order, with sessions spread throughout

260 daytime between 6:00am and 7:00pm. A special focus was given to early mornings 6:00am-
261 12:00pm (71.4%) and, to a lesser extent, to late afternoons 4:30pm-7:00pm (21.4%) known to
262 be the most active periods for cheetahs (Sunquist & Sunquist, 2002). For each group, 4 or 5
263 sessions were conducted prior to and throughout feeding, whereas all other sessions were
264 conducted out of feeding context. In total, 70 observation sessions (16–19 per group) were
265 conducted, lasting on average 3 hours each ($3h07 \pm 1h29$), summing up to 218h44 of
266 recordings (Table 1).

267 During these observation sessions, cheetah acoustic signals were recorded following the
268 *all-occurrences sampling* procedure (Altmann, 1974) using a directional microphone
269 Sennheiser K6/ME66 attached to a portable stereo digital recorder Marantz PMD661 MKII
270 (sampling frequency: 44100 Hz, resolution: 16 bits). We collected a total of 3297 sounds in the
271 four study groups. The identity of the caller was recorded whenever possible (that is, for 2656
272 sounds).

273

274 ***Data analysis***

275

276 Spectrograms of the calls were generated for auditory and visual inspection using
277 Ocenaudio audio editor (256-pt FFT Hanning window, sampling rate for inspection: 22050Hz).
278 A dichotomous classification key was established based on distinctive frequency, pulse and
279 temporal features, an approach commonly used to describe the acoustic repertoire of
280 mammal and bird species (Adret-Hausberger, 1989; André et al., 2020; Fournet et al., 2015;
281 Hausberger & Guyomarc'h, 1981; Lemasson & Hausberger, 2011). We distinguished between
282 vocal and non-vocal sounds: the former are sounds involving vibrations of the vocal cords,
283 either through phonation or by contraction of the vocalis muscle (Frazer Sissom et al., 1991;
284 Herbst et al., 2012; Weissengruber et al., 2008), whereas the latter are unvoiced sounds
285 produced by the airflow being forced through a vocal tract constriction (e.g. snort, snore and
286 blow in horses: Stomp et al., 2018; sneeze in African wild dogs: Walker et al., 2017).

287 We observed both single- and multi-unit sounds in our dataset consisting of 2656 sounds,
288 thus we coded all sounds at the unit level, in terms of unit types and number of units. As
289 transitions between expiratory and inspiratory phases have been estimated to be quite short
290 in cheetahs, with durations in the range of 50–200ms in purrs for example (Eklund et al., 2010),
291 we set up the threshold for two units (of any type) to be considered as parts of the same sound
292 to $\Delta=200$ ms. This way, we could code for single-type sounds, including either one (Single) or
293 several (Repeated, in series) units of the same type, as well as multi-type sounds made of a
294 mix of several units of different types, either produced joined (Transitions, with $\Delta=0$ ms) or
295 juxtaposed (Combinations, with $0<\Delta\leq 200$ ms). The level of agreement between two raters (HB,
296 KC) at classifying the single-type sounds was 90,28% (2164 sounds similarly labelled out of
297 2397).

298

299 ***Statistical analysis***

300

301 Statistical analysis was performed using R Studio 1.1.463 (R version 3.5.0) (R Core Team,
302 2016; RStudio Team, 2016), except for Chi-squared tests conducted using Microsoft Excel.

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

308 We aimed at evaluating the relative use of the different sound types by cheetahs with
309 different sex and early-life experiences. More specifically, we tested whether the different
310 types of single-type sounds (i.e. Single or Repeated) occurred in the same or different
311 proportions within the repertoire displayed by each category of individuals (females vs males,
312 early vs late-reared). A GLMM_{binomial-logit} model was built using the 'glmer' function (in R *lme4*
313 package), the response variable being the proportion of a given single-type sound type out of
314 the whole sample of sound (both single- and multi-type) recorded for a given individual on a
315 given day. All explanatory variables (sound type, subjects' sex and early-life experience) were
316 fitted in the model as fixed factors, alongside the corresponding two- and three-way
317 interactions. Subjects' identity as well as the day of observation (from Day-01, 1st day of
318 recording, onwards) were included in the model as random factors. We verified that the
319 model met the assumption of independence between the values of the residuals and the
320 values estimated by the model, and checked for overdispersion with an acceptable ratio of
321 residual deviance on degrees of freedom set to be <2 (using 'plotresid' and 'overdisp.glmer'
322 functions in R *RVAideMemoire* package, respectively). To test for the significance of the fixed
323 factors and their interactions, we applied a type III ANOVA to the model (using 'Anova'
324 function in R *car* package). We additionally verified the goodness of fit of the model (using
325 'r.squaredGLMM' in R *MuMIn* package that computes the pseudo-R-squared for GLMM), and
326 conducted comparisons with null models including either a constant value or including only
327 sound type as a fixed factor (using 'anova' function in R *stats* package). Then, we conducted
328 post-hoc pairwise comparisons between the different categories of individuals (females vs
329 males, early vs late-reared) within each sound type (using 'lsmeans' function in R *lsmeans*
330 package), with p-values adjusted for multiple comparisons (Sidak method). We further
331 confirmed these general results by comparing the frequency of use, out of the whole sample
332 of sounds recorded, of the four most frequently produced types of single-type sounds in the
333 different individuals using Chi-squared tests.

334 All tests were two tailed and we set the significance threshold at $\alpha = 0.05$.

335

336 ***Ethical note***

337

338 All applicable international, national, and institutional guidelines for the care and use of
339 animals were followed. This study was conducted in accordance with the current laws in
340 France and Namibia. It complies with the 2010/63/UE directive on the protection of animals
341 used for scientific purposes. Data collection was evaluated as non-invasive observations and

342 respecting the ethical rules by the “Comité Rennais d’Ethique en matière d’Expérimentation
343 Animale” (i.e. Rennes Ethical Comity for Experiments using Animals; CREEA approval
344 #201806081359001). The staff of the CCF centre was responsible for all animal husbandry and
345 care. Research at CCF was conducted under the authorization #201805701 awarded by the
346 Namibian National Commission on Research, Science and Technology.

347

348 **RESULTS**

349

350 ***Cheetahs’ acoustic repertoire***

351

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

356

357 Definition of the sound types

358

359 1. Vocal sound types

360

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

363 1.1. Tonal types – Nine of the expired vocal types were clearly tonal (with visible harmonics).

364 1.1.1. Unpulsed – Six of them displayed frequency bands with a continuous tracing (Figure
365 2a). Of the six unpulsed calls, four were high-pitched calls, of which three (**Mews**, **Meows**,
366 and **Screams**) were characterised by a modulated fundamental frequency: **Mews** were
367 shorter than **Meows** ($\approx 100\text{--}200\text{ms}$ and $\approx 200\text{--}700\text{ms}$, respectively), **Screams** were slightly
368 higher-pitched ($F0_{\text{mean}} > 500\text{Hz}$) and much noisier; and one, **Hoots**, had a slightly lower non-
369 modulated fundamental frequency ($F0_{\text{mean}} \approx 300\text{--}500\text{Hz}$) and a short duration ($\approx 100\text{--}$
370 200ms). Two calls were lower-pitched calls: **Hous** were shorter ($\approx 100\text{--}300\text{ms}$) than **Howls**
371 which could even exceed 2sec, sometimes developing into a slow wave-like modulation
372 pattern.

373 1.1.2. Pulsed – The other three tonal call types had a pulsed structure and were
374 distinguishable based on their pulse rate (Figure 2b), respectively fast (range: 30–45
375 pulses/sec) for **Trills** (also higher-pitched with $F0_{\text{mean}} > 400\text{Hz}$), medium (20–30) for **Chortles**
376 and slow (10–20) for **Stutters**.

377 1.2. Atonal types – Two expired vocal types were atonal, with more or less visible formants
378 (Figure 2c). **Growls** were low-pitched fast-pulsed calls (> 30 pulses/sec) and could exceed 2sec,
379 whereas **Barks** were relatively short and noisy units corresponding to an abrupt exhalation.

380 1.3. Expired/inspired type – The remaining vocal type, **Purr**, had a pulsed structure and had
381 the specificity to be produced continuously during both exhalation and inspiration phases

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

384

385 2. Non-vocal sound types

386

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

389 2.1. From the mouth – *Spits* were explosive sounds, whereas *Hisses* were aperiodic sounds
390 corresponding to a harsh blow with the mouth open.

391 2.2. From the nose – *Snuffs* and *Sneezes* were abrupt blowing nasal sounds, *Sneeze* being
392 characterised by an additional introductory unit (either a short tonal unit, or a short series of
393 pulses).

394

395 -- Figure 1 –

396

397 -- Figure 2 –

398

399 Single-type sounds: Single and Repeated

400

401 Although they were mostly produced as isolated utterances (Single = 79.4% of the dataset,
402 N=2108), sounds could also be made of a series of units of the same type (Repeated = 10.9%,
403 N=289). *Purrs* were the most frequent Repeated pattern, as they were produced mostly as
404 long series of expired units (94.6% of N=203, Figure 3), alternating with audible inspired units
405 in two-thirds of the cases, although isolated single expired units were produced occasionally
406 (5.4%). Some other sound types could be produced as series of same-type units: *Hous* (85.7%
407 of N=7, Figure 3), *Hoots* (37.1% of N=35), *Chortles* (34.8% of N=23), *Barks* (33.3% of N=3),
408 *Screams* (20% of N=30), *Trills* (14.3% of N=21), and to a lesser extent, *Mews* (5.2% of N=461,
409 Figure 3), *Stutters* (3.9% of N=541), *Growls* (3.9% of N=178), and *Meows* (1.1% of N=703). On
410 the contrary, *Howl* (N=30) as well as the unvoiced *Snuff* (N=79), *Sneeze* (N=67), *Hiss* (N=12)
411 and *Spit* (N=4) were never produced in series.

412

413 Multi-type sounds

414

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

420

421 -- Figure 3 --

422

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

432
433 -- Figure 4 --
434

435 ***Repertoire use at the population level***

436
437 Out of 3297 sounds recorded in the four study groups, caller's identity could be recorded
438 for a total of 2656 sounds (i.e. 80.6%). The number of sounds recorded per subject varied
439 greatly (range: 0.21–13.73 sounds per hour), with an average of 4.02 ± 3.98 sounds per hour
440 per individual (mean \pm sd across individuals). Early-reared animals tended to produce less
441 sounds (i.e. be less vocal) than late-reared individuals (Table 2; Mann-Whitney on hourly call
442 rates of early- vs. late-reared individuals: $W = 7$, $p=0.1061$). Individual repertoire sizes (for
443 single-type sounds) did not differ according to sex or rearing condition (Kruskal-Wallis on the
444 four "sex \times rearing" categories individuals: $H=5.3181$, $df=3$, $p=0.1499$) although the two early-
445 reared females had the smallest repertoire with only 7 and 4 different types of single-type
446 sounds (9 to 12 for all other individuals) (see Appendix 3: repertoire of single-type sounds).

447 Single-type sounds ($N=2397$) were largely predominant as they accounted for $90.5 \pm 6.6\%$
448 of the total sound production at the individual level (mean \pm sd across individuals), with 76.0
449 $\pm 14.6\%$ produced singly (Single) and $14.5 \pm 15.6\%$ as a sequence of the same repeated unit
450 (Repeated). Multi-type sounds ($N=259$) represented only $9.5 \pm 6.6\%$ of sound production
451 within individual repertoires, including $2.1 \pm 1.9\%$ of Combinations, $6.9 \pm 5.8\%$ of Transitions
452 and $0.6 \pm 1.1\%$ of Mixed pattern (Table 2).

453
454 -- Table 2 --
455

456 Overall, success rate at identifying the caller was 81.3% for single-type sounds (2397
457 identified out of the 2947 single-type sounds recorded in the four study groups). However,
458 some sound types were more difficult to assign to a given individual because of high levels of
459 sound overlap and excitation during the associated contexts of production, potentially leading
460 to being under-evaluated. This is the case for *Hoots*, *Howls*, *Hous*, *Growls*, *Trills*, and *Barks* (in
461 decreasing order of success rate for caller identification of single-type sounds, range: 71.4%-
462 42.8%).

463 Amongst these 2397 single-type sounds, the most frequently produced single-type sounds
464 were *Meows*, *Mews*, *Purrs*, *Growls*, *Stutters*, *Sneezes* and *Snuffs* (Figure 5). *Mews*, *Growls* and
465 *Sneezes* were emitted by all 12 study subjects (see Appendix 3: repertoire of single-type
466 sounds). *Meows*, *Purrs*, and *Hisses* were not given by all subjects but were nevertheless
467 recorded in individuals of all four classes (early- and late-reared of both sexes). More precisely,
468 most sounds (N=2108) were produced singly, and consisted then mostly in *Meows* and *Mews*
469 ($28.2 \pm 21.4\%$ and $23.3 \pm 12.6\%$ of Single production), whereas a smaller number of them
470 (N=289, produced by 11 out of 12 individuals; Table 2) were produced in repeated series,
471 consisting mostly in *Purrs* ($54.6 \pm 33.4\%$ of Repeated).

472
473 -- Figure 5 --
474

475 Although more anecdotal (N=259), multi-type sounds were emitted by all 12 study subjects,
476 with a predominance of the units *Meow*, *Stutter*, *Trill*, *Growl*, *Bark* and *Mew*, followed by *Howl*,
477 *Scream*, *Hoot* and *Hou* (see also Appendix 3: repertoire used within multi-type sounds). On
478 rare occasions, *Purr* units were combined or interspersed with *Chortle* or *Sneeze*. The unit
479 types *Meow*, *Trill* and *Growl* could be produced concurrently to almost all other unit types,
480 but the most frequently observed associations were *Stutter+Meow* (mainly transitional, N=82),
481 *Trill+Meow* (almost always transitional, N=62) and *Bark+Growl* (mainly transitional, N=33),
482 followed by the more rarely observed associations *Meow+Mew* (always combined, N=12),
483 *Howl+Growl* (almost always transitional, N=12), *Stutter+Mew* (mainly combined, N=9) and
484 *Trill+Scream* (almost always transitional, N=5) (Figure 4). Within these multi-type sound
485 patterns, units could be ordered both ways: for instance, *Stutter+Meow* can be produced as
486 either *Stutter-Meow* or *Meow-Stutter*.

487 ***Influence of sex and early-life experience on individual repertoire use***

488
489 Repertoire use varied across individuals depending on their sex and early-life experience.
490 A few single-type sounds were only produced by individuals of a given sex (see Appendix 3:
491 repertoire of single-type sounds). *Howls* and *Stutters* were produced by males only, and *Hous*
492 were emitted by one single late-reared male. *Screams* were produced by one single late-
493 reared female only (but note that another late-reared female and an early-reared male also
494 produced *Scream* units as part of transitional sounds). Moreover, only males produced series
495 of *Mews* (recorded in 3 early- and 3 late-reared subjects), *Stutters* (1 early- and 2 late-reared
496 males), *Hous* (a single late-reared male), *Chortles* (1 early- and 2 late-reared subjects) and *Trills*
497 (2 early-reared males). *Barks* and *Screams* were produced in series by one single late-reared
498 female. Lastly, only late-reared individuals produced *Meows* in series (recorded in 1 late-
499 reared female and 3 late-reared males).

500
501 Overall, the relative frequency of use (i.e. proportion of total acoustic production) of the
502 16 single-type sound types (i.e. Single or Repeated) appeared to differ across individuals
503 depending concurrently on their sex and early-life experience (ANOVA on $GLMM_{binomial-logit}$,

504 significant three-way interaction “SoundType × Sex × EarlyLife”: Table 3; post-hoc pairwise
505 comparisons: see Sidak-adjusted p-values in the text below).

506

507

-- Table 3 --

508

509 Thus, each category of individuals had a specific predominant use of some sound types in
510 particular (Fig. 6). Males used high proportions of *Meows* and *Stutters*, as well as *Mews* for
511 the late-reared males (>20% of the total number of sounds produced, based on GLMM model
512 estimates). Early reared females were characterized by a predominance of *Mews* and *Growls*
513 (>20%), and late-reared females by a predominance of *Meows* (38%). More specifically, post-
514 hoc statistical comparisons revealed that:

515 - early-reared males used a higher proportion of *Purr* (compared with late-reared males:
516 $p < 0.0001$, and late-reared females: $p < 0.0001$), *Meow* (than early-reared females: $p = 0.0098$),
517 *Stutter* and *Sneeze* (than late-reared males: $p = 0.0030$ and $p = 0.0111$ respectively) (Figure 6a).

518 - late-reared males used a greater proportion of *Meow* (than early-reared females: $p = 0.0043$),
519 *Mew* and *Growl* (compared with early-reared males: $p < 0.0001$ for both, and late-reared
520 females: $p = 0.0035$ and $p < 0.0001$ respectively), *Purr* (than late-reared females: $p = 0.0293$), and
521 *Howl* (than early-reared males: $p = 0.0036$) (Figure 6b).

522 - early-reared females used a higher proportion of *Mew*, *Growl* and *Hoot* (compared with late-
523 reared females: $p = 0.0030$, $p < 0.0001$ and $p = 0.0053$ respectively, and early-reared males:
524 $p < 0.0001$, $p < 0.0001$ and $p = 0.0003$ respectively), as well as *Sneeze* and *Hiss* (compared with
525 early-reared males: $p = 0.0078$ and $p = 0.0022$ respectively, and late-reared males: $p < 0.0001$ and
526 $p = 0.0036$ respectively) (Figure 6c).

527 - late-reared females used a greater proportion of *Meow* (compared with early-reared
528 females: $p = 0.0003$, early-reared males: $p < 0.0001$, and late-reared males: $p = 0.0007$), *Snuff* and
529 *Sneeze* (than late-reared males: $p = 0.0105$ and $p = 0.0009$ respectively) (Figure 6d).

530 No difference across categories of individuals could be found for the rare (N emitters ≤ 6 ,
531 see Appendix 3: repertoire of single-type sounds) *Scream*, *Trill*, *Chortle*, *Spit*, *Bark* and *Hou*
532 (Figure 6), possibly due to the limited sample size for these sound types.

533 Apart from the post-hoc pairwise comparisons reported above and illustrated in Figure 6a,
534 all others were statistically non-significant.

535

536

-- Figure 6 --

537

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

543

544

-- Figure 7 --

545

546 Finally, some differences appeared also in the production of multi-type sounds (see
547 Appendix 3: repertoire used within multi-type sounds). Although the *Trill+Meow*, *Bark+Growl*
548 and *Meow+Mew* were produced by both sexes ($N_{\text{ind}} = 7, 11, \text{ and } 6$ individuals respectively, for
549 a total of $N = 62, 33, \text{ and } 12$ recorded exemplars), some patterns were produced only by males
550 (with both types of early-life experience), namely *Stutter+Meow*, *Howl+Growl* and
551 *Stutter+Mew* ($N_{\text{ind}} = 3, 5, \text{ and } 2$ individuals respectively, for $N = 82, 12, \text{ and } 9$ exemplars),
552 whereas the *Trill+Scream* were recorded only in females ($N_{\text{ind}} = 2$ late-reared subjects, $N = 5$
553 exemplars). Besides, some multi-type sounds were occasionally recorded in just a few
554 individuals (often a single one), with some patterns limited to males: *Growl+Mew*,
555 *Stutter+Growl*, *Purr+Sneeze*, *Chortle+Purr*, *Hoot+Growl*, *Hoot+Meow*, *Hou+Growl*, *Hou+Howl*,
556 *Howl+Bark*, *Howl+Meow*, *Trill+Bark*, *Trill+Growl*, *Trill+Stutter*, *Bark+Howl+Growl*,
557 *Growl+Trill+Hoot*, *Stutter+Trill+Meow*, *Trill+Bark+Growl*, and *Trill+Meow+Growl* (recorded in
558 7 different subjects with both types of early-life experience; $N_{\text{ind}} \leq 3$ and $N \leq 3$ exemplars each);
559 and others to females: *Trill+Mew*, *Trill+Hoot*, *Scream+Trill+Growl*, *Meow+Scream+Trill*, and
560 *Hoot+Growl+Bark* (recorded in 3 different subjects with both types of early-life experience;
561 $N_{\text{ind}} \leq 2$ and $N \leq 4$ exemplars each). Other rare patterns, *Meow+Growl* and *Scream+Growl*,
562 were produced by individuals of both sexes ($N_{\text{ind}} = 3$ and 2 respectively; $N \leq 4$ exemplars).

563

564

565 DISCUSSION

566

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

578

579 *The cheetah acoustic repertoire: universal features?*

580

581 In our classification, based on acoustic structures, we identified 16 sound types, all but one
582 (*Hou*) emitted by at least three subjects. Repertoire size varied little between individuals and,
583 besides the *Hou* that was recorded here in a single male individual, the other two male-specific
584 call types in our study (*Howl* and *Stutter*) have been previously recorded in wild as well as
585 captive females, in contexts that we may have missed the chance to observe (i.e. stranger

586 intrusion for ‘howls’, and during male-female or mother-cubs interactions for ‘stutters’) (Caro,
587 1993; Eklund et al., 2012b; Sunquist & Sunquist, 2002; Volodina, 2000).

588

589 The repertoire we have established is twice larger (in terms of number of different sound
590 types identified) than what has been reported by Volodina (2000) and Smirnova et al. (2016)
591 for captive cheetahs. However, among the sounds that we added in the repertoire, some types
592 match what has been described, under the same or a different label, in other studies on adult
593 cheetahs (e.g. *Spit*: in Eklund et al., 2012b and Peters, 1991; *Mew*: labelled ‘Yelp’ in Stoeger-
594 Horwath & Schwammer, 2003 and Nagorzanski, 2018) (see Appendix 1). It is noteworthy that
595 several of the sound types described here in cheetahs have also been found in other felids
596 (Bradshaw & Cameron-Beaumont, 2000; Stanton et al., 2015), notably in the domestic cat
597 (Schötz et al., 2017; Tavernier et al., 2020): *Mew/Meow*, *Trill*, *Stutter*, *Purr*, *Growl*, *Howl*,
598 *Scream* (‘pain shriek’), *Hiss* and *Spit* for instance.

599

600 On the one hand, several sound types were easy to match with earlier published
601 descriptions of cheetahs’ communicative behaviour due to their distinctive and unambiguous
602 acoustic pattern. This was the case for the extensively studied *Purr* (Eklund et al., 2010, 2012a;
603 Eklund & Peters, 2013; Frazer Sissom et al., 1991; Peters, 2002), the frequently reported *Howl*,
604 *Stutter*, *Growl* and *Hiss* (Eklund et al., 2012b; Peters, 1991; Smirnova et al., 2016; Sunquist &
605 Sunquist, 2002; Volodina, 2000), and the occasionally reported *Spit* (Eklund et al., 2012b;
606 Peters, 1991) (see Appendix 1). On the other hand, discrepancies between our classification
607 and published ones likely originate from our attempt to clarify the cheetah vocal repertoire
608 regarding ambiguous structures not matching the commonly reported acoustic templates. For
609 instance, we divided high-pitched tonal calls into four types (*Mew*, *Meow*, *Scream* and *Hoot*),
610 and we added one low-pitched tonal (*Hou*), two tonal pulsed (*Trill* and *Chortle*), and one atonal
611 (*Bark*) types never reported so far (see Appendix 1). Unlike most previous studies however,
612 and despite extensive recordings, there is one call type (the ‘chirp’) that we could not identify
613 in our recordings. Rather than a specificity of our maternally-deprived subjects, we suspect
614 that it could have more to do with their age (> 5 years old, well beyond the juvenile stage) as
615 compared with previously studied populations which included young adults just 2-3 years old
616 (see Appendix 1). It could otherwise be due to methodological discrepancies in terms of
617 classification criteria (see Appendix 1).

618

619 Another novelty in our approach is to integrate more non-vocal sounds within the acoustic
620 repertoire in addition to *Hiss* and *Spit*, such as *Snuff* and *Sneeze*. Although included in the
621 repertoire for the first time here, they certainly do not constitute a peculiarity of our subjects
622 (see ‘snort/snuffle’ mentioned in Wachter et al., 2018). Recent studies revealed that ‘sneezes’
623 play a role in group movement coordination in the African wild dog (Walker et al., 2017) and
624 that ‘snorts’ reflect positive emotions in horses (Stomp et al., 2018) and possibly rhinos
625 (Policht et al., 2008), suggesting that such non-vocal sounds deserve more attention. Also,
626 nasal sounds used as friendly close-range calls (‘prusten’ and ‘puffing’) have been identified

627 in lions, leopards, jaguars and tigers (Peters & Tonkin-Leyhausen, 1999). For this reason,
628 although their context of emission requires further clarification, we recommend that *Snuff*
629 and *Sneeze* be included in the description of the cheetah acoustic repertoire.

630

631 It does not seem that the particular ontogenetic status of our subjects has influenced
632 repertoire size and composition, as their repertoire does not differ drastically from those
633 described in other studies (see Appendix 1). This supports the hypothesis of the cheetah as a
634 non- or limited-vocal learner, like many other terrestrial mammals, but still leaves open the
635 possibility for vocal production in a very broad sense (refinement of repertoire via parental
636 reinforcement) and/or use learning (Gultekin & Hage, 2018; Nieder & Mooney, 2020).

637

638 Unfortunately, the status (mother-reared vs hand-reared) of individuals is not always
639 mentioned in studies of captive cheetahs (e.g. Ruiz-Miranda et al., 1998; Smirnova et al., 2016;
640 Volodina, 2000) (see Appendix 2), although hand-rearing in both zoos and conservation
641 centres is a common necessity (Bell et al., 2012; Bircher & Noble, 1997; Woc Colburn et al.,
642 2018). Thus, most literature on cheetahs' acoustic behaviour is susceptible to be, for a large
643 part, based on hand-reared subjects. Interestingly, Eklund et al.'s extensive studies on 'purrs'
644 were conducted in captive, generally hand-reared individuals in the context of cheetah-human
645 interactions (Eklund et al., 2010, 2012a; Eklund & Peters, 2013), whereas their study on
646 agonistic calls was conducted in wild-caught, only semi-habituated individuals awaiting
647 relocation and managed under minimum human contact conditions (Eklund et al., 2012b) (see
648 Appendices 1 & 2). That choice of focus individuals may in fact explain the predominance of
649 either type of sounds in these populations with contrasting early-life backgrounds and
650 subsequent behaviours towards humans. It is also noteworthy that while most studies in
651 captivity have mentioned the 'meow' call type, this is not the case for studies conducted in
652 the wild (Peters, 1991; Sunkuist & Sunkuist, 2002). This may be either because this call type
653 is unusual in wild populations, or it may be that this soft call is harder to observe in natural
654 conditions. To get a better understanding of the factors driving variability in cheetahs' acoustic
655 communication patterns, future studies should make a practice of providing all relevant
656 background information for their study subjects (i.e. wild- vs captive-born, mother- vs hand-
657 reared, semi- vs fully-habituated to humans, housed singly or within a mixed- or same-sex
658 social group...). This would ease comparisons across populations, and also help disentangle
659 the influence of early-life experience and current social environment on cheetahs'
660 communicative behaviour.

661

662 Another aspect that remains poorly described in the literature is the existence of repeated
663 and multi-type calls (combinations or transitions). Repeated calls have not been mentioned in
664 the cheetah literature thus far (and were probably counted as distinct single utterances),
665 except for *Purrs* known to be produced in long series, unlimited in duration (Eklund et al.,
666 2012a; Volodina, 2000). Here, we found that 11 out of the 16 sound types could be produced
667 in series (that is all but *Howl* and the unvoiced *Snuff*, *Sneeze*, *Hiss* and *Spit*). Multi-type calls,

668 on the other hand, have already been described in cheetahs. Smirnova et al. (2016) reported
669 the most frequent transitional calls as being ‘purr-meow’, ‘growl-howl’ and ‘growl-meow’ calls.
670 Volodina (2000) reported transitional calls made of tonal sounds (‘miaowing’ or ‘chirping’)
671 alternating with pulsed sounds (‘churtling’, ‘growling’ or ‘gurgling’) as well as intermediate
672 sounds between ‘churtling-miaowing’, ‘howling-growling’, ‘howling-miaowing’, and
673 ‘miaowing-chirping’. Eklund et al. (2012b) also reported intermediate patterns between
674 ‘moan-growl’. In addition, we can find direct equivalents of cheetah multi-type calls in the
675 domestic cat vocal repertoire: Schötz et al. (2019) listed for example ‘trill-meow’, ‘growl-howl’,
676 ‘meow-howl’ and ‘meow-purr’ (see also “broadband hybrid units” in Owens et al., 2017).
677 These earlier findings are quite in accordance with our observations, where the most
678 frequently observed patterns were *Stutter+Meow*, *Trill+Meow*, and *Bark+Growl*, followed by
679 the less frequent *Meow+Mew* and *Howl+Growl*. These complex associative patterns definitely
680 deserve further investigation in cheetahs in order to determine whether or not they convey
681 messages that differ in some ways from those of single calls, as found in different mammal
682 species (Blumstein & Armitage, 1997; Manser, 2001; Ouattara et al., 2009; Schel et al., 2010),
683 or whether it may be a by-product of other factors such as adult deprivation and a lack of
684 canalization of acoustic patterns (Nelson, 1997).

685

686 ***Long term impact of early-life experience on repertoire use varies according to sex***

687

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

703

704 In most studies where parental/adult influence on vocal development was investigated, it
705 appeared that adults played a role in “pruning” the repertoires of innate call types by
706 canalizing varied immature production towards pertinent more restricted adult structures (e.g.
707 marmosets: Gultekin & Hage, 2017, 2018; Australian magpies: Kaplan, 2017; European
708 starlings: Bertin et al., 2007; cowbirds: West et al., 1997). Although the human caretakers here,

709 at the CCF centre, stimulated acoustic production in the early-reared animals, these actions
710 did not lead to higher vocal production (higher calling rates) nor diversity (larger repertoire
711 size and/or variety of associative acoustic patterns). It may be that the lack of appropriate
712 contingency, a crucial aspect for acoustic maturation in marmosets, humans and songbirds
713 (Goldstein et al., 2003; Gultekin & Hage, 2017, 2018; Kuhl et al., 2003), and/or the different
714 acoustic structure of the human imitations may have prevented any influence. When adopted,
715 the cubs had already had experience with their mother's voice, which is likely to convey
716 powerful emotional information as reported in degus (Ziabreva et al., 2003). In degus,
717 parentally-deprived animals vocalize less (Braun et al., 2003), which is also the case here for
718 early-reared cheetahs (see also Rose, 2012), revealing that age at separation may be an
719 important feature for acoustic development.

720
721 Although both sexes are supposedly able to produce all the call types of the species
722 repertoire as early as infancy (Volodina, 1998, 2000), we found that the acoustic repertoire of
723 early-reared females was less varied overall than that of all other categories, while males'
724 repertoire was enriched with a wide variety of associative acoustic patterns. This suggests
725 opposite effects of early deprivation on males and females: lack of canalization in males (as in
726 marmosets for instance: Gultekin & Hage, 2017) *versus* decreased acoustic production in
727 females (as in degus for example: Braun et al., 2003). The differential influence of maternal
728 deprivation on the acoustic repertoire of male and female cheetahs that we report here could
729 be in part attributable to differences in the maternal rearing of male and female cheetah cubs.
730 For instance, mothers have been found to make greater efforts to provision litters containing
731 two or more sons: not only do they spend increasing amounts of time hunting and thus
732 providing a greater number of meals to brothers (compared with litters comprising a single
733 son), but mothers also abstain from feeding on carcasses to favour their multiple sons (but
734 not their single son or daughters) (Caro, 1990). This bias in food provisioning would reflect a
735 preferential investment in favour of offspring of the cooperating sex (i.e. cheetah brothers
736 prone to form a life-long coalition) (Caro, 1990), and it is likely to not only influence offspring's
737 growth (as in e.g. macaques: Hinde, 2007; red deer: Landete-Castillejos et al., 2005) but also
738 to impact their social ontogeny (as in e.g. horses: Cameron et al., 2008; gorillas: Robbins et al.,
739 2007; mouse lemurs : Perret & Colas, 1997). The higher maternal investment may be
740 associated with an increased dependency on mother's care and a tendency to an increased
741 neotenic behaviour of young males relative to young females. While data on differences in
742 the impact of early social experience on vocal development according to sex are overall quite
743 scarce, some examples are known from other species as well. The impact of early deprivation
744 from adult contact differentially affects males and females in starlings (e.g. Cousillas et al.,
745 2006, 2008; Henry et al., 2008). Also, in degus, the broadcast of the mother's voice led to
746 opposite effects in young separated males and females, modulating the effects of separation
747 in males, but increasing them in females (Ziabreva et al., 2003). It is possible that the mother's
748 emotional buffering is more important for males, or that these gender-specific responses may
749 be due to interactions of gonadal hormones.

750

751 An alternative cause for the observed differences between the repertoire use of males and
752 females (i.e. differences in preferentially produced sound types and in their levels of acoustic
753 diversity regarding associative patterns) could be related to their contrasting “social
754 dispositions” (Mason, 1978). Male cheetahs have a greater propensity at interacting and
755 bonding, and unlike females, are prone to form long-term coalitions (Caro, 1994; Sunquist &
756 Sunquist, 2002; Wachter et al., 2018), which could lead to differential use of acoustic signals
757 with different social values. Indeed, social organisation and bonding propensities can translate
758 into a differential expression of the vocal repertoire across classes of individuals (e.g. in
759 primates: Bouchet et al., 2010, 2012; Hohmann, 1991). Also, these higher levels of variability
760 in communicative patterns in males could be directly linked to the higher frequency of social
761 interactions they experience, and the tighter bonds they maintain with their peers (Caro,
762 1993), compared with females whose social tolerance level remains low even when housed in
763 a single-sex group in captivity (Wielebnowski et al., 2002).

764

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

779

780 Several of the sounds expressed differentially by cheetahs based on early vs late maternal-
781 deprivation are related to positive intraspecific interactions. In cheetahs, *Purrs* are produced
782 by wild and captive animals when resting, before or after a meal, and during friendly
783 encounters or mutual grooming with conspecifics (Caro, 1993; Smirnova et al., 2016; Sunquist
784 & Sunquist, 2002). In captivity however, according to Eklund & Peters (2013) and Smirnova et
785 al. (2016), cheetahs of all ages purr primarily in the context of physical contact with humans.
786 But the early experience of these captive subjects, notably regarding hand-rearing, needs to
787 be clarified (see Appendix 2). Indeed, the redirection of purring towards humans may well be
788 related to the amount of human contact and/or lack of contact to conspecifics experienced at
789 earlier stages. Whether the increased purring in males is attributable to increased effects of
790 maternal deprivation/persistence of neotenic behaviours or a greater propensity at

791 interacting and bonding among male peers still remains to be understood. In domestic cats,
792 purring is known to emerge almost from birth, its production by kittens while suckling
793 stimulating maternal care. Later in life, cats purring towards a familiar partner is viewed as a
794 sign of contentment from an animal “feeling well” and “comfortable”, or alternatively as a
795 contact- and care-soliciting signal like in neonates (Bradshaw & Cameron-Beaumont, 2000;
796 Little et al., 2014; Peters, 2002).

797
798 *Stutters* and *Mews* also relate to signals known to be used in the context of interactions
799 between mother and cubs, among social partners or during courting (Ruiz-Miranda et al.,
800 1998; Smirnova et al., 2016; Sunquist & Sunquist, 2002; Volodina, 1997, 2000; Volodina &
801 Volodin, 1996) (see Appendix 1 for correspondence between call terminologies). In our
802 maternally-deprived hand-reared subjects, the increased production of *Stutters* in early-
803 reared males and *Mews* in early-reared females relative to their late-reared counterparts may
804 again be a redirection from intra- to inter-specific communication towards humans, as for
805 *Purrs*, similarly to the way domestic cats use ‘meows’ (Bradshaw & Cameron-Beaumont, 2000;
806 Nicastro, 2004).

807
808 Another sound associated with mother-cub interactions in cheetahs are the ‘meows’.
809 ‘Meows’ are notably produced by juvenile cheetahs in an attempt to attract attention and
810 care (Volodina, 1997). In adults, ‘meows’ are emitted to call over a conspecific or when in
811 contact with a social partner, as well as during courting (Ruiz-Miranda et al., 1998; Smirnova
812 et al., 2016; Volodina & Volodin, 1996) (see Appendix 1 for correspondence between call
813 terminologies). ‘Meows’ are also produced by captive animals when calling to humans in the
814 context of food anticipation, both by juveniles and adults (Smirnova et al., 2016; Stoeger-
815 Horwath & Schwammer, 2003). In interspecific communication, the efficiency of ‘meows’ at
816 attracting human attention is suggested to have enhanced its production by domestic cats
817 (Bradshaw & Cameron-Beaumont, 2000; Nicastro, 2004). Ongoing analyses of the context of
818 production will help understand the increased proportion of *Meows* in late-reared cheetahs
819 of both sexes, produced not only as single but also within repeated calls, with late-reared
820 females using them in proportions significantly greater than any other class of individuals. The
821 communicative value of *Meows* is expected to be either as a social signal (notably among male
822 coalition partners) or as an inter-specific communication signal (towards human caretakers
823 who provision them). In addition, further investigation in naturalistic conditions would be
824 needed to decipher the prevalence and contextual use of *Meow* calls, not explicitly reported
825 in wild cheetah populations so far (see Appendix 1). Of note, in other species, ‘meows’ are
826 rarely heard either during felids’ intraspecific interactions among adults (Bradshaw, 2016).

827
828 Other sounds are associated with aggressive interactions, which can be both intra- or inter-
829 specific. *Growls* and *Hisses*, which are produced more by early-reared females than any other
830 categories of cheetahs are considered to be agonistic signals (Eklund et al., 2012b; Volodina,
831 2000). Deprivation of adult influence at an early stage has been found to be associated with

832 higher frequencies of aggressive behaviours in most species studied (e.g. cats: Ahola et al.,
833 2017; chimpanzees: van Leeuwen et al., 2014; macaques: Mason, 1960; Suomi, 1997;
834 elephants: Slotow et al., 2000; horses: Bourjade et al., 2009; rats: Tóth et al., 2008; cichlids:
835 Arnold & Taborsky, 2010; Hesse & Thünken, 2014). It is probable that, like in other species,
836 the cheetah mother plays a major role in regulating aggressive interactions within the litter
837 once the youngsters have left the den. In cheetahs, females are the “asocial” sex, which means
838 that they are more likely to develop aggressive behaviours towards conspecifics
839 (Wielebnowski et al., 2002), as a result of their “social dispositions” (Mason, 1978). The
840 absence of the canalizing influence of the mother when these behaviours develop may explain
841 the higher frequency of these agonistic signals in the acoustic repertoire of the early-reared
842 females.

843
844 *Growls* and *Howls* (or ‘moans’), which are produced in higher proportion by late-reared
845 males than by their early-reared counterparts, have previously been reported to be produced
846 in agonistic contexts by cheetahs, towards either conspecifics, predators or humans (Eklund
847 et al., 2012b; Smirnova et al., 2016; Sunkuist & Sunkuist, 2002; Volodina, 2000). Males living
848 within a coalition, which is the case for all of our male subjects housed with same-sex peers,
849 are more likely to become territorial (Caro, 1990; Caro & Collins, 1987). The more extensive
850 experience gained alongside their mother by late-reared individuals, and possibly also along
851 adult males encountered while away from the den (Hunter & Skinner, 2003), may have helped
852 them acquire more advanced “typically male” social skills in terms of dominance and
853 territoriality (Caro, 1993; Caro & Collins, 1987).

854
855 The functional value of the non-vocal sound *Sneeze* remains to be explored, as it is the case
856 for *Snuff* (but see ‘snort/snuffle’ mentioned in Wachter et al., 2018). Further studies are
857 therefore needed to elucidate the reason for an increased production of *Sneezes* in females
858 relative to males, irrespective of their early-life experience.

859
860 ***Limitations, conclusion and future directions***

861
862 This description of cheetah acoustic repertoire provides a thorough view of the different
863 sounds produced by adult hand-reared cheetahs, based on a large sample of recordings. This
864 is, to our knowledge, the first study to provide a quantitative representation of the relative
865 use of the different sound types at the individual level in cheetahs. Unfortunately, this
866 precludes any direct comparison with previously published studies. Therefore, reporting
867 quantitative data from other captive and wild cheetah populations, with various living
868 conditions and developmental histories, should be the aim of future studies. The further
869 finding that both early experience and sex strongly influence repertoire use opens important
870 new lines of thought and raises methodological questions, notably regarding the lack of
871 consideration for developmental history in studies using data from captive animals. However,
872 we must acknowledge that the four classes of individuals (early/late reared females vs

873 early/late reared males) were represented by a low sample of subjects (N = 2–5) within our
874 population, which is however rather usual for captive cheetah studies and other
875 developmental studies in primates (e.g. Gultekin & Hage, 2017, 2018). In fact, one of the
876 limitations in conducting such an investigation is that information about early-life experience
877 of captive individuals is generally sparse and lacking details about when exactly they were
878 separated from their mother and how they were subsequently taken care of by surrogates
879 (e.g. hand-reared by wildlife professionals or any person, bottle-fed or directly meat-fed, kept
880 in a social group with age-peers or with adult conspecifics, isolated and raised by humans in
881 the absence of conspecifics...). The results obtained here emphasizes how important it would
882 be for future studies to access and report this information, and to consider all these individual
883 factors of variations when investigating vocal behaviour even in a so-called limited-vocal
884 learner. This is especially critical in the context of captivity, in zoological parks and
885 conservation centres, where animals are likely to have experienced early maternal/adult
886 deprivation, or other disrupted social conditions of life that may have a long-lasting influence
887 on not only their social but also their communicative skills.

888

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1265 **TABLES**

1266

1267 *Table 1. Characteristics of the study subjects.*

Group [†]	Individual	NAAJU identifier	Sex	Rearing condition [‡]	Estimated age (yrs) [§]	Relatedness (siblings)	Observation time (N sessions)
G1	Harry	1474	F	Early	14.4	a	52h32 (N=19)
G1	Hermione	1475	F	Early	14.4	a	52h32 (N=19)
G1	Aurora	1641	F	Late	7.1	—	52h32 (N=19)
G1	Rainbow	1640	F	Late	7.1	—	52h32 (N=19)
G2	Shunga	1549	M	Early	11.8	b	55h58 (N=18)
G2	N'Dunge	1548	M	Early	11.8	b	55h58 (N=18)
G2	LittleC	1532	M	Early	12.5	—	55h58 (N=18)
G2	Ron	1473	M	Early	14.4	a	55h58 (N=18)
G3	Phoenix	1565	M	Early	11.3	—	56h36 (N=17)
G3	B2	1646	M	Late	5.8	—	56h36 (N=17)
G4	Mischief	1581	M	Late	10.7	c	53h38 (N=16)
G4	Phil	1583	M	Late	10.7	c	53h38 (N=16)

1268 [†] Physical contacts between subjects were limited to individuals belonging to the same group (either G1, G2,
 1269 G3 or G4), but visual and auditory contacts were possible across groups (both study groups and unobserved
 1270 ones within the CCF centre).

1271 [‡] Rescued before ('Early-reared') or after ('Late-reared') 2 months old.

1272 [§] Age at the end of the study (December 2019), based on first estimation at the time of rescue.

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1275 *Table 2. Proportion of sounds (percentage of total production) within each category (single,
 1276 repeated, combined, transitional) for the 12 study subjects.*

Sex [†]	Rearing [‡]	Subject (NAAJU)	Single-type		Multi-type			N Total
			Single (%)	Repeated (%)	Combination (%)	Transition (%)	Mixed [§] (%)	
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

1277 [†] Sex: 'F' = female, 'M' = male.

1278 [‡] Rearing: 'Early' = rescued before 2 months old, 'Late' = rescued between 2 and 6 months old.

1279 [§] 'Mixed' are multi-type sounds of three units or more, some being produced juxtaposed (alike combinations)
 1280 and other joined (alike transitions).

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Table 3. Factors influencing individual use of the acoustic repertoire (GLMM_{binomial-logit}: Analysis of deviance table, Type III Wald Chi-square tests)

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’ vs ‘male’. **EarlyLife:** ‘early’ vs ‘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))

	Chi ²	df	p-value
<i>(Intercept)</i>	0.0000	1	0.9954
SoundType	33.1925	15	0.0044
Sex	0.0000	1	0.9968
EarlyLife	0.0000	1	0.9967
SoundType × Sex	58.4729	15	< 0.0001
SoundType × EarlyLife	42.0043	15	0.0002
Sex × EarlyLife	0.0001	1	0.9939
SoundType × Sex × EarlyLife	83.3293	15	< 0.0001

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Goodness of fit: conditional pseudo-R-squared for GLMM (delta method) = 0.7749.

Pairwise comparisons with null models: Akaike’s information criterion (AIC) and between-models comparisons (Chi² 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))

	Df	AIC	Deviance	Chi ²	Df	p-value
Null model 1	3	11378.0	11372.0			
Model	66	6350.9	6218.9	5153.1	63	< 0.0001

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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))

	Df	AIC	Deviance	Chi ²	Df	p-value
Null model 2	18	7146.9	7110.9			
Model	66	6350.9	6218.9	892	48	< 0.0001

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1303 **FIGURE LEGENDS**

1304

1305 **Figure 1. Classification key established for cheetah acoustic signals.** The letters, from a) to e),
1306 refer to the associated group of spectrograms in Figure 2.

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1308 **Figure 2. Cheetah single-type sounds can be divided into a) vocal tonal unpulsed, b) vocal**
1309 **tonal pulsed, c) vocal atonal, d) purring, and e) non-vocal sounds.** Spectrograms were drawn
1310 using ‘spectro’ function in R seewave package (512-pt FFT Hanning window, sampling rate:
1311 44100Hz, y-axis range: 0–11kHz for vocal sounds, 0–22kHz for non-vocal sounds).

1312

1313 **Figure 3. Examples of single-type cheetah sounds produced in series (‘Repeated’).** Top: 9-
1314 expired units *Purr*, bottom left: 2-units *Hou*, bottom right: 2-units *Mew*. Spectrograms were
1315 drawn using ‘spectro’ function in R seewave package (512-pt FFT Hanning window, sampling
1316 rate: 22050Hz).

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1318 **Figure 4. Examples of multi-type cheetah sounds.** From left to right: *Trill-Meow* (transition),
1319 *Meow-Stutter* (combination), *Bark-Howl-Growl* (transition). Spectrograms were drawn using
1320 ‘spectro’ function in R seewave package (512-pt FFT Hanning window, sampling rate:
1321 22050Hz).

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1323 **Figure 5. Average proportion of each sound type in individual repertoires for single-type**
1324 **sounds only** (for each sound type: mean value across individuals \pm sd, N = total number of
1325 sounds recorded in the population).

1326

1327 **Figure 6. Relative frequency of use (GLMM model estimates, percentage of total acoustic**
1328 **production) of the 16 different single-type sound types according to sex and early-life**
1329 **experience.** a) The central chart represents only the 10 call types for which statistically
1330 significant differences were found across classes (post-hoc pairwise comparisons following
1331 the GLMM). b–e) To illustrate repertoire use within each sex/rearing category, one chart is
1332 drawn per class: F = females, M = males, Early = early-reared, Late = late-reared.

1333

1334 **Figure 7. Comparison of individual relative frequencies of use (percentage of total acoustic**
1335 **production) for the four most frequently produced call types: *Meow* (a), *Mew* (b), *Purr* (c),**
1336 ***Growl* (d).** Individuals are grouped by class: F = females, M = males, Early = early-reared, Late
1337 = late-reared. Significance: * is used when standardized Chi-squared residuals are > 2 (see
1338 Agresti, 2002, p.81).

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FIGURE 1

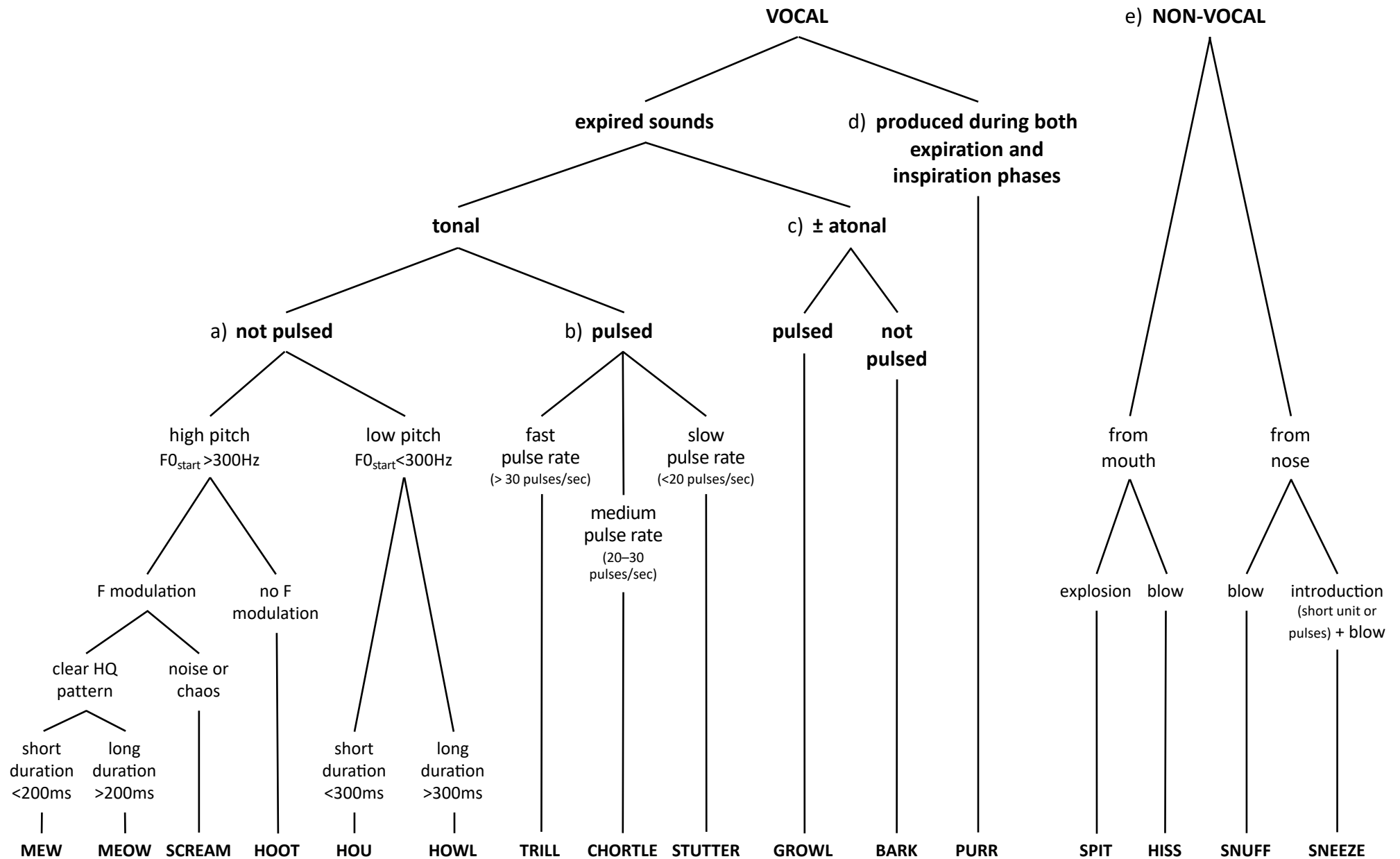


FIGURE 2

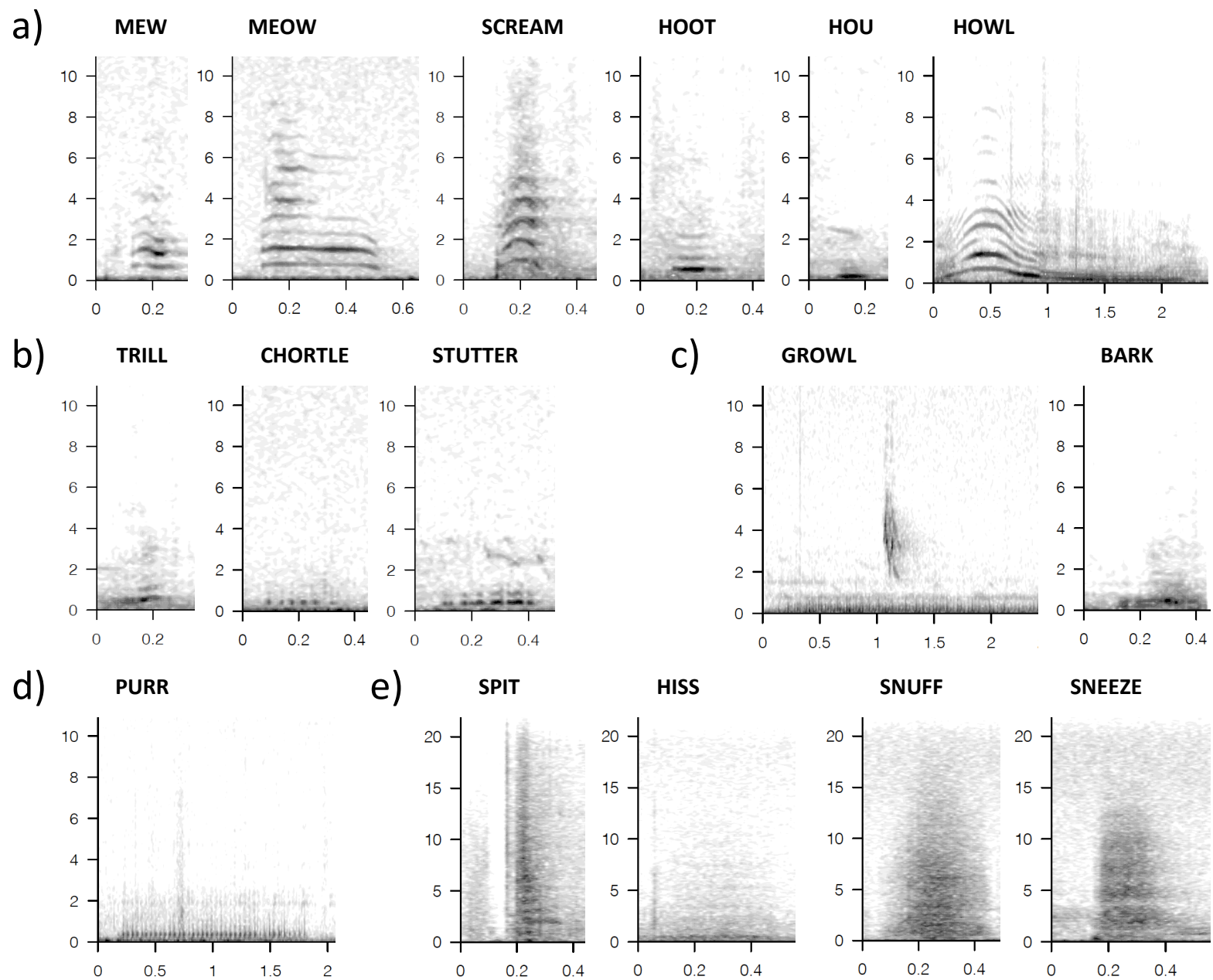


FIGURE 3

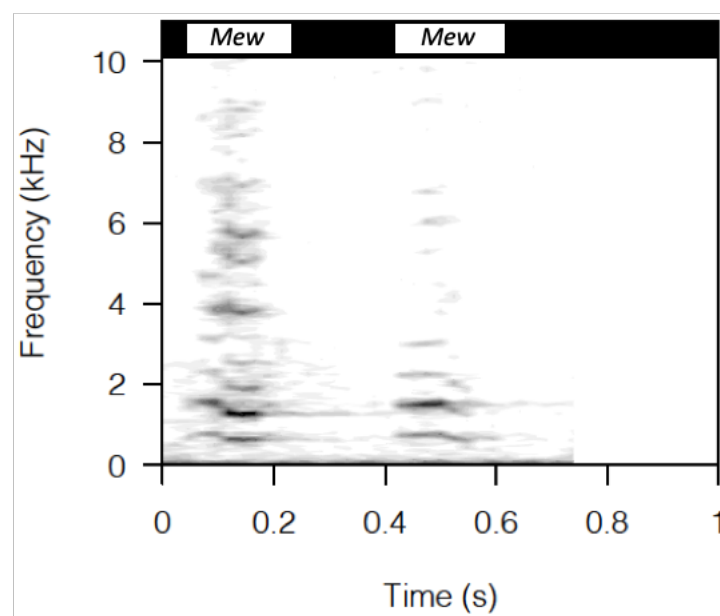
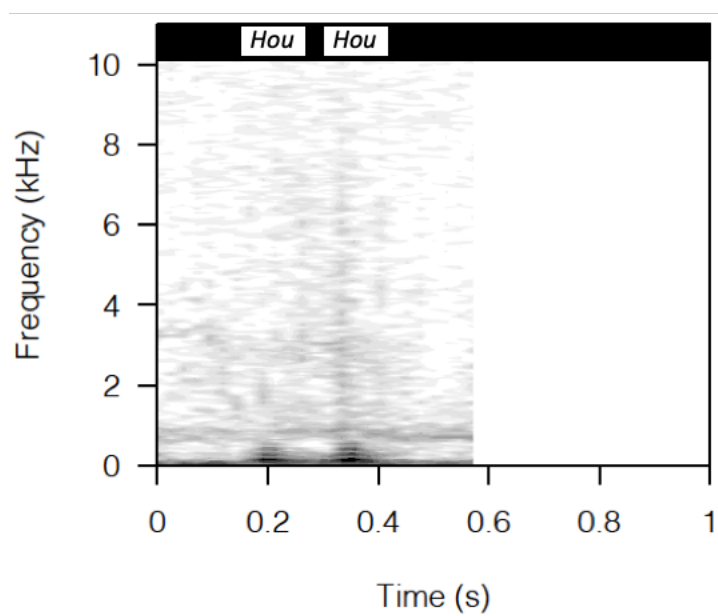
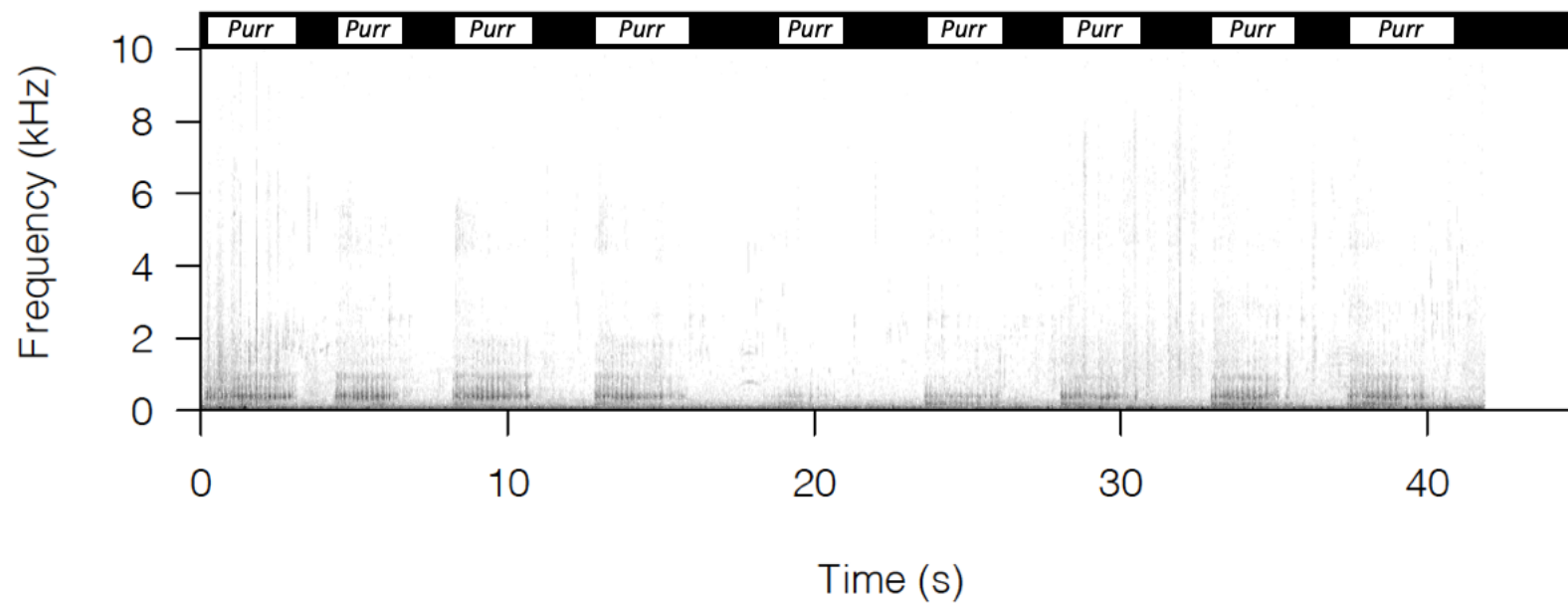


FIGURE 4

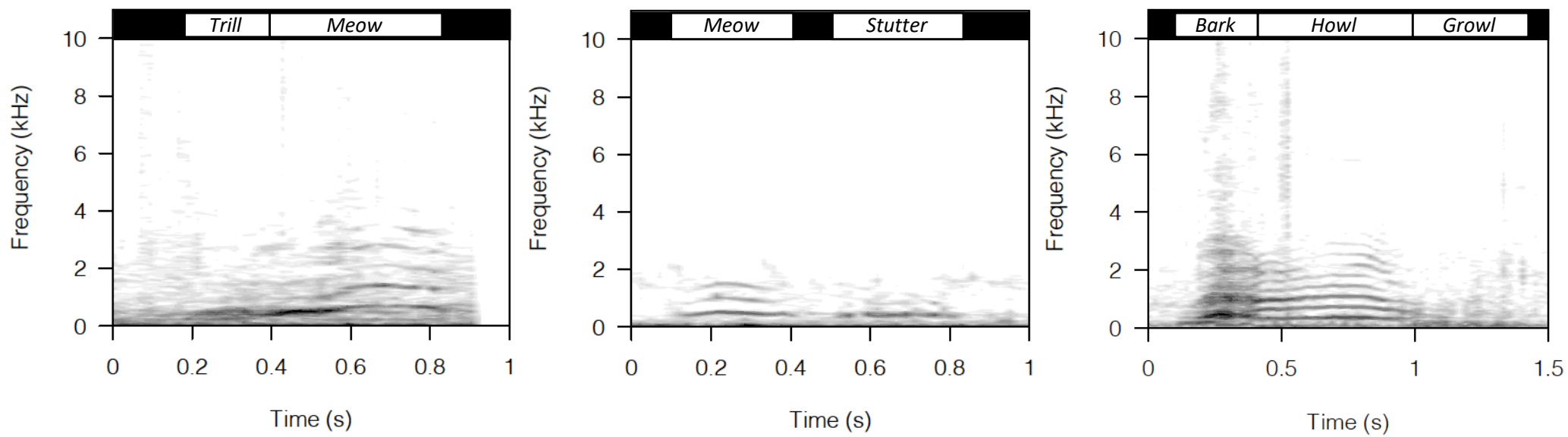


FIGURE 5

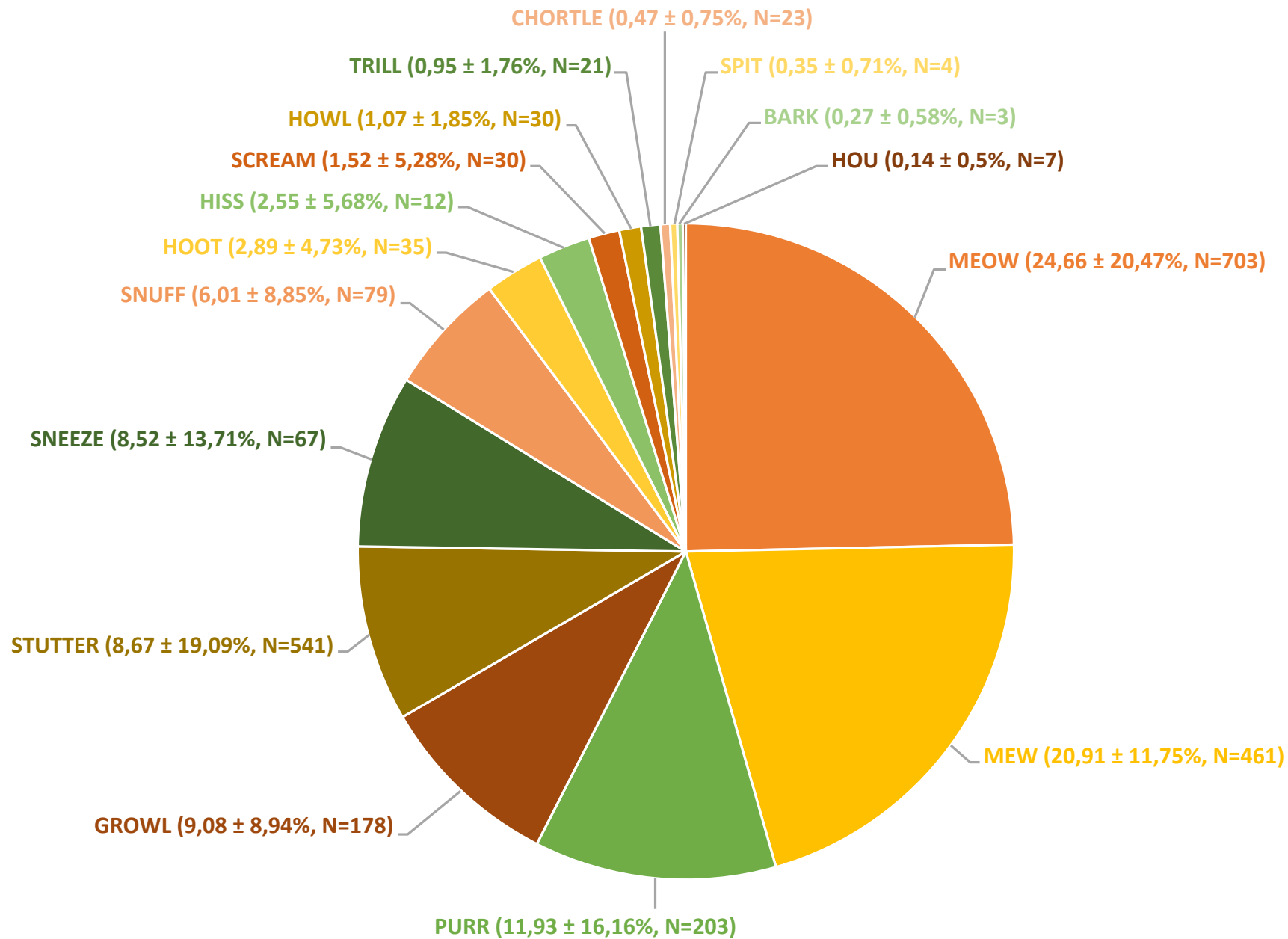


FIGURE 6

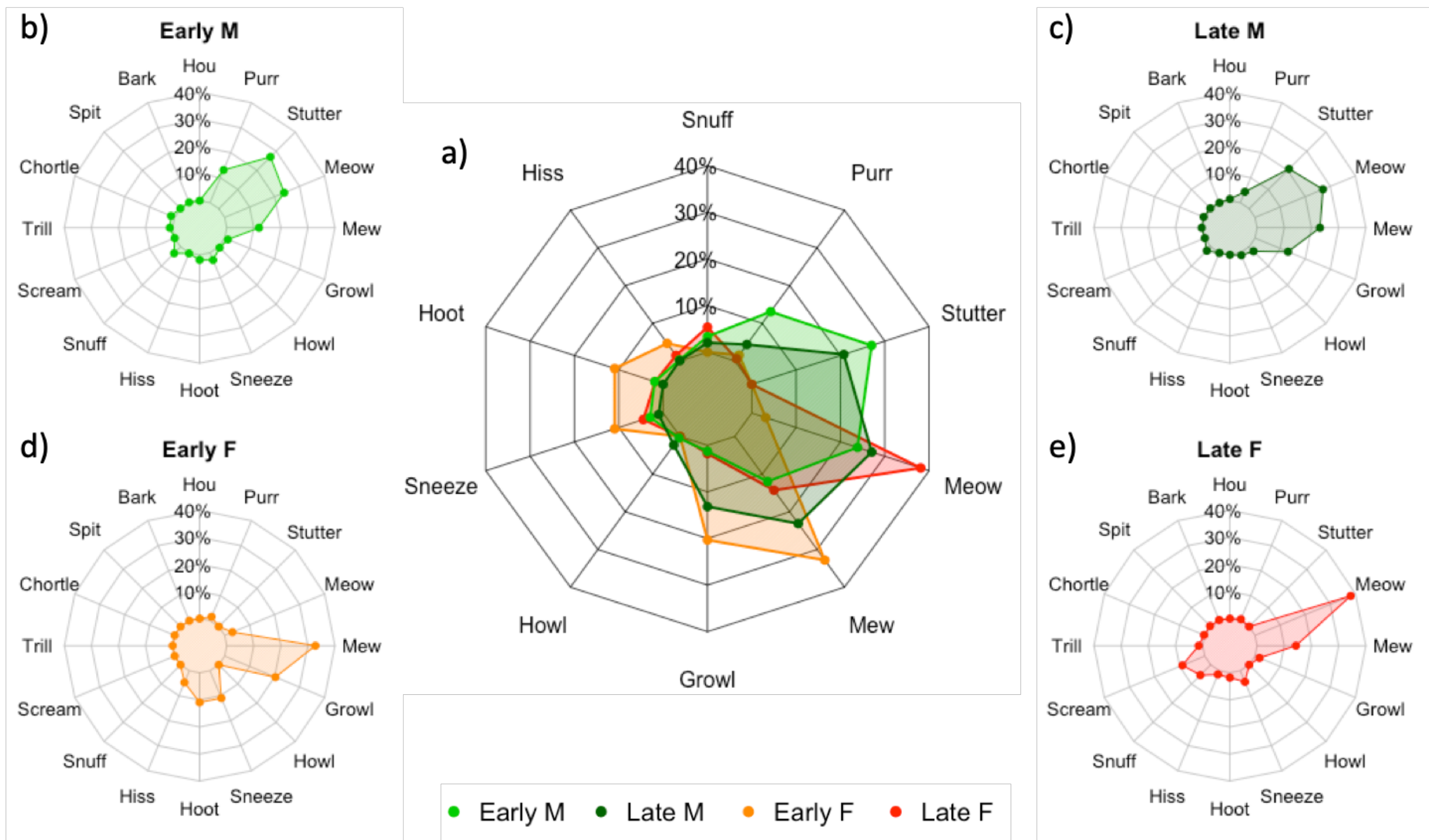
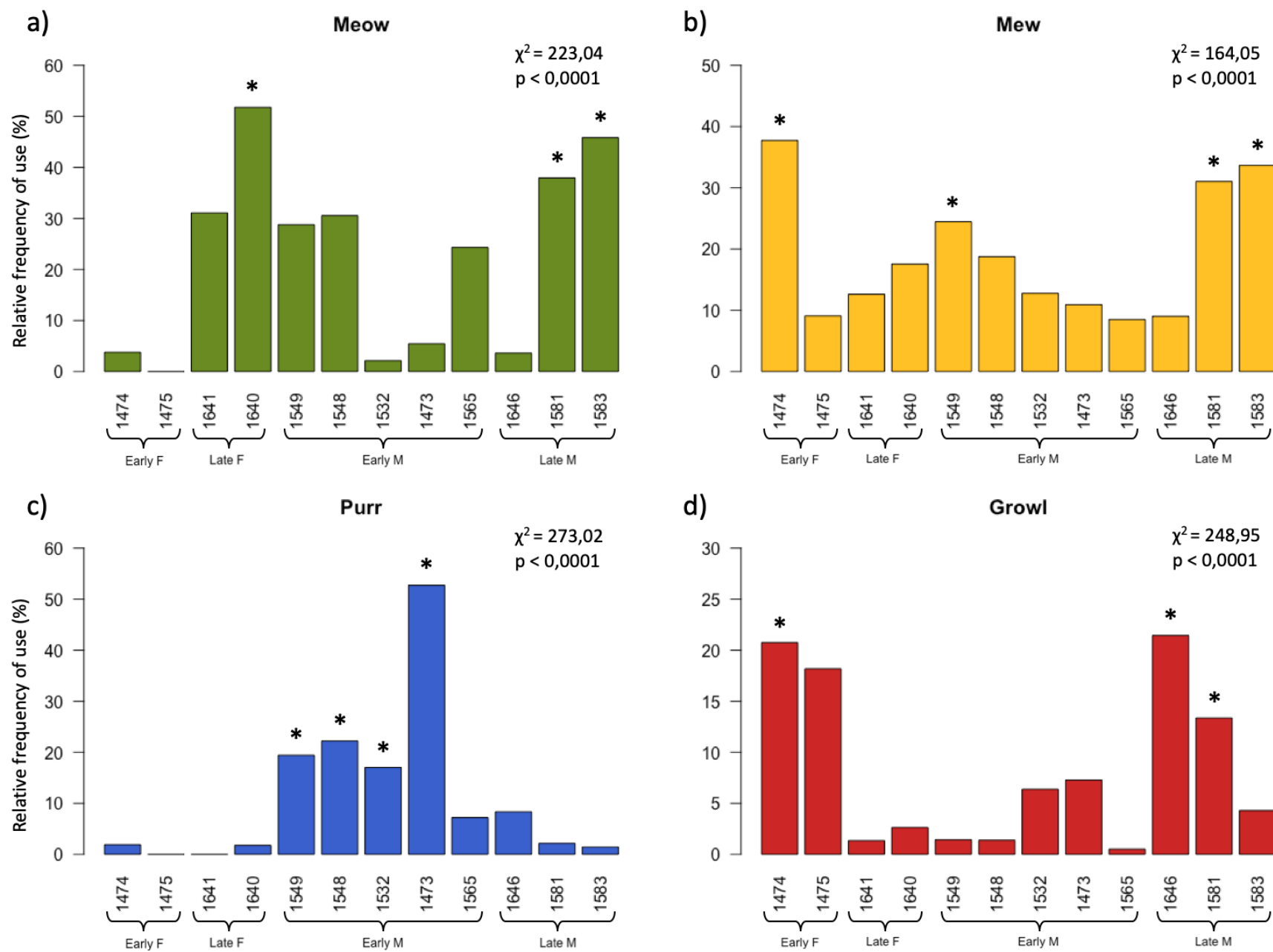


FIGURE 7



APPENDICES

Appendix 1. Synopsis of the cheetah's vocal repertoire established in our study and presumptive equivalences in the pre-existing literature

✓: 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 (yo) or months (mo) when available.

	Studies in captivity								Studies in the wild		
	<i>Our team</i>	<i>Volodina's team</i>		<i>Ruiz-Miranda</i>	<i>Stoeger's team</i>		<i>Peters' team</i>		<i>Sunquist</i>		
	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
Subjects	8M 4F	6M 7F	6M 8F	14M/F + 1M	4M	4 cubs	26M 28F	5M 5F	1M 5F	M/F	M/F
Age	A: 5-15yo	A: >2yo	A: >3yo	J: 1.5-3mo + 1 N	A: 3-6yo	J: 14mo	A/J: 1-16yo	A/J: 0.5-13yo	A: 2-9yo	A/J	A/J
VOCAL	Mew ^{ab}	Meow [S+]	Miaowing [S]	Miaowing [S]	Eeaoow [S]	Yelp [S]	Yelp [S] ^b				Yelp "yow" ? ^b
	Meow ^a										
	Scream ^a										Bleating ?
	Hoot ^a										
	Hou										
	Howl	✓ [S+]	✓ [S]	✓ [S]					Moaning [W]	Moaning	Moan
	Trill ^c										
	Chortle ^d	Gurgle ?	Gurgling [S] ?								Gurgle ?
	Stutter	Chirr [S+]	Churtling [S]	Churtling [S]	✓	Churr [S]				Churring	✓ or Churr
	Growl	✓ [S+]	✓ [S]	✓ [S]					✓ [W]	✓ and Snarling	✓
	Bark ^e										
	- NA - ^f	Chirp [S+]	Chirping [S] (explosive yelp)	Chirping [S]	Chirp [S]	Chirp [S]	Chirp [S]			Chirping or Yelping	Yelp "yow" ? ^b
Purr	✓ [S+]	✓ [S]	✓					✓ [W,S]	✓	✓	
NON-VOCAL	Spit								✓ [W]	✓	
	Hiss	✓ [S+]	✓ [S]	✓ [S]					✓ [S]	✓	
	Snuff										
	Sneeze										

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

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

Appendix 1. Synopsis of the cheetah's vocal repertoire established in our study and presumptive equivalences in the pre-existing literature

Notes:

^a 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'.

^b 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 & Sunquist, 2002 may correspond to *Mew* or *Chirp* types (Nagorzanski, 2018).

^c The acoustic pattern of *Trills*, not reported elsewhere, may have been mistaken for short *Purrs* in previous studies given that whereas 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).

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

^e *Bark* has not been counted as a distinct type so far, although Volodina (2000) reported that *Growl* can occasionally fuse in a noisy vocalisation.

^f We did not identify 'chirp' calls in our dataset. We see two plausible explanations to account for this discrepancy:

- 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 > 2kHz (Stoeger-Horwath & Schwammer, 2003). Now, when comparing the 'chirps' recorded in 3 and 6 years old cheetahs by Ruiz-Miranda et al. (1998), calls of the youngest are high-pitched (F0 > 2kHz), but those of the older individuals seem to match 'meow' ('eeaoow') 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.

- 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...) 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 2. Background information given for the subjects in our study and in previously published studies

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

	Studies in captivity									Studies in the wild	
	This study	Smirnova et al., 2016	Volodina, 2000 ¹	Volodina, 1998	Ruiz-Miranda et al., 1998	Stoeger-Horwath & Schwammer, 2003	Nagorzanski, 2018	Eklund et al., 2010, 2012a; Eklund & Peters, 2013 ²	Eklund et al., 2012b ²	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: 5-15yo	A: >2yo	A: >3yo	J: 1.5-3mo + 1 N	A: 3-6yo	J: 14mo	A/J: 1-16yo	A/J: 0.5-13yo	A: 2-9yo	A/J	A/J
Wild-born ↳ Parent-reared ↳ Hand-reared ↳ Early ↳ Late	✓ (all) ✓ orphaned ✓ (all) ↳ Early ↳ Late ✓ (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- vs hand-reared subjects not detailed	no information for the other 6 subjects (2010 and 2013 studies)	managed under minimum human contact conditions		

Appendix 3. Presence/absence of the 16 types of sounds in the 12 study subjects (grey cell: recorded within single-type sounds, cell crossed out in black: recorded within multi-type sounds, white cell: not recorded in this individual)

† Sex: 'F' = female, 'M' = male.

‡ Rearing: 'Early' = rescued before 2 months old, 'Late' = rescued between 2 and 6 months old.

Sex [†]	Rearing [‡]	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	Grey	Grey	Grey	White	Grey	White	Grey	Grey	White	White	White	White	White	White	White	White	7	6
F	Early	1475	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	White	4	2
F	Late	1641	Grey	Grey	Grey	Grey	White	Grey	Grey	Grey	Grey	White	Grey	White	Grey	White	Grey	Grey	11	7
F	Late	1640	White	Grey	White	Grey	White	White	White	White	White	White	White	White	White	White	White	White	9	6
M	Early	1549	Grey	Grey	White	Grey	White	White	White	White	White	White	White	White	White	White	White	White	9	7
M	Early	1548	Grey	Grey	Grey	Grey	White	White	White	White	White	White	White	White	Grey	Grey	White	White	9	7
M	Early	1532	White	Grey	White	White	White	White	White	White	White	White	White	White	White	White	White	White	9	4
M	Early	1473	Grey	Grey	White	Grey	White	White	White	White	White	White	White	White	Grey	White	White	White	10	4
M	Early	1565	Grey	Grey	Grey	Grey	White	White	White	White	White	White	White	White	White	White	White	White	12	12
M	Late	1646	Grey	Grey	White	White	White	White	White	White	White	White	White	White	White	White	White	White	9	7
M	Late	1581	Grey	Grey	White	White	White	White	White	White	White	White	White	White	White	White	White	White	11	7
M	Late	1583	Grey	Grey	White	Grey	White	White	White	White	White	White	White	White	White	White	White	Grey	11	9
<i>Number of emitting individuals within single-type sounds</i>			12	12	12	11	10	10	7	7	6	6	5	5	3	3	1	1		
<i>Number of emitting individuals within multi-type sounds</i>			9	11	2	10	2	0	0	5	4	11	3	6	11	0	3	1		