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1 **Title: Honest signaling in mouse lemur vocalizations?**

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19 **Abstract**

20 Animal vocalizations may provide information about a sender's condition or motivational
21 state and, hence, mediate social interactions. In this study, we examined whether
22 vocalizations of gray mouse lemurs (*Microcebus murinus*) emitted in aggressive contexts
23 (grunts, tsaks) co-vary with physical condition, which would underly and indicate honest
24 signaling. We recorded calls from captive individuals that were subjected to a caloric restricted
25 (CR) or *ad libitum* (AL) diet, assuming that individuals on an *ad libitum* dietary regime were in
26 better condition. We analyzed 828 grunts produced by 7 CR and 9 AL individuals and 270 tsaks
27 by 8 CR and 5 AL individuals. Grunts consisted of two separate elements, with the 1st element
28 having more energy in higher frequencies than the 2nd element. Body mass correlated
29 negatively with acoustic features of grunts, and heavier individuals produced lower-frequency
30 grunts. Acoustic features of grunts did not differ between sexes. Acoustic features of tsaks
31 were predicted by neither body mass nor sex. However, tsaks produced by AL individuals were
32 noisier than those of CR individuals. Hence, manipulation of body condition via dietary
33 regimes affected acoustic features of calls given during aggression in different ways: acoustic
34 features of grunts varied according to the rule of acoustic allometry, and can be considered as
35 honest signals. Acoustic features of tsaks, however, varied according to motivational
36 structural rules. Longitudinal studies are now indicated to examine whether intra-individual
37 changes in body mass are also reflected in the acoustic structure of calls, allowing callers to
38 signal more flexible variation in condition.

39

40 **Keywords:** communication, honest signaling, acoustic allometry, motivational structural
41 rules, vocalizations, primates, mouse lemurs

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45 **Introduction**

46 A central objective in animal communication research is to understand what information is
47 conveyed in signals, and what function communication may serve during social interactions
48 (Cheney and Seyfarth 2003). Among a wide range of taxa, acoustic cues in vocal signals are
49 associated with rather stable, long-term attributes of callers, such as individual or species
50 identity, sex, age, kin, and body size (Charlton *et al.* 2020; Clarke *et al.* 2006; Ey *et al.* 2007;
51 Fichtel 2014; Masters *et al.* 1995; Rendall *et al.* 1996; Ryan and Brenowitz 1985; Zimmermann
52 *et al.* 2000). In contrast, acoustic cues in vocalizations are also associated with more flexible
53 attributes of the caller, such as their motivational (Fichtel *et al.* 2001; Fichtel and
54 Hammerschmidt 2002; 2003; Scheumann *et al.* 2007) or physiological state (Barelli *et al.* 2013;
55 Buesching *et al.* 1998; Charlton *et al.* 2010a; Semple *et al.* 2002; Zimmermann 1996),
56 dominance status (Kitchen *et al.* 2003; Vannoni and McElligott 2008), or fighting ability
57 (Fischer *et al.* 2004; Reby and McComb 2003; Reby *et al.* 2005).

58 Fighting ability is often operationalized through body size, and it is well established that
59 frequencies in vocalizations co-vary with body size across frogs, birds and mammals (Bowling
60 *et al.* 2017; Charlton and Reby 2016; Fitch and Hauser 1995; Garcia *et al.* 2018; Gingras *et al.*
61 2013; Hauser 1993; Wallschläger 1980). According to this rule of acoustic allometry, larger
62 animals tend to produce lower-frequency calls than smaller animals, because they have longer
63 vocal tracts producing lower resonances and longer vocal folds oscillating at lower frequencies
64 (Fitch 1997; Taylor and Reby 2010). For example, among primates and carnivores, the
65 fundamental frequency and the frequency with the maximum amplitude correlate negatively
66 with body size (Bowling *et al.* 2017). Among primates, the fundamental frequency correlates
67 negatively with body size and vocal fold length, but the latter predicts more precisely the
68 fundamental frequency, indicating a potential for decoupling between larynx and body size
69 (Garcia *et al.* 2018). Such a decoupling of larynx and body size has been documented in several
70 mammalian species (Charlton and Reby 2016). For example, the hypertrophied larynges in
71 howler monkeys (*Alouatta* ssp.) allow them to produce much lower formant frequencies than
72 expected for their body size (Dunn *et al.* 2015).

73 Acoustic cues that provide accurate information about animal attributes, such as body
74 size, may convey honest information because only individuals in better condition are capable
75 to bear any costs associated with signal production (Zahavi 1977). Accordingly, vocal
76 performance has been suggested to reflect individual quality (Bradbury and Vehrencamp

77 Since body mass reflects individual's fighting ability (Arnott and Elwood 2009; Jonart *et*
78 *al.* 2007; Vieira and Peixoto 2013), acoustic correlates of these traits are biologically relevant
79 for senders and receivers. For example, giant pandas (*Ailuropoda melanoleuca*) produce
80 'bleats' when they encounter and compete over estrous females that encode cues about the
81 caller's sex, age and body size (Charlton *et al.* 2009). Playback experiments with bleats showed
82 that males as well as females respond more strongly to calls indicating larger male size
83 (Charlton *et al.* 2010b). Similarly, male red deer (*Cervus elaphus*) respond more strongly to
84 acoustic features of roars that indicate larger size and better fighting ability (Reby *et al.* 2005).
85 Finally, among anthropoid primates, sexual dimorphism in fundamental frequency is
86 associated with variation in the mating system. It increases during evolutionary transitions
87 towards polygyny and decreases with transitions towards monogamy, suggesting that low
88 male fundamental frequencies signal condition and have evolved in response or in parallel to
89 changes in the intensity of mating competition (Puts *et al.* 2016).

90 Many species experience periodic changes in body mass due to variable food availability
91 in the lean versus the rich season, but little is known about how such changes are reflected in
92 the acoustic structure of animal vocalizations and whether these dynamics represent flexible
93 indicators of fighting ability. Mouse lemurs are a suitable study species for this question
94 because they have to cope with low food availability and high climatic unpredictability in their
95 natural environment in Madagascar (Dewar and Richard 2007). During the dry season, the
96 austral winter, mouse lemurs experience shortfalls in food availability and lose body mass
97 accordingly (Dammhahn and Kappeler 2008; Schmid and Kappeler 2008). However, seasonal
98 body and tail fattening in combination with energy saving strategies such as torpor, which is
99 photoperiodically controlled, enables them to face these unfavourable environmental
100 conditions (Aujard *et al.* 1998; Schmid and Kappeler 1998; Vuarin *et al.* 2013). As a
101 consequence, mouse lemurs experience fluctuations of about one third in body mass across
102 winter and summer in both captivity and the wild (Perret and Aujard 2001; Schmid and
103 Kappeler 1998).

104 Moreover, mouse lemurs are sexually monomorphic, nocturnal, solitary foragers
105 exhibiting an unusual mating system; they are polygynandrous and females are sexually
106 receptive for only a few hours once a year (Eberle and Kappeler 2004a; Schmid and Kappeler
107 1998). In the wild, body mass crucially impacts mating strategies of males, with heavier males
108 having higher reproductive success (Eberle and Kappeler 2004b). In captivity, copulation

109 success, however, is not influenced by body mass but by male competitiveness and aggression
110 (Gomez *et al.* 2012). In addition, females in better condition are more polyandrous than
111 females in weaker condition, which might result in elevated genetic diversity or quality of
112 offspring (Huchard *et al.* 2012; Jennions and Petrie 2000). Hence, signalling condition in
113 acoustic displays during competition over and with mates might be beneficial for both sexes.
114 Males may benefit by signalling condition to deter rival males but also to advertise quality to
115 females, which preferentially mate with more competitive and aggressive males (Gomez *et al.*
116 2012). Since up to 14 males can solicit matings with an oestrous female, females may also
117 benefit by signalling condition to deter unwanted mating attempts of males (Eberle and
118 Kappeler 2004 a,b; Huchard *et al.* 2012).

119 During agonistic interactions, mouse lemurs produce grunts and tsaks and sometimes
120 whistles. Grunts are considered as defensive threat calls, given during disturbances at their
121 sleeping sites and during aggressive interactions (Leliveld *et al.* 2011; Zimmermann 2010).
122 Tsaks are given during aggressive interactions with conspecifics but also during encounters
123 with predators (Rahlf and Fichtel 2010; Zimmermann 2010). Whistles are harmonic calls that
124 are given in several contexts and may serve to recruit conspecifics (Radespiel 2000; Rahlf and
125 Fichtel 2010; Zimmermann 1996).

126 During the mating season mouse lemurs produce so-called trills that serve to attract
127 mates. In males, calling rate of trills is associated with rank and may serve to advertise quality
128 (Zimmerman 1996; Buesching *et al.* 1998). Hence, it is likely that also call types given during
129 agonistic interactions may contain cues about the sender's quality. We, therefore,
130 investigated whether caloric reduction influences acoustic features of vocalizations in gray
131 mouse lemurs (*Microcebus murinus*). We recorded vocalizations given during agonistic
132 contexts in captive mouse lemurs that were exposed to different dietary regimes, i.e. an *ad*
133 *libitum* and caloric restricted diet. These dietary restriction experiments were implemented
134 to study the effect of caloric restriction on physiology, cognitive abilities or female mating
135 strategies (Canale *et al.* 2011; Giroud *et al.* 2008; Huchard *et al.* 2012). According to the rule
136 of acoustic allometry, we predicted that mouse lemurs that were exposed to a dietary
137 restriction, and, hence, assumed to be in a weaker condition, should produce higher-
138 frequency calls than those exposed to an *ad libitum* diet. Since mouse lemurs are
139 monomorphic, we did not predict that acoustic features co-vary with sex.

140

141 **Methods**

142 *Subjects*

143 Subjects were housed under standard breeding conditions in the breeding colony at the
144 Muséum National d'Histoire Naturelle in Brunoy, France, IBISA platform, agreement
145 E91.114.1, DDPP Essonne. Animals were kept with 14h of light and 10h of dark during the six
146 month period of long days and 10h of light and 14h of dark during the six month period of
147 short days (Perret and Aujard 2001). Animals were kept under two different feeding regimes:
148 *Ad libitum* (AL), where animals were fed with a homemade standard diet with a caloric value
149 of 4.8 kJg⁻¹, containing 50% carbohydrates, 20% proteins, and 30% lipids. In the caloric
150 restricted (CR) regime, animals were exposed to a 80% caloric restriction with a daily food
151 supply of 20% of the food mass offered to the group under the *ad libitum* regime (Giroud *et*
152 *al.* 2008; Huchard *et al.* 2012). CR individuals were housed individually in cages (50 cm x 50
153 cm x 50 cm) with branches and two nest-boxes to control caloric intake. Studies of the short-
154 and long-term effects of caloric restriction on the endocrine system and energy balance
155 revealed that mouse lemurs have pronounced physiological flexibility, enabling them to adapt
156 to acute food shortage (Giroud *et al.* 2008; Canale *et al.* 2011; Dal-Pan *et al.* 2011). Notably,
157 the food-restricted individuals were not found to experience chronic stress, as urinary cortisol
158 excretion (Canale *et al.* 2011) and plasma testosterone levels (Dal-Pan *et al.* 2011) remained
159 unaffected by dietary treatment.

160 We recorded and analyzed the vocalizations of 25 individuals (13 AL and 12 CR, Table 1)
161 during mild disturbances at the sleeping box, i.e., when animals were taken out of their home
162 cage in their sleeping box to either clean the cage or to inspect their well-being. During this
163 procedure, we opened the door of the sleeping box to about one third of the full opening and
164 positioned the microphone about 30 cm in front of it.

165 Some individuals were related with a maternal relatedness coefficient ranging from
166 0.125-0.5. For grunts, 2 of 36 dyads were related in the AL condition, whereas none of the
167 dyads (N=28) was related in the CR condition. For tsaks, 2 of 10 dyads were related in the AL
168 condition, whereas only 3 of 36 dyads were related in the CR condition. Since only a few dyads
169 were related, we did not control for relatedness in the statistical analyses.

170

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172

173 Table 1: Individual identity, sex, diet and number of calls analyzed in a study of mouse lemur
 174 vocalizations housed at the CNRS, MNHN, Brunoy (2010).

Diet	Sex	ID	N Grunts		N Tsaks
			1 st element	2 nd element	
AL	F	1	27	26	-
AL	F	4	30	30	-
AL	F	5	-	-	6
AL	F	6	-	-	19
AL	F	7	28	18	18
AL	F	8	20	17	-
AL	F	12	20	11	-
AL	F	13	29	16	-
AL	M	16	-	-	30
AL	M	18	-	-	21
AL	M	20	27	22	-
AL	M	21	22	12	-
AL	M	22	27	7	-
CR	F	2	53	51	14
CR	F	3	23	23	-
CR	F	9	41	35	15
CR	F	10	23	21	31
CR	F	11	54	45	-
CR	M	14	-	-	30
CR	M	15	-	-	24
CR	M	17	-	-	24
CR	M	19	-	-	25
CR	M	23	20	15	-
CR	M	24	23	12	-
CR	M	25	-	-	13

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185 **Recordings and acoustic analyses**

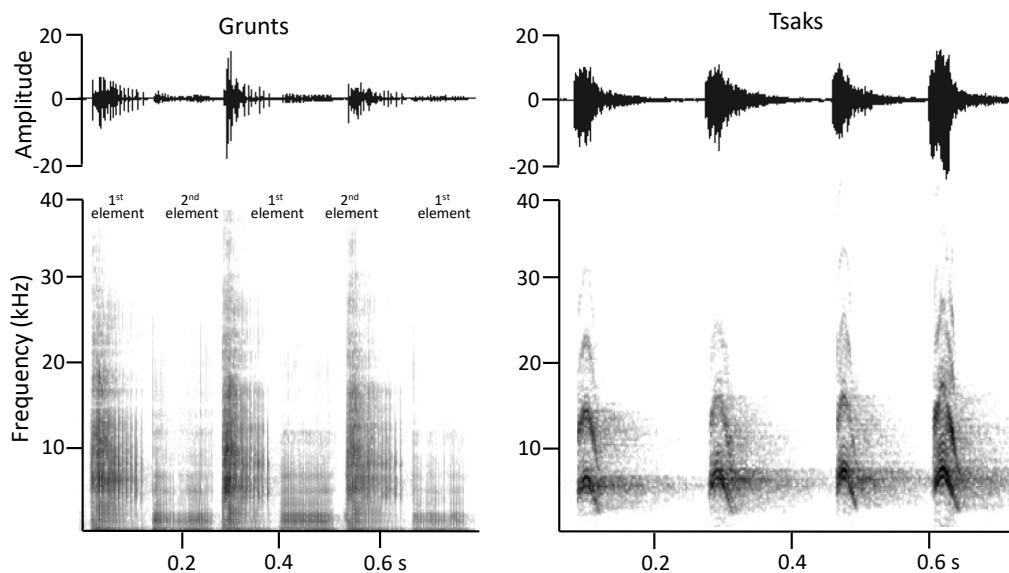
186 We recorded vocalizations with an ultrasound microphone (polarized condenser microphone
187 CMPA, Avisoft, Germany) in combination with an Avisoft-UltraSoundGate 116 (Avisoft,
188 Germany) recording device resulting in a frequency range of 20-200 kHz that was connected
189 to a Toshiba Satellite Pro laptop (Toshiba Europe GmbH, Germany) with 'AVISOFT-RECORDER
190 v.2.96' software (Avisoft, Germany). We digitized call recordings with a sampling rate of 500
191 kHz at 16 bit resolution and converted them into spectrograms with 1024-point fast Fourier
192 transforms (window function: Hanning, 93.75% overlap; time resolution: 0.64 ms; frequency
193 range: 100 kHz) using AVISOFT-SASLab Pro 4.2 (Avisoft, Germany). We visually inspected and
194 sampled only calls of good quality and low background noise for acoustic analysis. We derived
195 acoustic variables from frequency-time spectra with a time resolution of 5 ms for each time
196 window across the call using LMA 9.2, a custom software tool to extract different sets of
197 variables from acoustic signals (Schrader and Hammerschmidt 1997).

198 To avoid potential effects of a group-signature in the acoustic structure of vocalizations,
199 we recorded vocalizations from AL individuals that were housed in different groups and kept
200 CR individuals in individual cages in different rooms. Mouse lemurs produced three different
201 call types during these mild disturbances: grunts, tsaks, and whistles. Grunts are noisy low-
202 frequency calls, that consist of two clearly separated elements which are usually uttered
203 together, but sometimes mouse lemurs produce only the first element (Fig. 1a). Therefore,
204 we digitized and analyzed the two elements separately, referring to them as the 1st and 2nd
205 elements of grunts. Tsaks are harmonic calls which are commonly described as chevron-
206 shaped, because they increase in frequency, up to a local peak, followed by a decrease in
207 frequency (Fig. 1b). Whistles are harmonic calls that are given in several contexts and may
208 serve to recruit conspecifics in the mating season, when meeting members of sleeping
209 associations at the sleeping site (Radespiel 2000), or during an escalating predator encounter
210 to recruit other individuals to mob the predator (Rahlf and Fichtel 2010). Since only a few
211 individuals produced whistles (N=6), we did not include them in the analysis.

212 To characterize the acoustic structure of grunts and tsaks (Fig. 1a, b), we measured
213 acoustic variables that characterize the general call structure and are comparable with
214 acoustic variables measured in other studies characterizing the structure of mammalian
215 vocalizations (Fichtel and Hammerschmidt 2002; Fichtel *et al.* 2005; Manser *et al.* 2001). Since
216 the fundamental frequency can only be measured for vocalizations that are produced by

regular vocal fold vibration, we could not measure it in grunts. Because tsaks are noisy calls that also contain harmonic energy, we could only measure the fundamental frequency reliably in 83 of 270 calls. Instead, we measured the frequency with the maximum amplitude (peak frequency) for both calls, which has been suggested to be associated with body size in several primates and carnivores (Bowling *et al.* 2017).

222
223



224
225 Figure 1: Spectrograms and oscillograms of grunts and tsaks of mouse lemurs housed at the
226 CNRS, MNHN, Brunoy (2010). For grunts, two examples of calls with the 1st and 2nd element
227 and one example with only the 1st element are shown.

228
229 For each element of grunts, we measured the duration, the mean frequency range, the mean
230 peak frequency, the mean lower, central, and upper frequency distribution, as well as the 2nd
231 dominant frequency band (Table 2). To characterize the acoustic structure of tsaks, we also
232 measured the duration, the mean frequency range and the mean peak frequency. Because
233 tsaks have a narrow frequency bandwidth, we measured only the central frequency but
234 included measurements of the start, end and maximum of the central frequency to
235 characterize the chevron-shaped acoustic structure of these calls. Because tsaks are noisy calls
236 containing harmonic elements, we also measured the percentage of noisy parts in the call
237 (Table 2).

238

239

240 Table 2: Definitions of acoustic variables measured for grunts and/or tsaks produced by mouse
 241 lemurs housed at the CNRS, MNHN, Brunoy (2010).

Acoustic variable	Definition	Call type
Duration (ms)	Time between the onset and end of call	Grunts, tsaks
Mean frequency range (kHz)	Difference between the maximum and minimum frequency	Grunts, tsaks
Mean lower frequency (kHz)	Distribution of frequency amplitudes across the spectrum obtained by calculating the cumulative sum of the frequency amplitudes per time segments. Frequency at which the distribution reached the 1. quartile (25%), averaged across time segments.	Grunts
Mean central frequency (kHz)	Frequency at which the distribution of frequency amplitudes across the spectrum reached the 2. quartile (50%), mean value over all time segments	Grunts, tsaks
Start, end, maximum central frequency (kHz)	Frequency of the central frequency at the beginning and the end of the call as well as the maximum, the highest frequency of central frequency	Tsaks
Mean upper frequency (kHz)	Frequency at which the distribution reached frequency amplitudes across the spectrum reached the 3. quartile (75%), mean value over all time segments	Grunts
2 nd dominant frequency band (kHz)	The dominant frequency bands are characterized by amplitudes that exceed a given threshold in a consecutive number of frequency bins.	Grunts
Mean peak frequency (kHz)	Mean frequency with the highest amplitude across time segments	Grunts, tsaks
% noise	Percentage of time segments in which no harmonic structure could be detected	Tsaks
Mean fundamental frequency (kHz)	Mean lowest frequency across tonal time segments	Tsaks

242

243 Statistical analyses

244 Because some individuals produced only grunts or tsaks and some produced both call types,
 245 we used a Fisher exact test to investigate whether the number of individuals producing either
 246 only one call type or both varies as a function of the dietary regime. We tested for differences

247 in body mass of individuals exposed to the two dietary regimes with an exact Mann Whitney
248 U test.

249 To summarize multiple acoustic variables of a call into a single composite index, we first
250 ran a Principal Component Analysis (PCA) using the package “rela” (Chajewski 2009). We
251 included only acoustic variables that describe the distribution of frequencies and not the
252 duration of calls and log-transformed values of the acoustic variables. The PCAs were justified
253 as shown by the Kaiser-Meyer-Olkin measure of sampling adequacy (grunts: KMO=0.82; tsaks:
254 KMO=0.80) and Bartlett's test of sphericity (grunts: p<0.01; tsaks: p<0.001).

255 To estimate the influence of body mass, sex and call element (1st and 2nd element) on
256 variation in the acoustic structure of grunts, we fitted two linear mixed models (LMMs) with
257 either the first (PC1) or second (PC2) extracted principal component as the response variable
258 using the packages “lme4” and “lmerTest” (Bates *et al.* 2015; Kuznetsova *et al.* 2017). We
259 fitted body mass, sex, and call element as fixed factors, individual identity as a random
260 intercept effect, and a random slope of call element (Schielzeth and Forstmeier 2009; Barr *et*
261 *al.* 2013).

262 To estimate the influence of body mass and sex on variation in the acoustic structure of
263 tsaks, we fitted another two LMMs with PC1 or PC2 as the response variable, body mass and
264 sex as fixed factors and individual identity as random factor. For calls in which we could
265 measure the fundamental frequency, we calculated the mean and correlated it with body
266 mass using a Spearman rank correlation. Since we could not include body mass and diet in the
267 models because they were collinear, we fitted four additional models for grunts and tsaks
268 including diet instead of body mass. We estimated the effect of diet *per se* because in another
269 study, caloric restricted females mated only with one male, whereas *ad libitum* fed females
270 mated with several males (Huchard *et al.* 2012). Since mating is costly and body mass loss
271 during mating correlated with the number of mating partners (Huchard *et al.* 2012), caloric
272 restricted females might be less likely to engage in energetic costly behavior, such as
273 displaying aggression during disturbances. In these models we set either PC1 or PC2 as
274 response variable, diet and sex as fixed factors, individual identity as random factor, and call
275 element as random slope for models on acoustic variation of grunts. Following Perneger
276 (1998), we did not apply corrections for multiple testing.

277 We conducted all statistical tests in R (version 4.0.3; R Core Team 2020). For all models
278 (LMM), we checked the assumptions of normality distributions and homogeneity by visual

279 inspection of a QQ-plot of residuals and residuals plotted against fitted values (Queen *et al.*
280 2002). We assessed model stability through the level of estimated coefficients and standard
281 deviations (Nieuwenhuis *et al.* 2012). Furthermore, we checked collinearity issues by deriving
282 Variance Inflation Factors (VIF) (Fox and Weisberg 2019) of the standard linear model lacking
283 the random effects. To test the significance of the predictors as a whole, we compared the fit
284 of the full model with that of the null model comprising only the random factor and the
285 intercept (Forstmeier and Schielzeth 2011).

286

287 Ethical note

288 This study adhered to the Guidelines for the Treatment of Animals in Behavioral Research and
289 Teaching (Animal Behaviour 2020) and the legal requirements of the country (France) in which
290 the work was carried out. All the procedures were carried out in accordance with the
291 European Communities Council Directive (86/609/EEC) and were done by authorized
292 experimenters (license numbers 91-439 and 91-455 delivered by the departmental veterinary
293 service). Animal housings were equipped with foliage, branches and several nest-boxes.
294 Caloric restriction over a short period is physiologically sustainable for mouse lemurs and does
295 not induce chronic stress (cortisol release), because mouse lemurs are adapted to drastic
296 temporal changes in energy availability (Canale *et al.* 2011).

297

298 Data availability statement

299 The datasets generated and analysed during the current study are not publicly available due
300 to further analyses but are available from the corresponding author on reasonable request.

301

302 Results

303 In the AL condition, 8 individuals produced only grunts, 4 only tsaks and 1 both call types,
304 whereas in the CR condition 4 individuals produced only grunts, 5 only tsaks and 3 both call
305 types. The number of individuals giving either only one call type, tsaks or grunts, or both did
306 not differ between the dietary regimes (Fisher exact test: p=0.32). Individuals exposed to the
307 CR diet had a lower body mass than those exposed to the AL diet (exact Mann Whitney U-test:
308 Z=1.32, p<0.001, mean body mass ± SD: CR= 76.2 ± 17.5 g, AL=99.6 ± 10.4 g).

309

310

311 *Grunts*

312 We analyzed 828 calls (1st element=467, 2nd element=361) produced by 9 AL and 7 CR
313 individuals. Measurements of acoustic variables are presented in (Table 3).

314

315 Table 3: Acoustic variables measured in grunts and tsaks in a study of mouse lemur
316 vocalizations housed at the CNRS, MNHN, Brunoy (2010).

Acoustic variables Mean ± SD	Grunts		Tsaks
	1 st element	2 nd element	
Duration (ms)	75.01 ± 24.23	106.13 ± 52.6	54.11 ± 19.44
Frequency range (kHz)	35.50 ± 11.07	14.69 ± 6.11	-
Mean peak frequency (kHz)	2.76 ± 3.82	0.74 ± 0.2	1.88 ± 2.84
2 nd dominant frequency band (kHz)	14.89 ± 2.27	13.66 ± 3.51	-
Mean lower frequency (kHz)	5.94 ± 4.41	1.04 ± 0.53	-
Mean central frequency (kHz)	13.68 ± 5.17	2.94 ± 1.92	-
Mean upper frequency (kHz)	22.16 ± 5.03	8.54 ± 4.02	-
Start lower frequency (kHz)	-	-	19.41 ± 2.79
End lower frequency (kHz)	-	-	18.67 ± 2.57
Mean lower frequency (kHz)	-	-	20.54 ± 2.66
Maximum lower frequency (kHz)	-	-	23.31 ± 3.28
Noise %	-	-	91.27 ± 11.61

317

318 The PCA extracted two principal components with Eigenvalues higher than 1, which
319 explained in total 85% of the variance (PC1=68%, PC2=17%). PC1 correlated most strongly with
320 variables characterizing the general energy distribution of the calls (Table 4), with higher
321 values of the PC1 characterizing calls that had a higher peak, lower, central, and upper
322 frequency and a broader frequency range. The 2nd dominant frequency band loaded most
323 strongly on PC2, with higher values characterizing higher pitched calls (Table 4).

324

325

326 Table 4: Loadings of each variable on the first (PC1) and second (PC2) principal component for
 327 each acoustic variable measured in grunts and tsaks in a study of mouse lemur vocalizations
 328 housed at the CNRS, MNHN, Brunoy (2010).

Acoustic variables	Grunts		Tsaks	
	PC1	PC2	PC1	PC2
Frequency range	0.48	-0.01	0.36	0.28
Peak frequency	0.36	-0.10	0.43	-0.19
2 nd dominant frequency band	0.03	0.99	-	-
	0.47	-0.08	-	-
	0.48	0.01	0.48	0.06
	0.44	0.10		
	-	-	0.35	0.23
	-	-	0.39	-0.27
	-	-	0.41	0.21
	-	-	0.13	-0.84
% of variance explained	68	17	59	16

329

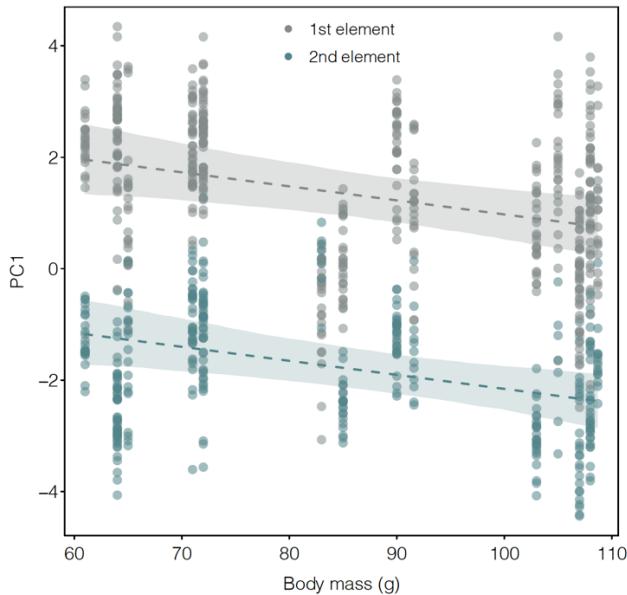
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331 Overall, the model investigating variation in the PC1 of grunts with regard to body mass,
 332 sex, and call element was significant (likelihood ratio test comparing full-null model
 333 comparison: $\chi^2=39.1$, df=3 p<0.001). PC1 correlated negatively with body mass, with grunts
 334 produced by heavier individuals having more energy in lower frequencies than calls produced
 335 by lighter individuals (Table 4a, Fig 2). PC1 co-varied significantly with call element. The 1st
 336 element of grunts had more energy in higher frequencies than the 2nd element.

337

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339



340

341 Figure 2: Values of the PC1 (1st Principal Component) plotted against body mass for both call
 342 elements of grunts recorded in a study of mouse lemur vocalizations housed at the CNRS,
 343 MNHN, Brunoy (2010). Dashed lines indicate the regression lines and confidence intervals for
 344 the 1st element in grey and the 2nd element in turquoise.

345

346 The model investigating the influence of body mass, sex and call element on variation of
 347 the PC2 of grunts was also significant (likelihood ratio test comparing full-null model
 348 comparison: $\chi^2=10.8$, df=3, p=0.013). PC2 differed significantly between call elements, with
 349 the 1st element containing more energy in higher frequencies than the 2nd element (Table 5b).
 350 Variation in PC2 co-varied only by trend (p=0.07) with body mass, and did not co-vary with sex
 351 (Table 5b).

352 The model estimating the influence of diet, sex and call element on variation in PC1 was
 353 significant (likelihood ratio test comparing full-null model comparison: $\chi^2=37.7$, df=3 p<0.001;
 354 Table 5c). Diet and call element significantly influenced variation in PC1. AL individuals that
 355 were heavier produced grunts that had lower PC1 values, and the 1st element had more energy
 356 in higher frequencies than the 2nd element. The model estimating the influence of diet, sex
 357 and call element on variation in PC2 was also significant (likelihood ratio test comparing full-
 358 null model comparison: $\chi^2=8.52$, df=3 p=0.037; Table 5d). Call element but not diet or sex
 359 influenced variation in PC2.

360

361

362 Table 5: Results of LMMs testing the influence of body mass, diet, call element and sex on
 363 variation in PC1 and PC2 (1st and 2nd Principal Component; N=836; N_{ID} = 16) of grunts in a study
 364 of mouse lemur vocalizations housed at the CNRS, MNHN, Brunoy (2010). We tested body
 365 mass and diet in separate models due to collinearity. Bold indicates p < 0.05.

366

Response variable	Term	Est	SE	P
a) PC1	Intercept	3.37	0.88	^b
	Body mass	-0.03	0.01	0.021
	Call element (2nd) ^a	-3.02	0.31	<0.001
	Sex (male) ^a	-0.26	0.36	0.488
b) PC2	Intercept	-1.01	0.65	^b
	Body mass	0.02	0.01	0.063
	Call element (2nd) ^a	-0.50	0.16	0.007
	Sex (male) ^a	-0.27	0.28	0.347
c) PC1	Intercept	0.85	0.30	^b
	Diet	0.81	0.34	0.035
	Call element (2nd) ^a	-3.02	0.31	<0.001
	Sex (male) ^a	-0.03	0.37	0.943
d) PC1	Intercept	0.25	0.22	^b
	Diet	0.08	0.27	0.768
	Call element (2nd) ^a	-0.51	0.16	0.007
	Sex (male) ^a	-0.16	0.29	0.598

367 ^a 1st element and females as reference categories

368 ^b Not shown as has no meaningful interpretation

369

370 *Tsaks*

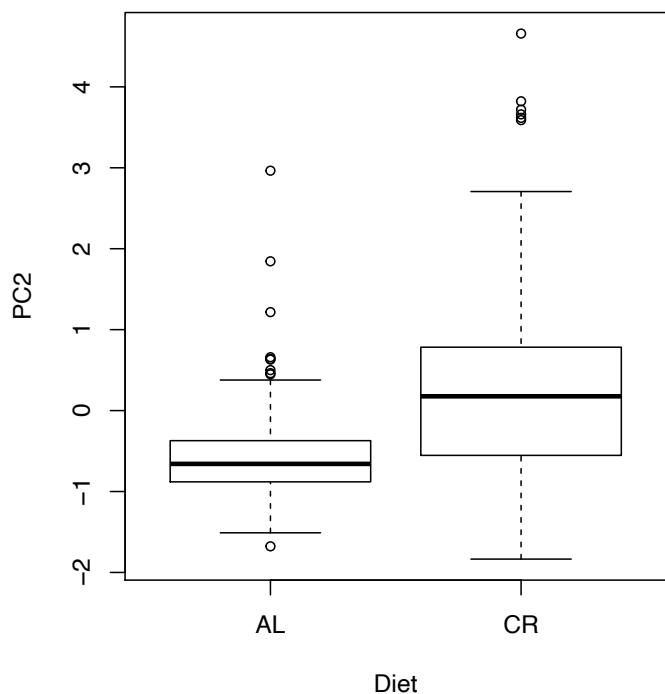
371 We analyzed 270 calls given by 5 AL and 8 CR individuals. Measurements of acoustic variables
 372 are presented in (Table 3). The first two principal components of the PCA had Eigenvalues
 373 higher than 1, which explained 75% of the variance in total (PC1=59%, PC2=16%). Similar to
 374 grunts, the PC1 of tsaks correlated most strongly with variables characterizing the general
 375 energy distribution within calls (Table 4), with higher values of the PC1 characterizing calls that
 376 had a higher start, end, maximum, and mean lower frequency, a higher mean central and peak
 377 frequency. PC2 loaded most strongly with noise, with higher values characterizing calls that
 378 were less noisy (Table 4).

379 The models investigating the influence of body mass and sex on variation of the PC1 and
 380 PC2 of tsaks were not significant (likelihood ratio test comparing full-null model comparison:
 381 PC1: $\chi^2=1.25$, df=2 p=0.530, PC2: $\chi^2=3.43$, df=2, p=0.180; Table 6a, b). In the subset of calls
 382 (N=83), for which we could measure the fundamental frequency, body mass did not correlate
 383 with the mean fundamental frequency (Spearman rank, N=11, R=-0.24, p=0.484). This result

384 should be considered carefully, however, because we could only measure the fundamental
385 frequency in one call in 3 of 11 individuals.

386 PC1 co-varied neither with diet or sex (likelihood ratio test comparing full-null model
387 comparison: $\chi^2=0.42$, df=2 p=0.810; Table 6c). PC2, however, had lower values in tsaks given
388 by AL individuals than by CR individuals (likelihood ratio test comparing full-null model
389 comparison: $\chi^2=10.70$, df=2 p=0.005; Table 6d), suggesting that tsaks given by AL individuals
390 were noisier than those given by CR individuals (Fig. 3).

391



392

393 Figure 3: PC2 (2nd Principal Component) of tsaks recorded in a study of mouse lemur
394 vocalizations housed at the CNRS, MNHN, Brunoy (2010) as a function of dietary regimes
395 (AL=ad libitum, CR= caloric restriction). Depicted are boxplots showing medians (solid lines),
396 inter-quartile ranges (boxes), ranges (whiskers) and outliers (open circles) of PC2.

397

398

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400

401

402 Table 6: Results of LMMs testing the influence of body mass, diet, call element and sex on
 403 variation in PC1 and PC2 (1st and 2nd Principal Component; N=272; N_{ID} = 15) of tsaks in a study
 404 of mouse lemur vocalizations housed at the CNRS, MNHN, Brunoy (2010). We tested body
 405 mass and diet in separate models due to collinearity. Bold indicates p < 0.05.

406

Response variable	Term	Est	SE	P
a) PC1	Intercept	-1.45	2.95	^b
	Body mass	0.02	0.02	
	Sex (male) ^a	-0.85	0.91	
b) PC2	Intercept	0.04	0.68	^b
	Body mass	-0.01	0.01	
	Sex (male) ^a	0.58	0.34	
c) PC1	Intercept	0.12	0.81	^b
	Diet (CR) ^a	-0.11	0.93	
	Sex (male) ^a	-0.46	0.91	
d) PC2	Intercept	-0.67	0.21	^b
	Diet (CR) ^a	0.68	0.24	
	Sex (male) ^a	0.38	0.23	

407 ^asex and dietary regime: males and *ad libitum* (AL) as reference categories

408 ^b Not shown as has no meaningful interpretation

409

410

411 Discussion

412 We showed in this study, that mouse lemurs under caloric restriction had a lower body mass
 413 than individuals under the *ad libitum* diet, suggesting that they were in poorer body condition
 414 than individuals under the *ad libitum* diet. In grunts, the 1st element was characterized by
 415 more energy in higher frequencies than the 2nd element. Body mass correlated negatively with
 416 both principal components, with heavier individuals producing lower-frequency grunts.
 417 Accordingly, AL individuals produced lower-frequency grunts than CR individuals. Acoustic
 418 features of tsaks were predicted by neither body mass nor sex. However, tsaks produced by
 419 AL individuals were noisier than those produced by CR individuals. Noisiness in vocalizations
 420 has been suggested to be associated with aggressiveness, suggesting that mouse lemurs in
 421 comparatively better condition might have been able to afford to be more aggressive. Hence,
 422 manipulation of body condition via dietary regimes affected acoustic features of calls given
 423 during aggression in different ways: acoustic features of grunts varied according to the rule of
 424 acoustic allometry similar to what has been proposed for many other species. Acoustic
 425 features of tsaks, however, varied according to motivational structural rules.

426

427 *Grunts*

428 Grunts consist of two elements that differ in distribution of energy, with the 1st element having
429 more energy in higher frequencies than the 2nd element. Body mass correlated negatively with
430 the distribution of energy in both elements, with heavier individuals producing lower-
431 frequency grunts. These results are in line with the rule for acoustic allometry, supporting
432 earlier studies in many other species (Bowling *et al.* 2017; Charlton and Reby 2016; Fitch and
433 Hauser 1995; Garcia *et al.* 2018; Gingras *et al.* 2013; Hauser 1993; Wallschläger 1980).
434 Although many studies have focused on fundamental frequency or formant dispersion to
435 assess acoustic allometry (Fitch 1997; Fitch and Hauser 1995; Fitch and Reby 2001), a more
436 recent comparative study revealed that the frequency with the highest amplitude also co-
437 varies with body mass in carnivores and primates (Bowling *et al.* 2017). Here, we show that a
438 general shift in frequencies, summarized as principal components, also co-varies with body
439 mass in mouse lemur grunts.

440 In grey mouse lemurs in the wild, body mass predicts several fitness proxies such as
441 survival (Hämäläinen *et al.* 2014; Rakotonaina *et al.* 2017), the ability to cope better with
442 environmental constraints through physiological mechanisms, such as torpor (Vuarin *et al.*
443 2013) or allostatic load in males (Hämäläinen *et al.* 2015), reproductive success in males
444 (Eberle and Kappeler 2004b) and the relative proportion of polyandrous mating in females in
445 captivity (Huchard *et al.* 2012). Hence, acoustic features that convey information about body
446 mass might serve as honest signals (Zahavi 1977). Similarly, call rates of mouse lemur trills that
447 are produced in the mating season to attract mates have been suggested to be associated
448 with rank and to advertise quality (Zimmerman 1996). Hence, calling rates of advertisement
449 calls and acoustic features of aggressive grunts may serve to advertise quality in mouse
450 lemurs.

451 Mouse lemurs may benefit from signaling their current body condition during agonistic
452 interactions, in particular. During the mating season, males roam widely in search of receptive
453 females by enlarging their home ranges to cover the center of activity of up to 21 females
454 (Eberle and Kappeler, 2004a). Once they encounter an estrous female, they attempt to mate
455 guard her by staying close to her and trying to fend off rivals. An estrous female is usually
456 guarded by several males, and the longer a male can guard a female, the fewer mating
457 partners she has. During mate guarding, males fight with several other males and male

458 mortality increases during the brief mating season because of this risky mating strategy (Kraus
459 et al. 2008). In addition, in captivity females preferentially accepted copulations from more
460 competitive, aggressive males (Gomez et al. 2012). Hence, males clearly benefit from signaling
461 condition and fighting ability in vocalizations both during agonistic interactions with rivals and
462 to obtain access to matings.

463 In contrast, females may face male harassment during the mating season. They are
464 receptive for only one night, but males harass and inspect female's reproductive state over
465 the whole mating season (Eberle and Kappeler 2004a). In addition, estrous females are
466 guarded by several males but may try to escape guarding males (Eberle and Kappeler 2004a)
467 to mate with other males (Huchard et al. 2012). Hence, signaling their condition during such
468 conflicts might also be beneficial for females. Outside the mating season, both males and
469 females produce grunts during aggressive interactions and during disturbances at the sleeping
470 site (Radespiel and Zimmermann 2001, Zimmermann 2010). In both contexts individuals might
471 benefit from signaling condition and fighting ability. Playback experiments are now required
472 to determine whether mouse lemurs also respond to acoustic cues indicating differently sized
473 callers, as in other species (Reby et al. 2005; Charlton et al. 2010b).

474

475 *Tsaks*

476 In contrast to grunts, acoustic features of tsaks did not correlate with body mass. Neither shifts
477 in the general energy distribution nor the mean fundamental frequency co-varied with body
478 mass. Tsaks have a relatively narrow frequency bandwidth with little variation across calls.
479 Their mean central frequency, for example, varied on average only by about 2 kHz, whereas
480 the mean central frequency in grunts varied by about 5 kHz. Hence, the production of tsaks
481 may be too constrained to co-vary with changes in body mass. Unfortunately, we could only
482 measure the fundamental frequency in a subset of calls, and the lack of a significant
483 correlation between fundamental frequency and body mass might be due to the small sample
484 size. Additional recordings are required to understand whether acoustic features of tsaks co-
485 vary principally with body mass, for example during the development from infancy to
486 adulthood.

487 Dietary treatment predicted the amount of noisy energy in tsaks. Individuals on the *ad*
488 *libitum* diet produced noisier calls than caloric restricted individuals. According to the
489 motivational-structural rules (Morton 1977), noisiness is associated with aggression. More

490 aggressive calls are characterized by noisier acoustic structure in squirrel monkeys (*Saimiri*
491 *sciureus*) and Geoffroy's spider monkeys (*Ateles geoffroyi*) (Fichtel *et al.* 2001; Ordóñez-Gómez
492 *et al.* 2015). Since mouse lemurs on the *ad libitum* dietary regime were in better condition,
493 they might have been able to afford to be more aggressive and hence produced more noisy
494 calls. Moreover, in another study including some females that also participated in this study,
495 caloric restricted females mated only with one male, whereas females on the *ad libitum*
496 dietary regime mated with several males (Huchard *et al.* 2012). Since mating is costly and body
497 mass loss during mating correlated with the number of mating partners (Huchard *et al.* 2012),
498 caloric restricted females might be less likely to engage in energetic costly aggressive behavior
499 during disturbances.

500 Vocalizations that contain more nonlinear dynamics, such as noise, have been suggested
501 to be more unpredictable, and this unpredictability may function to prevent receivers from
502 ignoring such calls (Fitch and Hauser 1995; Fitch *et al.* 2002). Playback experiments revealed
503 that yellow-bellied marmots (*Marmota flaviventris*) responded more strongly to alarm calls
504 including noise than to control calls, supporting the notion that the adaptive value of non-
505 linearities might be to prevent habituation (Blumstein and Récapet 2008). Again, playback
506 experiments are required to examine whether mouse lemurs also respond more strongly to
507 noisier tsaks. In principle, signaling condition or the motivational state is beneficial both during
508 competition over mates and to defend resources such as feeding or sleeping sites or to deter
509 predators, contexts in which both call types are produced (Eberle and Kappeler 2008; Rahlfs
510 and Fichtel 2010; Zimmermann 2010).

511 Finally, variation in acoustic features can also be due to group membership or relatedness
512 (Mitani *et al.* 1992; Levréro *et al.* 2015). However, we think it is unlikely that group
513 membership or relatedness explains variation in acoustic features across dietary regimes
514 because only a few dyads of mouse lemurs were closely related in our study, and individuals
515 were either housed individually or we recorded only individuals from different groups if they
516 were housed in groups.

517 In conclusion, manipulation of body condition via dietary regimes affected acoustic
518 features of calls given during aggression in different ways: mouse lemurs in better condition
519 produced lower pitched grunts than those in weaker condition, supporting the rule of acoustic
520 allometry. In contrast, the acoustic features of tsaks did not support the rule of acoustic
521 allometry but did follow motivational structural rules. Mouse lemurs in better condition might

522 have been able to show more aggression and produced more noisy calls. However, we only
523 compared vocalizations of different individuals in which body mass was manipulated via
524 caloric restriction. Since mouse lemurs undergo seasonal changes of up one third of their body
525 mass in their natural habitat (Hämäläinen *et al.* 2014), a longitudinal study is needed to
526 examine how much changes in body mass within individuals are also reflected in the acoustic
527 structure of aggressive vocalizations. This would also allow us to investigate whether acoustic
528 cues indicate stable, long-term attributes of callers as well as more flexible variation in
529 condition and, hence, fighting ability.

530

531

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539

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542 wrote the manuscript; other authors provided editorial advice.

543

544 **Conflict of Interest**

545 The authors declare that they have no conflict of interest.

546

547

548 **References**

- 549 Animal Behaviour (2020). Guidelines for the treatment of animals in behavioural research
550 and teaching. *Animal Behaviour*, 159, I-XI. <https://doi.org/10.1006/anbe.1996.0293>
- 551 Arnott, G., Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal*
552 *Behaviour*, 77, 991-1004. <https://doi.org/10.1016/j.anbehav.2009.02.010>
- 553 Aujard, F., Perret, M. & Vanier, G. (1998). Thermoregulatory responses to variations of
554 photoperiod and ambient temperature in the lesser mouse lemur: a primitive or an
555 advanced adaptive character? *Journal of Comparative Physiology B*, 168, 540–548.
556 <https://link.springer.com/article/10.1007/s003600050175>

- 557 Barelli, C., Mundry, R., Heistermann, M., & Hammerschmidt, K. (2013). Cues to androgens
558 and quality in male gibbon songs. *PLoS ONE*, 8, e82748–9.
559 <https://doi.org/10.1371/journal.pone.0082748>
- 560 Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for
561 confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68,
562 255–278. <https://doi.org/10.1016/j.jml.2012.11.001>
- 563 Bates D, Mächler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models using
564 lme4. *Journal of Statistical Software*, 67, 1–48.
565 <https://www.jstatsoft.org/article/view/v067i01>
- 566 Blumstein, D. T., & Récapet, C. (2009). The sound of arousal: the addition of novel non-
567 linearities increases responsiveness in marmot alarm calls. *Ethology*, 115, 1074–1081.
568 <https://doi.org/10.1111/j.1439-0310.2009.01691.x>
- 569 Bowling, D. L., Garcia, M., Dunn, J. C., Ruprecht, R., Stewart, A., Frommolt, K. H., & Fitch, W.
570 T. (2017). Body size and vocalization in primates and carnivores. *Scientific Reports*, 7,
571 41070. <https://www.nature.com/articles/srep41070>
- 572 Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication*.
573 2nd. Sunderland, Massachusetts: Sinauer.
- 574 Buesching, C. D., Heistermann, M., Hodges, J.K. & Zimmermann E. (1998). Multimodal
575 oestrus advertisement in a small nocturnal prosimian, *Microcebus murinus*. *Folia
576 Primatologica*, 69, 295–308. <https://doi.org/10.1159/000052718>
- 577 Canale, C. I., Perret, M., Thiéry, M. & Henry, P.-Y. (2011). Physiological flexibility and
578 acclimation to food shortage in a heterothermic primate. *Journal of Experimental Biology*,
579 214, 551–560. <https://jeb.biologists.org/content/214/4/551>
- 580 Chajewski, M. (2009). rela: Scale item analysis. R package version 4.1.
- 581 Charlton, B. D., Zhihe, Z. & Snyder, R. J. (2009). The information content of giant panda,
582 *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. *Animal Behaviour*, 78,
583 893–898. <https://doi.org/10.1016/j.anbehav.2009.06.029>
- 584 Charlton, B. D., Keating, J. L., Rengui, L., Huang, Y., & Swaisgood, R. R. (2010a). Female giant
585 panda (*Ailuropoda melanoleuca*) chirps advertise the caller's fertile phase. *Proceedings of
586 the Royal Society B: Biological Sciences*, 277, 1101–1106.
587 <https://doi.org/10.1098/rspb.2009.1431>
- 588 Charlton, B. D., Zhihe, Z., & Snyder, R. J. (2010b). Giant pandas perceive and attend to
589 formant frequency variation in male bleats. *Animal Behaviour*, 79, 1221–1227.
590 <https://doi.org/10.1016/j.anbehav.2010.02.018>
- 591 Charlton, B. D. & Reby, D. (2016). The evolution of acoustic size exaggeration in terrestrial
592 mammals. *Nature Communication*, 7, 12739, <https://doi.org/10.1038/ncomms12739>
- 593 Charlton, B. D., Pisanski, K., Raine, J., & Reby, D. (2020). Coding of static information in
594 terrestrial mammal vocal signals. In *Coding Strategies in Vertebrate Acoustic
595 Communication* (Vol. 7, pp. 115–136). Cham: Springer International Publishing.
- 596 Seyfarth, R. M., & Cheney, D. L. (2003). Signalers and receivers in animal
597 communication. *Annual Review of Psychology*, 54, 145–173.
- 598 Clarke, E., Reichard, U. H., Zuberbühler, K., & Emery, N. (2006). The syntax and meaning of
599 wild gibbon songs. *PLoS ONE*, 1, e73. <https://doi.org/10.1371/journal.pone.0000073>
- 600 Dal-Pan, A., Terrien, J., Pifferi, F., Botalla, R., Hardy, I., Marchal, J., Zahariev, A., Chery, I.,
601 Zizzari, P., Perret, M., Picq, J. L., Epelbaum, J., Blanc, S. & Aujard, F. (2011). Caloric
602 restriction or resveratrol supplementation and ageing in a non-human primate: first-year
603 outcome of the RESTRIKAL study in *Microcebus murinus*. *Age (Dordrecht, Netherlands)*,
604 33, 15–31. DOI: [10.1007/s11357-010-9156-6](https://doi.org/10.1007/s11357-010-9156-6)

- 605 Dammhahn, M., & Kappeler, P. M. (2008). Small-scale coexistence of two mouse lemur
606 species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive
607 environment. *Oecologia*, 157, 473–483. <https://dx.doi.org/10.1007%2Fs00442-008-1079-x>
- 609 Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of
610 Madagascar. *Proceedings of the National Academy of Sciences of the United States of
611 America*, 104, 13723–13727. <https://doi.org/10.1073/pnas.0704346104>
- 612 Dunn, J. C., Halenar, L. B., Davies, T. G., Cristobal-Azkarate, J., Reby, D., Sykes, D., Dengg, S.,
613 Fitch, W.T., Knapp, L. A. (2015). Evolutionary trade-off between vocal tract and testes
614 dimensions in howler monkeys. *Current Biology*, 25, 2839-2844.
<https://www.sciencedirect.com/science/article/pii/S0960982215011094>
- 616 Gomez, D., Huchard, E., Henry, P.-Y., & Perret, M. (2012). Mutual mate choice in a female-
617 dominant and sexually monomorphic primate. *American Journal of Physical
618 Anthropology*, (147), 370–379. <https://doi.org/10.1002/ajpa.21653>
- 619 Eberle, M., & Kappeler, P. M. (2004a). Selected polyandry: female choice and inter-sexual
620 conflict in a small nocturnal solitary primate (*Microcebus murinus*). *Behavioral Ecology
621 and Sociobiology*, 57, 91–100. <https://link.springer.com/article/10.1007/s00265-004-0823-4>
- 623 Eberle, M., & Kappeler, P. M. (2004b). Sex in the dark: determinants and consequences of
624 mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate.
625 *Behavioral Ecology and Sociobiology*, 57, 77–90.
<https://link.springer.com/article/10.1007/s00265-004-0826-1>
- 627 Eberle, M., & Kappeler, P. M. (2008). Mutualism, reciprocity, or kin selection? Cooperative
628 rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur.
629 *American Journal of Primatology*, 70, 410–414. <https://doi.org/10.1002/ajp.20496>
- 630 Ey, E., Hammerschmidt, K., Seyfarth, R. M., & Fischer, J. (2007). Age- and sex-related
631 variations in clear calls of *Papio ursinus*. *International Journal of Primatology*, 28(4), 947–
632 960. <https://link.springer.com/article/10.1007/s10764-007-9139-3>
- 633 Fichtel, C. (2014). Acoustic differences in loud calls of Decken's and Crowned sifakas
634 (*Propithecus deckenii* and *P. coronatus*) at two sites in Madagascar, 1–7.
<https://doi.org/10.1896/052.028.0105>
- 636 Fichtel, C., Hammerschmidt, K., & Jürgens, U. (2001). On the expression of emotion. A multi-
637 parametric analysis of different states of aversion in the squirrel monkey. *Behaviour*, 138,
638 97–116. <https://doi.org/10.1163/15685390151067094>
- 639 Fichtel, C., & Hammerschmidt, K. (2002). Responses of redfronted lemurs to experimentally
640 modified alarm calls: evidence for urgency-based changes in call structure. *Ethology*, 108,
641 763–777. <https://doi.org/10.1046/j.1439-0310.2002.00816.x>
- 642 Fichtel, C., & Hammerschmidt, K. (2003). Responses of squirrel monkeys to their
643 experimentally modified mobbing calls. *The Journal of the Acoustical Society of America*,
644 113(5), 2927–2932. <https://doi.org/10.1121/1.1548158>
- 645 Fichtel, C., Perry, S., & Gros Louis, J. (2005). Alarm calls of white-faced capuchin monkeys: an
646 acoustic analysis. *Animal Behaviour*, 70, 165–176.
<https://doi.org/10.1016/j.anbehav.2004.09.020>
- 648 Fischer, J., Kitchen, D. M., Seyfarth, R. M. & Cheney, D. L. (2004). Baboon loud calls advertise
649 male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral
650 Ecology and Sociobiology*, 56, 140–148. <https://link.springer.com/article/10.1007/s00265-003-0739-4>

- 652 Fitch, W. (1997). Vocal tract length and formant frequency dispersion correlate with body
653 size in rhesus macaques. *The Journal of the Acoustical Society of America*. 102, 1213.
654 <https://doi.org/10.1121/1.421048>
- 655 Fitch, W. T. & Hauser, M. D (1995) Vocal production in nonhuman primates: acoustics,
656 physiology, and functional constraints on “honest” advertisement. *American Journal of*
657 *Primateology*, 37, <https://doi.org/10.1002/ajp.1350370303>
- 658 Fitch, T. W., & Reby, D. (2001). The descended larynx is not uniquely human. *Proceedings of*
659 *the Royal Society of London. Series B: Biological Sciences*, 268, 1669-1675.
660 <https://doi.org/10.1098/rspb.2001.1704>
- 661 Fitch, W. T., Neubauer, J. & Herzel, H. (2002). Calls out of chaos: the adaptive significance of
662 nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, 63, 407—418.
663 <https://doi.org/10.1006/anbe.2001.1912>
- 664 Forstmeier, W. Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models:
665 overestimated effect sizes and the winner’s curse. *Behavioral Ecology & Sociobiology*, 65,
666 47–55. <https://doi.org/10.1007/s00265-010-1038-5>
- 667 Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage,
668 Thousand Oaks CA <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- 669 Garcia, M., Herbst, C. T., Bowling, D. L., Dunn, J. C., & Fitch, W. T. (2018). Acoustic allometry
670 revisited: morphological determinants of fundamental frequency in primate vocal
671 production, *Scientific Reports*, 7, 10450. <https://www.nature.com/articles/s41598-017-11000-x>
- 672 Gingras, B., Boeckle, M., Herbst, C. T., & Fitch, W. T. (2013). Call acoustics reflect body size
673 across four clades of anurans. *Journal of Zoology*, 289, 143-
674 150. <https://doi.org/10.1111/j.1469-7998.2012.00973.x>
- 675 Giroud, S., Blanc, S., Aujard, F., Bertrand, F., Gilbert, C. & Perret, M. (2008). Chronic food
676 shortage and seasonal modulations of daily torpor and locomotor activity in the grey
677 mouse lemur (*Microcebus murinus*). *American Journal of Physiology Regulatory*
678 *Integrative and Comparative Physiology*, 294, R1958–R1967.
679 <https://doi.org/10.1152/ajpregu.00794.2007>
- 680 Gomez, D., Huchard, E., Henry, P.-Y., & Perret, M. (2012) Mutual mate choice in a female-
681 dominant and sexually monomorphic primate. *American Journal of Physical*
682 *Anthropology*, 147, 370–379. <https://doi.org/10.1002/ajpa.21653>
- 683 Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: effects of
684 phylogeny, body weight, and social context. *The American Naturalist*, 142, 528–542.
685 <https://doi.org/10.1086/285553>
- 686 Hämäläinen, A., Dammhahn, M., Aujard, F., Eberle, M., Hardy, I., Kappeler, P. M., Perret, M.,
687 Schliehe-Diecks, S. & Kraus, C. (2014). Senescence or selective disappearance? Age
688 trajectories of body mass in wild and captive populations of a small-bodied
689 primate. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140830.
690 <https://doi.org/10.1098/rspb.2014.0830>
- 691 Hämäläinen, A., Heistermann, M., & Kraus, C. (2015). The stress of growing old: sex-and
692 season-specific effects of age on allostatic load in wild grey mouse
693 lemurs. *Oecologia*, 178, 1063-1075. DOI: [10.1007/s00442-015-3297-3](https://doi.org/10.1007/s00442-015-3297-3)
- 694 Huchard, E., Canale, C. I., Le Gros, C., Perret, M., Henry, P.-Y. & Kappeler, P. M. (2012).
695 Convenience polyandry or convenience polygyny? Costly sex under female control in a
696 promiscuous primate. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1371–
697 1379. <https://doi.org/10.1098/rspb.2011.1326>

- 699 Jennions, M. D. & Petrie, M. (2000). Why do females mate multiply? A review of the genetic
700 benefits. *Biological Reviews*, 75, 21–64. [https://doi.org/10.1111/j.1469-
701 185X.1999.tb00040.x](https://doi.org/10.1111/j.1469-185X.1999.tb00040.x)
- 702 Jonart, L. M., Hill, G. E., & Badyaev, A. V. (2007). Fighting ability and motivation:
703 determinants of dominance and contest strategies in females of a passerine bird. *Animal
704 Behaviour*, 74(6), 1675–1681
<https://www.sciencedirect.com/science/article/abs/pii/S0003347207003144>
- 705 Kitchen, D., Seyfarth, R., Fischer, J., & Cheney, D. (2003). Loud calls as indicators of
706 dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and
707 Sociobiology*, 53, 374–385. <https://doi.org/10.1007/s00265-003-0588-1>
- 708 Kraus, C., Eberle, M., & Kappeler, P. M. (2008). The costs of risky male behaviour: sex
709 differences in seasonal survival in a small sexually monomorphic primate. *Proceedings of
710 the Royal Society London B*, 275, 1635–1644. <https://doi.org/10.1098/rspb.2008.0200>
- 711 Kuznetsova A., Brockhoff P.B., & Christensen, R.H.B. (2017). “lmerTest Package: Tests in
712 Linear Mixed Effects Models.” *Journal of Statistical Software*, 82, 1–26.
<https://doi.org/10.18637/jss.v082.i13>.
- 713 Leliveld, L M., Scheumann, M., & Zimmermann, E. (2011). Acoustic correlates of individuality
714 in the vocal repertoire of a nocturnal primate (*Microcebus murinus*). *The Journal of the
715 Acoustical Society of America*, 129, 2278–2288. <https://doi.org/10.1121/1.3559680>
- 716 Levréro, F., Carrete-Vega, G., Herbert, A., Lawabi, I., Courtiol, A., Willaume, E., Kappeler,
717 P.M., Charpentier, M. J. E. (2015). Social shaping of voices does not impair phenotype
718 matching of kinship in mandrills. *Nature Communications*, 6, 1–7.
<https://www.nature.com/articles/ncomms8609?origin=ppub>
- 719 Malalaharivony HS, Fichtel C, Heistermann M, Kappeler PM (2021) Maternal stress effects on
720 infant development in wild Verreaux's sifaka (*Propithecus verreauxi*). *Behavioral Ecology
721 & Sociobiology* 75: 143
- 722 Manser, M. (2001). The acoustic structure of suricates' alarm calls varies with predator type
723 and the level of response urgency. *Proceedings of the Royal Society London B*: 268: 2315–
724 2324. <https://doi.org/10.1098/rspb.2001.1773>
- 725 Masters, W. M., Raver, K. A. S. & Kazial, K. A. (1995). Sonar signals of big brown bats,
726 *Eptesicus fuscus*, contain information about individual identity, age and family affiliation.
727 *Animal Behaviour*, 50, 1243–1260. [https://doi.org/10.1016/0003-3472\(95\)80041-7](https://doi.org/10.1016/0003-3472(95)80041-7)
- 728 Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P., Byrne, R. (1992). Dialects in wild
729 chimpanzees? *American Journal of Primatology*, 27, 233–
730 243. <https://doi.org/10.1002/ajp.1350270402>
- 731 Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in
732 some bird and mammal sounds. *American Naturalist*, 111, 855–869.
<https://www.jstor.org/stable/2460385>
- 733 Nieuwenhuis, R., te Grotenhuis, M., and Pelzer, B. (2012). Influence.me: Tools for detecting
734 influential data in mixed effects models. *The R Journal*, 4:38–47. <https://journal.r-project.org/archive/2012/RJ-2012-011/index.html>
- 735 Ordóñez-Gómez, J. D., Dunn, J. C., Arroyo-Rodríguez, V., Méndez-Cárdenas, M. G., Márquez-
736 Arias, A., & Santillán-Doherty, A. M. (2015). Role of emitter and severity of aggression
737 influence the agonistic vocalizations of Geoffroy's spider monkeys (*Ateles geoffroyi*).
738 *International Journal of Primatology*, 36(2), 429–440.
<https://link.springer.com/article/10.1007/s10764-015-9833-5>
- 739 Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. *Bmj*, 316(7139), 1236–
740 1238. <https://doi.org/10.1136/bmj.316.7139.1236>

- 747 Perret, M. & Aujard, F. (2001). Regulation by photoperiod of seasonal changes in body mass
748 and reproductive function in gray mouse lemurs (*Microcebus murinus*): differential
749 responses by sex. *International Journal of Primatology*, 22, 5–24.
750 <https://doi.org/10.1023/A:1026457813626>
- 751 Puts, D. A., Hill, A. K., Bailey, D. H., Walker, R. S., Rendall, D., Wheatley, J. R., et al. (2016).
752 Sexual selection on male vocal fundamental frequency in humans and other anthropoids.
753 *Proceedings of the Royal Society London B*, 283, 20152830–8.
754 <https://doi.org/10.1098/rspb.2015.2830>
- 755 Queen, J. P., Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for*
756 *biologists*. Cambridge university press.
- 757 R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. R
758 Foundation for Statistical Computing. Vienna, Austria.
- 759 Radespiel, U. (2000). Sociality in the gray mouse lemur (*Microcebus murinus*) in
760 northwestern Madagascar. *American Journal of Primatology*, 51, 21–40.
761 [https://doi.org/10.1002/\(SICI\)1098-2345\(200005\)51:1<21::AID-AJP3>3.0.CO;2-C](https://doi.org/10.1002/(SICI)1098-2345(200005)51:1<21::AID-AJP3>3.0.CO;2-C)
- 762 Radespiel, U., & Zimmermann, E. (2001). Female dominance in captive gray mouse lemurs
763 (*Microcebus murinus*). *American Journal of Primatology*, 54, 181–192.
764 <https://doi.org/10.1002/ajp.1029>
- 765 Rahlfs, M. & Fichtel, C. (2010). Anti-Predator Behaviour in a Nocturnal Primate, the Grey
766 Mouse Lemur (*Microcebus murinus*). *Ethology*, 116, 429–439.
767 <https://doi.org/10.1111/j.1439-0310.2010.01756.x>
- 768 Rakotonaina, J. H., Kappeler, P. M., Kaesler, E., Hämäläinen, A. M., Kirschbaum, C., & Kraus,
769 C. (2017). Hair cortisol concentrations correlate negatively with survival in a wild primate
770 population. *BMC ecology*, 1–13. <https://doi.org/10.1186/s12898-017-0140-1>
- 771 Reby, D. & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to
772 age and weight in the roars of red deer stags. *Animal Behaviour*, 65, 519–530.
773 <https://doi.org/10.1006/anbe.2003.2078>
- 774 Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W., & Clutton-Brock, T. (2005). Red
775 deer stags use formants as assessment cues during intrasexual agonistic interactions.
776 *Proceedings of the Royal Society London B*, 272, 941.
777 <https://doi.org/10.1098/rspb.2004.2954>
- 778 Rendall, D., Rodman, P. S. & Emond, R. E. (1996). Vocal recognition of individuals and kin in
779 free-ranging rhesus monkeys. *Animal Behaviour*, 51, 1007–1015.
780 <https://doi.org/10.1006/anbe.1996.0103>
- 781 Ryan, M. J. & Brenowitz, E. A. (1985). The role of body size, phylogeny, and ambient noise in
782 the evolution of bird song. *American Naturalist*, 87–100.
783 <https://www.jstor.org/stable/2461564>
- 784 Scheumann, M., Zimmermann, E., & Deichsel, G. (2007). Context-specific calls signal infants'
785 needs in a strepsirrhine primate, the gray mouse lemur (*Microcebus murinus*).
786 *Developmental Psychobiology*, 49, 708–718. <https://doi.org/10.1002/dev.20234>
- 787 Schielzeth, H. & Forstmeier, W. 2009. Conclusions beyond support: overconfident estimates
788 in mixed models. *Behavioral Ecology*, 20, 416–420.
789 <https://doi.org/10.1093/beheco/arn145>
- 790 Schmid, J. & Kappeler, P. M. (1998). Fluctuating sexual dimorphism and differential
791 hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*). *Behavioral*
792 *Ecology and Sociobiology*, 43, 125–132. <https://doi.org/10.1007/s002650050474>

- 793 Schrader, L., & Hammerschmidt, K. (1997). Computer-aided analysis of acoustic parameters
794 in animal vocalisations: a multi-parametric approach. *Bioacoustics*, 7, 247-265.
795 <https://doi.org/10.1080/09524622.1997.9753338>
- 796 Semple, S., Mccomb, K., Alberts, S., & Altmann, J. (2002). Information content of female
797 copulation calls in yellow baboons. *American Journal of Primatology*, 56, 43–56.
798 <https://doi.org/10.1002/ajp.1062>
- 799 Taylor, A. & Reby, D. (2010). The contribution of source–filter theory to mammal vocal
800 communication research. *Journal of Zoology*, 280, 221–236.
801 <https://doi.org/10.1111/j.1469-7998.2009.00661.x>
- 802 Vannoni, E. & McElligott, A. G. (2008). Low frequency groans indicate larger and more
803 dominant fallow deer (*Dama dama*) males. *PloS One*, 3, e3113.
804 <https://doi.org/10.1371/journal.pone.0003113>
- 805 Vieira, M. C., & Peixoto, P. E. (2013). Winners and losers: a meta-analysis of functional
806 determinants of fighting ability in arthropod contests. *Functional Ecology*, 27(2), 305-313.
- 807 Vuarin, P., Dammhahn, M., & Henry, P.-Y. (2013). Individual flexibility in energy saving: body
808 size and condition constrain torpor use. *Functional Ecology*, 27, 793-799.
809 <https://doi.org/10.1111/1365-2435.12069>
- 810 Wallschläger, D. (1980). Correlation of song frequency and body weight in passerine birds.
811 *Experientia*, 36, 412. <https://doi.org/10.1007/BF01975119>
- 812 Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). *Journal of
813 Theoretical Biology*, 67, 603–605. DOI: [10.1016/0022-5193\(77\)90061-3](https://doi.org/10.1016/0022-5193(77)90061-3)
- 814 Zimmermann, E. 1996. Castration affects the emission of an ultrasonic vocalization in a
815 nocturnal primate, the grey mouse lemur (*Microcebus murinus*). *Physiology & Behavior*,
816 60, 693-697. DOI: [10.1016/0031-9384\(96\)81674-x](https://doi.org/10.1016/0031-9384(96)81674-x)
- 817 Zimmermann, E., Vorobieva, E., Wrogemann, D., & Hafen, T. (2000). Use of vocal
818 fingerprinting for specific discrimination of gray (*Microcebus murinus*) and rufous mouse
819 lemurs (*Microcebus rufus*). *International Journal of Primatology*, 21, 837–852.
820 <https://doi.org/10.1023/A:1005594625841>
- 821 Zimmermann, E. (2010). Vocal expression of emotion in a nocturnal prosimian primate
822 group, mouse lemurs. In: Ed. by Brudzynski, S. M, *Handbook of Mammalian Vocalization:
823 An Integrative Neuroscience Approach*, (pp. 215–226). Oxford: Academic Press.
- 824
- 825