

Sussex Research

Function and evolution of vibrato-like frequency modulation in mammals

Benjamin D Charlton, Anna M Taylor, David Reby

Publication date

11-09-2017

Licence

This work is made available under the [CC BY-NC-ND 4.0](#) licence and should only be used in accordance with that licence. For more information on the specific terms, consult the repository record for this item.

Document Version

Accepted version

Citation for this work (American Psychological Association 7th edition)

Charlton, B. D., Taylor, A. M., & Reby, D. (2017). *Function and evolution of vibrato-like frequency modulation in mammals* (Version 1). University of Sussex. <https://hdl.handle.net/10779/uos.23447189.v1>

Published in

Current Biology

Link to external publisher version

<https://doi.org/10.1016/j.cub.2017.07.046>

Copyright and reuse:

This work was downloaded from Sussex Research Open (SRO). This document is made available in line with publisher policy and may differ from the published version. Please cite the published version where possible. Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners unless otherwise stated. For more information on this work, SRO or to report an issue, you can contact the repository administrators at sro@sussex.ac.uk. Discover more of the University's research at <https://sussex.figshare.com/>

Figure S1

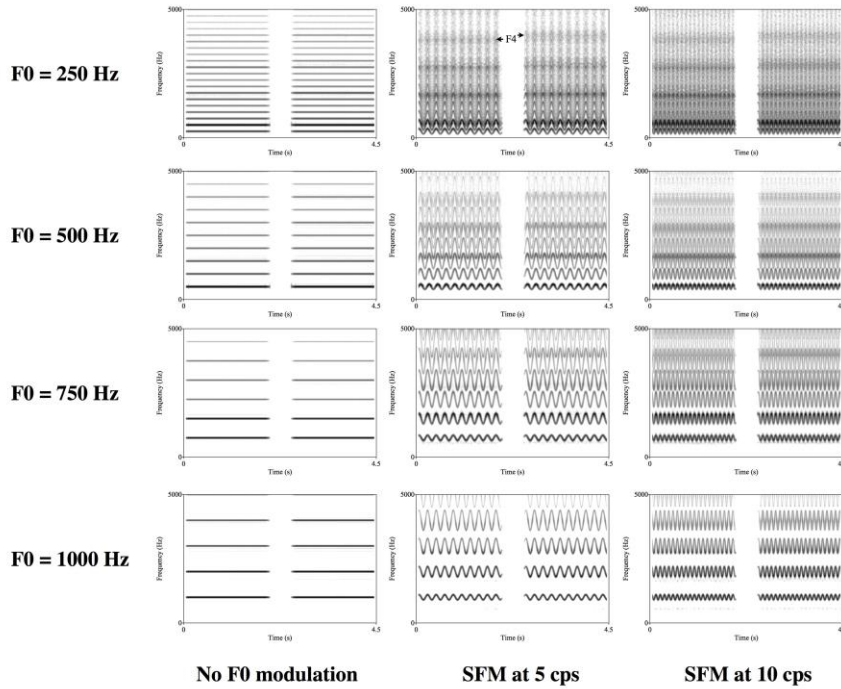


Figure S1. Stimuli used in psychoacoustic tests. The vocal stimuli were synthesised using scripts written by BDC that generated voice-like stimuli with or without SFM. Four different mean F0s (250, 500, 750 and 1000 Hz) and two levels of SFM rate (5 and 10 cycles per second) were presented to the participants. The stimuli were presented in pairs that had identical mean F0 and SFM cps, but either differed only in the value of the fourth formant (shifted up 3%, or down 3%, from its original value of 3850 Hz) or had exactly the same formant pattern. F4 denotes the position of the fourth formant, which has been shifted up 3% in all the stimuli presented. The mean F0 of the stimuli is given vertically and the level of F0 modulation is given horizontally: cps = cycles per second. Also see Figure 2 in the main text.

Figure S2

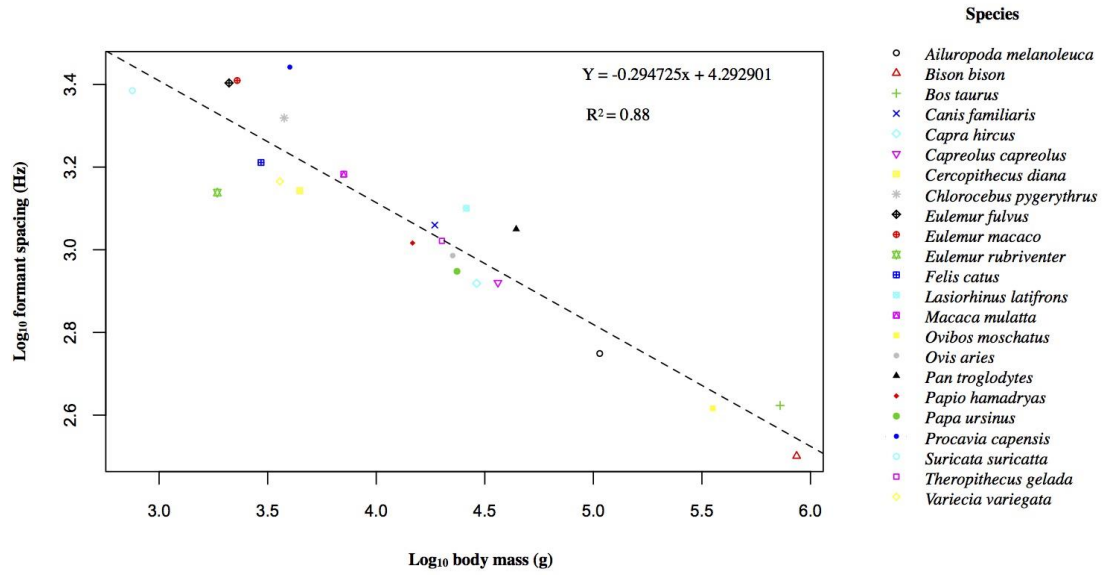


Figure S2. Relationship between log₁₀ formant spacing (ΔF) and log₁₀ body mass across 23 mammal species. A non-phylogenetic Ordinary Least Squares (OLS) model without the species' typical habitat and social structure proved to be the best supported model (Table S5). The regression equation from this model was subsequently used to predict ΔF.

Table S1. Acoustic, morphological and ecological data for all mammal species in the dataset

Species	Call type	Habitat	Context	Body mass (g)	Mean F0 (Hz)	ΔF (Hz)	pred $\Delta F/F0$ ratio	References for acoustic data	Source of weight data
<i>Ailuropoda melanoleuca</i>	SFM	Terrestrial	Contact promoting	107000	366	561	1.77	[S1]	[S1]
<i>Ailurus fulgens</i>	SFM	Terrestrial	Contact promoting	5000	3046	1595	0.52	[S2]	[S3]
<i>Alces alces</i>	Other	Terrestrial	Sexual	573785	125	394	3.15	[S4]	[S3]
<i>Alopex lagopus</i>	Other	Terrestrial	Territorial	4261	1283	1672	1.30	[S5]	[S3]
<i>Arctocephalus australis</i>	SFM	Terrestrial	Contact promoting	51750	871	801	0.92	[S6]	[S3]
<i>Ateles geoffroyi</i>	Other	Arboreal	Various	7627	1509 ^s	1408	0.93	[S7]	[S7]
<i>Bison bison</i>	Other	Terrestrial	Sexual	863410	55	317	6.32	[S8]	[S8]
<i>Bos taurus</i>	Other	Terrestrial	Contact promoting	725000	117	420	3.15	[S9]	Wikipedia
<i>Brachyteles hypoxanthus</i>	Other	Arboreal	Contact promoting	9000	1723	1341	0.78	[S7]	[S7]
<i>Callithrix geoffroyi</i>	Other	Arboreal	Contact promoting	307	7353	3630	0.49	[S7]	[S7]
<i>Callithrix jacchus</i>	Other	Arboreal	Feeding	269	6957	3774	0.54	[S7]	[S7]
<i>Callithrix kuhlii</i>	Other	Arboreal	Feeding	271	4853	3766	0.78	[S7]	[S7]
<i>Callithrix pygmaea</i>	SFM	Arboreal	Contact promoting	133	9831 [^]	4645	0.47	[S10]	[S3]
<i>Callorhinus ursinus</i>	SFM	Terrestrial	Contact promoting	149333	250 [#]	586	4.21	[S11]	[S3]
<i>Canis familiaris</i>	Other	Terrestrial	Aggression	18603	133	1148	8.17	[S12]	[S12]
<i>Canis latrans</i>	SFM	Terrestrial	Contact promoting	12197	725 [^]	1226	1.69	[S13]	[S3]
<i>Canis lupus dingo</i>	Other	Terrestrial	Various	35280	1950 ^s	897	0.46	[S14]	[S3]
<i>Capra hircus</i>	SFM	Terrestrial	Contact promoting	45162	223	829	3.74	[S15]	Wikipedia
<i>Capreolus capreolus</i>	Other	Terrestrial	Territorial	36346	175	833	5.08	[S16]	[S3]
<i>Cebus apella</i>	Other	Arboreal	Fear	2929	1826	1867	1.02	[S7]	[S7]
<i>Cebus capucinus</i>	SFM	Arboreal	Feeding	3036	7546	1848	0.24	[S17]	[S3]
<i>Cercocebus atys</i>	Other	Arboreal	Feeding	10553	129	1280	9.96	[S7]	[S7]
<i>Cercopithecus campbelli</i>	Other	Arboreal	Various	3600	658 ^s	1757	2.67	[S7]	[S7]
<i>Cercopithecus diana</i>	SFM	Arboreal	Contact promoting	4445	1500 [#]	1390	1.10	[S18]	[S3]
<i>Cercopithecus mitis</i>	Other	Arboreal	Various	5187	835 ^s	1578	1.89	[S7]	[S7]
<i>Cercopithecus mona</i>	Other	Arboreal	Sexual	4566	534	1638	3.07	[S7]	[S7]
<i>Cervus nippon</i>	Other	Terrestrial	Various	34583	940 [^]	902	0.96	[S19]	[S3]
<i>Chlorocebus pygerythrus</i>	Other	Terrestrial	Alarm	3768	330	2083	5.25	[S20]	[S3]
<i>Crocota crocuta</i>	Other	Terrestrial	Feeding	58167	547	774	1.41	[S21]	[S3]
<i>Enhydra lutris</i>	Other	Terrestrial	Various	25848	888 ^s	983	1.11	[S22]	[S3]

<i>Equus caballus</i>	SFM	Terrestrial	Contact promoting	479350	399	416	1.04	[S23]	[S23]
<i>Equus przewalskii</i>	Other	Terrestrial	Contact promoting	270000	296	492	1.66	[S24]	[S3]
<i>Erythrocebus patas</i>	Other	Terrestrial	Contact promoting	9740	212	1310	6.20	[S7]	[S7]
<i>Eulemur fulvus</i>	Other	Arboreal	Group coordination	2100	566	2532	3.64	[S25]	[S26]
<i>Eulemur macaco</i>	Other	Arboreal	Contact promoting	2289	75	2567	26.77	[S25]	[S3]
<i>Eulemur rubriventer</i>	Other	Arboreal	Contact promoting	1854	52	1375	41.09	[S27]	[S3]
<i>Felis catus</i>	Other	Terrestrial	Contact promoting	2947	609	1626	3.06	[S28]	[S3]
<i>Felis chaus</i>	Other	Terrestrial	Contact promoting	7600	440	1410	3.20	[S29]	[S29]
<i>Felis margarita</i>	Other	Terrestrial	Contact promoting	3000	580	1854	3.20	[S29]	[S29]
<i>Felis nigripes</i>	Other	Terrestrial	Contact promoting	1550	320	2252	7.04	[S29]	[S29]
<i>Felis silvestris lybica</i>	Other	Terrestrial	Contact promoting	4500	356	1645	4.62	[S29]	[S29]
<i>Felis silvestris ornata</i>	Other	Terrestrial	Contact promoting	3300	245	1803	7.36	[S29]	[S29]
<i>Felis silvestris silvestris</i>	Other	Terrestrial	Contact promoting	6500	335	1476	4.41	[S29]	[S29]
<i>Geomys breviceps</i>	SFM	Terrestrial	Sexual	139	2090	4587	2.19	[S30]	[S3]
<i>Gorilla gorilla</i>	Other	Terrestrial	Group coordination	109909	264	641	2.43	[S31]	[S3]
<i>Heterocephalus glaber</i>	Other	Terrestrial	Group coordination	41	4100	6557	1.60	[S32]	[S3]
<i>Homo sapiens</i>	Other	Terrestrial	Various	71900	162 ^s	727	4.48	[S33]	[S33]
<i>Hydrochoerus hydrochaeris</i>	SFM	Terrestrial	Contact promoting	48700	1945	815	0.42	[S34]	[S3]
<i>Hylobates klossii</i>	Other	Arboreal	Sexual	5792	811	1527	1.88	[S7]	[S7]
<i>Hylobates lar</i>	Other	Arboreal	Sexual	5457	968	1554	1.61	[S7, 35]	[S3]
<i>Hylobates moloch</i>	Other	Arboreal	Sexual	6120	951	1503	1.58	[S7]	[S7]
<i>Hylobates muelleri</i>	Other	Arboreal	Sexual	5847	839	1523	1.82	[S7]	[S7]
<i>Hylobates pileatus</i>	Other	Arboreal	Sexual	5495	778	1551	1.99	[S7]	[S7]
<i>Indri indri</i>	Other	Arboreal	Sexual	8896	637	1346	2.11	[S36]	[S3]
<i>Lasiiorhinus latifrons</i> **	Other	Terrestrial	Mild distress	26000	-	1260	-	[S37]	[S3]
<i>Lemur catta</i>	Other	Arboreal	Group coordination	2549	626	1945	3.11	[S38]	[S3]
<i>Lycaon pictus</i>	SFM	Terrestrial	Greeting call	20643	1526	1050	0.69	[S39]	[S3]
<i>Macaca fascicularis</i>	Other	Terrestrial	Sexual	4369	179	1660	9.27	[S7]	[S7]
<i>Macaca fuscata</i>	Other	Terrestrial	Contact promoting	10342	763	1287	1.69	[S7]	[S7]
<i>Macaca mulatta</i>	Other	Terrestrial	Contact promoting	7086	215	1524	6.71	[S7]	[S7]
<i>Marmota flaviventris</i>	Other	Terrestrial	Alarm	3967	1302	1707	1.31	[S40]	[S3]
<i>Meles meles</i>	Other	Terrestrial	Various	11869	348* ^s	1236	3.55	[S41]	[S3]
<i>Mesocricetus auratus</i>	Other	Terrestrial	Sexual	97	36150	5095	0.14	[S42]	[S3]
<i>Microcebus murinus</i>	SFM	Arboreal	Sexual	78	19200	5436	0.28	[S43]	[S43]

<i>Microcebus rufus</i>	Other	Arboreal	Sexual	43	21800 [^]	6479	0.30	[S44]	[S26]
<i>Mungos mungo</i>	SFM	Terrestrial	Alarm	1364	2000 [#]	2339	1.86	[S45]	[S3]
<i>Mus musculus</i>	Other	Terrestrial	Sexual	20	62338	8145	0.13	[S46]	[S3]
<i>Nasalis larvatus</i>	Other	Arboreal	Aggression	14659	136	1162	8.57	[S7]	[S7]
<i>Neophoca cinerea</i>	SFM	Terrestrial	Contact promoting	170275	534	564	1.06	[S47]	[S3]
<i>Odobenus rosmarus</i>	Other	Terrestrial	Contact promoting	828000	118	354	3.00	[S48]	[S3]
<i>Odocoileus virginianus</i>	Other	Terrestrial	Sexual	88914	209	683	3.27	[S4]	[S3]
<i>Ovibos moschatus</i>	Other	Terrestrial	Aggression	354884	92	414	4.96	[S49]	[S3]
<i>Ovis aries</i>	SFM	Terrestrial	Contact promoting	22500	181	968	5.67	[S50]	[S3]
<i>Pan troglodytes</i>	Other	Terrestrial	Various	44127	247 ^{\$}	1122	3.40	[S7]	[S7]
<i>Papio hamadryas</i>	Other	Terrestrial	Contact promoting	14699	72	1039	16.14	[S51]	[S3]
<i>Papio ursinus</i>	Other	Terrestrial	Group coordination	23550	84	887	12.10	[S52]	[S52]
<i>Phodopus sungorus</i>	Other	Terrestrial	Aggression	32	58925	7068	0.12	[S53]	[S3]
<i>Pongo pygmaeus</i>	Other	Arboreal	Alarm	56882	46	779	16.93	[S7]	[S7]
<i>Procavia capensis</i>	Other	Terrestrial	Sexual	4000	1280	2766	1.33	[S54]	[S3]
<i>Propithecus diadema</i>	Other	Arboreal	Contact promoting	6230	1229	1495	1.22	[S55]	[S3]
<i>Pteronotus parnellii</i>	Other	Terrestrial	Navigation	12	63500	9437	0.15	[S56]	[S56]
<i>Pteronura brasiliensis</i>	SFM	Terrestrial	Aggression	26000	347	981	2.83	[S57]	[S3]
<i>Pteropus poliocephalus</i>	SFM	Arboreal	Contact promoting	719	3000	2825	0.94	[S58]	[S3]
<i>Rattus rattus</i>	Other	Terrestrial	Contact promoting	275	2500	3749	1.50	[S59]	[S59]
<i>Saguinus oedipus</i>	Other	Arboreal	Contact promoting	456	1856	3230	1.74	[S7]	[S7]
<i>Saimiri sciureus</i>	SFM	Terrestrial	Contact promoting	760	7500 [^]	2779	0.37	[S60]	[S3]
<i>Suricata suricatta</i>	Other	Terrestrial	Contact promoting	753	556	2427	4.96	[S61]	[S3]
<i>Sus scrofa</i>	Other	Terrestrial	Various	95700	133 ^{\$}	668	5.01	[S62]	[S62]
<i>Tamias striatus</i>	SFM	Terrestrial	Alarm	104	7000	498	0.71	[S63]	[S3]
<i>Theropithecus gelada</i>	Other	Terrestrial	Sexual	20075	111	1051	9.54	[S64]	[S3]
<i>Tupaia belangeri</i>	Other	Terrestrial	Various	200	3343 [^]	4118	1.23	[S65]	[S3]
<i>Varecia variegata</i>	Other	Arboreal	Group coordination	3600	222	1464	7.91	[S66]	[S3]
<i>Vulpes vulpes</i>	Other	Terrestrial	Various	5077	748 ^{\$}	1588	2.12	[S67]	[S3]

** the southern hairy-nosed wombat (*Lasiornhinus latifrons*) was used in the formant model but does not have a measurable F0 in its “harsh cough” vocalizations.

ΔF = derived from published data, normal font = ΔF predicted from body mass using the formant model (Figure S2). Data on species habitat were taken from the Encyclopedia of Life website (<http://eol.org/>). Data on species social structure were taken from the Animal Diversity Website (<http://animaldiversity.org/>). \$Average F0 from vocal repertoire. ^ F0 calculated as the mid point between reported minimum and maximum values. #F0 values measured from a published spectrogram using a clear ruler to extrapolate from the axes. Also see Figure 3 in the main text.

Table S2. Results from the ten best supported PGLS regression models fitted to explain variance in \log_{10} harmonics to formants ratio with call type across 92 mammal species.

Model	(Intercept)	Call type	Habitat	Log ₁₀ male body mass	Social structure	df	logLik	AICc	Delta	Weights
BM + λ	-0.34	+	-	0.16	-	5.00	-44.40	99.50	0.00	0.32
BM + λ	0.20	+	-	-	-	4.00	-45.93	100.32	0.81	0.21
BM + λ	-0.39	+	-	0.16	+	6.00	-45.03	103.04	3.54	0.05
BM + λ	0.18	+	-	-	+	5.00	-46.73	104.16	4.66	0.03
BM + λ	-0.42	+	+	0.15	-	7.00	-44.73	104.80	5.30	0.02
BM + λ	0.06	+	+	-	-	6.00	-45.94	104.86	5.36	0.02
BM + ρ	-0.33	+	-	0.17	-	5.00	-48.66	108.03	0.05	0.28
BM + λ	-0.46	+	+	0.16	+	8.00	-45.51	108.75	9.25	0.00
BM + λ	0.04	+	+	-	+	7.00	-46.80	108.93	9.43	0.00
BM + ρ	0.27	+	-	-	-	4.00	-50.82	110.11	2.13	0.10

The PGLS regression models are ordered by AICc value so that the best supported model (with the lowest AICc value) is first in the list. “+” denotes factor included in the model and statistically significant independent variables are indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). BM + λ = Brownian motion + Pagel’s lambda model, BM + ρ = Brownian motion + Grafen’s rho model.

Table S3. Acoustic measures for SFM calls. Data on mean F0 and F0 modulation extent were taken from the same source. Also see Figure 3 in the main text.

Species	Context	Mean F0 (Hz)	F0 modulation extent (Hz)	% F0 modulation	pred Δ F/F0 ratio	Source of recordings	N	SFM acoustics
<i>Ailuropoda melanoleuca</i>	Contact promoting	365	101	28	1.54		245	[S1]
<i>Ailurus fulgens</i>	Contact promoting	1450	442	30	1.1	CS, AT	6	Data not available
<i>Arctocephalus australis</i>	Contact promoting	871	353	41	0.92		276	[S6]
<i>Callithrix pygmaea</i>	Contact promoting	9831	3264	33	0.47		12	[S10]
<i>Callorhinus ursinus</i>	Contact promoting	139	40	29	4.21	ML	20	Data not available
<i>Canis latrans</i>	Contact promoting	778	271	35	1.58	AT, ASA	15	Data not available
<i>Capra hircus</i>	Contact promoting	223	49	22	3.72		88	[S15]
<i>Cebus capucinus</i>	Feeding	6163	2258	37	0.3	AT	5	Data not available
<i>Cercopithecus diana</i>	Contact promoting	1163	312	27	1.2	ASA	13	Data not available
<i>Equus caballus</i>	Contact promoting	494	126	26	0.84	AT	7	Data not available
<i>Geomys breviceps</i>	Sexual	2090	966	46	2.19		30	[S30]
<i>Hydrochoerus hydrochaeris</i>	Contact promoting	1495	1007	67	0.55	CW	13	Data not available
<i>Lycaon pictus</i>	Greeting call	1506	579	38	0.7	ASA	8	Data not available
<i>Microcebus murinus</i>	Sexual	22000	12050	55	0.25		138	[S43]
<i>Mungos mungo</i>	Alarm	1260	611	48	1.86	ASA	11	Data not available
<i>Neophoca cinerea</i>	Contact promoting	534	180	34	1.06		61	[S47]
<i>Ovis aries</i>	Contact promoting	256	28	11	3.79	AT	16	Data not available
<i>Pteronura brasiliensis</i>	Aggression	300	55	18	3.27	ML	3	Data not available
<i>Pteropus poliocephalus</i>	Contact promoting	3000	2000	67	0.94		27	[S58]
<i>Saimiri sciureus</i>	Contact promoting	2689	1006	37	1.03	ASA	5	Data not available
<i>Tamias striatus</i>	Alarm	1211	435	36	4.12	AT	8	Data not available

CS = Cao et al 2016 Anim. Biol. 66, 145-155 supplementary material

AT = Animal Trax audio CD (Hollywood Edge, CA, USA)

ASA = Berlin Animal Sound Archive (http://www.animalsoundarchive.org/tsa/content_16_en.html)

ML = Macaulay Library (<https://www.macaulaylibrary.org/>)

CW = Capybara World website (<https://capybaraworld.wordpress.com/>)

Table S4. Results from the ten best supported PGLS regression models fitted to explain variance in \log_{10} harmonics to formants ratio with % F0 modulation in SFM calls across 21 mammal species.

Model	(Intercept)	\log_{10} harmonics to formant ratio	\log_{10} male body mass	Social structure	Habitat	df	logLik	AICc	Delta	Weights
BM	56.11	+	-3.05	-13.25	+	6.00	-64.04	146.09	0.00	0.33
BM	46.74	+	-	-12.53	+	5.00	-66.58	147.16	1.07	0.19
BM	57.34	-	-4.16	-14.30	+	5.00	-66.71	147.43	1.34	0.17
BM	53.63	+	-2.64	-13.49	-	5.00	-67.08	148.17	2.08	0.12
BM + λ	55.77	+	-2.88	-11.92	+	7.00	-63.28	149.18	0.00	0.34
BM	45.88	+	-	-12.77	-	4.00	-69.48	149.47	3.38	0.06
BM	54.89	-	-3.74	-14.52	-	4.00	-69.74	149.97	3.88	0.05
BM + ρ	48.95	+	-	-17.99	+	6.00	-65.99	149.98	0.00	0.34
BM + λ	58.16	-	-4.38	-12.84	+	6.00	-65.99	149.98	0.80	0.23
BM	42.18	-	-	-14.21	+	4.00	-69.80	150.11	4.02	0.04

The PGLS regression models are ordered by AICc value so that the best supported model (with the lowest AICc value) is first in the list. “+” denotes factor included in the model and statistically significant independent variables are indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). BM = pure Brownian motion model, BM + λ = Brownian motion + Pagel’s lambda model, BM + ρ = Brownian motion + Grafen’s rho model.

Table S5. Results from the ten best supported PGLS regression models fitted to explain variance in \log_{10} formant spacing with \log_{10} body mass across 23 mammal species.

Model	(Intercept)	\log_{10} male body mass	Social structure	Habitat	df	logLik	AICc	Delta	Weights
OLS	4.29	-0.29	-	-	3.00	17.51	-27.76	0.00	0.90
BM + λ	4.38	-0.31	-	-	4.00	18.10	-25.98	0.00	0.88
BM + ρ	4.29	-0.29	-	-	4.00	17.64	-25.06	0.00	0.91
OU	4.29	-0.29	-	-	4.00	17.51	-24.80	0.00	0.92
OLS	4.28	-0.29	+	-	4.00	16.34	-22.45	5.31	0.06
BM + λ	4.26	-0.29	-	+	5.00	17.25	-20.96	5.02	0.07
OLS	4.30	-0.30	-	+	4.00	15.57	-20.91	6.85	0.03
BM + λ	4.36	-0.31	+	-	5.00	16.95	-20.37	5.61	0.05
BM + ρ	4.27	-0.28	+	-	5.00	16.47	-19.41	5.65	0.05
OU	4.28	-0.29	+	-	5.00	16.34	-19.14	5.65	0.05

The PGLS regression models are ordered by AICc value so that the best supported model (with the lowest AICc value) is first in the list. “+” denotes factor included in the model and statistically significant independent variables are indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). OLS = non-phylogenetic (ordinary least squares) model, BM + λ = Brownian motion + Pagel’s lambda model, OU = Ornstein-Uhlenbeck model. BM + ρ = Brownian motion + Grafen’s rho model.

Supplemental references

- S1. Charlton, B., Zhang, Z., and Snyder, R. (2009). Vocal cues to identity and relatedness in giant pandas (*Ailuropoda melanoleuca*). *J. Acoust. Soc. Am.* *126*, 2721-2732.
- S2. Cao, D., Zhou, H., Wei, W., and Lei, M. (2016). Vocal repertoire of adult captive red pandas (*Ailurus fulgens*). *Anim. Biol.* *66*, 145-155.
- S3. Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Neil, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., et al. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. In *Ecology*, Volume 90. (Ecological Society of America), pp. 2648-2648.
- S4. Cap, H., Deleporte, P., Joachim, J., and Reby, D. (2008). Male vocal behavior and phylogeny in deer. *Cladistics* *24*, 917-931.
- S5. Frommolt, K.H., Goltsman, M.E., and MacDonald, D.W. (2003). Barking foxes, *Alopex lagopus*: field experiments in individual recognition in a territorial mammal. *Anim. Behav.* *65*, 509-518.
- S6. Phillips, A.V., and Stirling, I. (2000). Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*. *Marine Mammal Science* *16*, 592-616.
- S7. Puts, D.A., Hill, A.K., Bailey, D.H., Walker, R.S., Rendall, D., Wheatley, J.R., Welling, L.L., Dawood, K., Cárdenas, R., Burriss, R.P., et al. (2016). Sexual selection on male vocal fundamental frequency in humans and other anthropoids. *Proceedings of the Royal Society B* *283*.
- S8. Wyman, M., Mooring, M., McCowan, B., Penedo, M., Reby, D., and Hart, L. (2012). Acoustic cues to size and quality in the vocalizations of male North American bison, *Bison bison*. *Anim. Behav.* *84*, 1381-1391.
- S9. Padilla de la Torre, M., Briefer, E.F., Reader, T., and McElligott, A.G. (2015). Acoustic analysis of cattle (*Bos taurus*) mother-offspring contact calls from a source-filter theory perspective. *Appl. Anim. Behav. Sci.* *163*, 58-68.
- S10. De La Torre, S., and Snowdon, C.T. (2009). Dialects in pygmy marmosets? Population variation in call structure. *Am. J. Primatol.* *71*, 333-342.
- S11. Insley, S.J. (2001). Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Anim. Behav.* *61*, 129-137.
- S12. Taylor, A., Reby, D., and McComb, K. (2008). Human listeners attend to size information in domestic dog growls. *The Journal of the Acoustical Society of America* *123*, 2903-2909.
- S13. Mitchell, B.R., Makagon, M.M., Jaeger, M.M., and Barrett, R.H. (2006). Information content of coyote barks and howls. *Bioacoustics* *15*, 289-314.
- S14. Déaux, É.C., and Clarke, J.A. (2013). Dingo (*Canis lupus dingo*) acoustic repertoire: form and contexts. *Behaviour* *150*, 75-101.
- S15. Briefer, E., and McElligott, A.G. (2011). Mutual mother offspring vocal recognition in an ungulate hider species (*Capra hircus*). *Animal Cognition* *14*, 585-598.
- S16. Reby, D., and Cargnelutti, B. (1999). Des voix dans la forêt. Un guide sonore des Cervides d'Europe.
- S17. Gros-Louis, J.J., Perry, S.E., Fichtel, C., Wikberg, E., Gilkenson, H., Wofsy, S., and Fuentes, A. (2008). Vocal repertoire of *Cebus capucinus*: acoustic structure, context, and usage. *Int. J. Primatol.* *29*, 641-670.
- S18. Zuberbühler, K., Noë, R., and Seyfarth, R. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Anim. Behav.* *53*, 589-604.
- S19. Minami, M., and Kawamichi, T. (1992). Vocal repertoires and classification of the sika deer *Cervus nippon*. *Journal of the Mammalogical Society of Japan* *17*, 71-94.
- S20. Owren, M.J., and Bernacki, R.H. (1988). The acoustic features of vervet monkey alarm calls. *J. Acoust. Soc. Am.* *83*, 1927-1935.
- S21. Mathevon, N., Koralek, A., Weldele, M., Glickman, S.E., and Theunissen, F.E. (2010). What the hyena's laugh tells: Sex, age, dominance and individual signature in the giggling call of *Crocuta crocuta*. *BMC Ecology* *10*, 1-16.
- S22. McShane, L.J., Estes, J.A., and Riedman, M.L. (1995). Repertoire, structure, and individual variation of vocalizations in the sea otter. *J. Mammal.* *76*, 414-427.
- S23. Briefer, E.F., Maigrot, A.-L., Mandel, R., Freymond, S.B., Bachmann, I., and Hillmann, E. (2015). Segregation of information about emotional arousal and valence in horse whinnies. *Sci Rep* *4*, 9989-9911.

- S24. Alberghina, D., Caudullo, E., Bandi, N., and Panzera, M. (2014). A comparative analysis of the acoustic structure of separation calls of Mongolian wild horses (*Equus ferus przewalskii*) and domestic horses (*Equus caballus*). *Journal of Veterinary Behavior: Clinical Applications and Research* 9, 254-257.
- S25. Gamba, M., and Giacoma, C. (2008). Subspecific divergence in the black lemur's low-pitched vocalizations. *The Open Acoustics Journal* 1, 49-53.
- S26. Smith, R.J., and Junkers, W.L. (1997). Body mass in comparative primatology. *Journal of Human Evolution* 32, 523-559.
- S27. Gamba, M., Friard, O., and Giacoma, C. (2012). Vocal tract morphology determines species-specific features in vocal signals of lemurs (*Eulemur*). *Int. J. Primatol.* 33, 1453-1466.
- S28. Nicastro, N. (2004). Perceptual and acoustic evidence for species-level differences in meow vocalizations by domestic cats (*Felis catus*) and African wild cats (*Felis silvestris lybica*). *J Comp Psychol* 118, 287-296.
- S29. Peters, G., Baum, L., Peters, M., and Tonkin-Leyhausen, B. (2009). Spectral characteristics of intense mew calls in cat species of the genus *Felis* (*Mammalia: Carnivora: Felidae*). *J. Ethol.* 27, 221-237.
- S30. Devries, M.S., and Sikes, R.S. (2008). Vocalisations of a North American subterranean rodent *Geomys breviceps*. *Bioacoustics* 18, 1-15.
- S31. Salmi, R., and Doran-Sheehy, D.M. (2014). The function of loud calls (Hoot Series) in wild western gorillas (*Gorilla gorilla*). *Am. J. Phys. Anthropol.* 155, 379-391.
- S32. Judd, T., and Sherman, P. (1996). Naked mole-rats recruit colony mates to food sources. *Anim. Behav.* 52, 957-969.
- S33. Pisanski, K., Jones, B.C., Fink, B., O'Connor, J.J.M., Debruine, L.M., Röder, S., and Feinberg, D.R. (2016). Voice parameters predict sex-specific body morphology in men and women. *Anim. Behav.* 112, 13-22.
- S34. Barros, K.S., Tokumaru, R.S., Pedroza, J.P., and Nogueira, S.S.C. (2010). Vocal Repertoire of Captive Capybara (*Hydrochoerus hydrochaeris*): Structure, Context and Function. *Ethology* 117, 83-94.
- S35. Barelli, C., Mundry, R., Heistermann, M., and Hammerschmidt, K. (2013). Cues to androgens and quality in male gibbon songs. *PLoS ONE* 8, e82748.
- S36. Giacoma, C., Sorrentino, V., Rabarivola, C., and Gamba, M. (2010). Sex differences in the song of *Indri indri*. *Int. J. Primatol.* 31, 539-551.
- S37. Charlton, B. (2014). Vocal distinctiveness in the harsh coughs of southern hairy-nosed wombats (*Lasiorhinus latifrons*). *Acta Acustica United With Acustica* 100, 719-723.
- S38. Oda, R. (2002). Individual distinctiveness of the contact calls of ring-tailed lemurs. *Folia Primatol.* 73, 132-136.
- S39. Hugh Sinclair, W. (2009). Vocal communication and cognitive abilities in a "fugitive" species: the African wild dog. In *Psychology*, Volume PhD. (University of Sussex), pp. 1-254.
- S40. Blumstein, D.T., and Munos, O. (2005). Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. *Anim. Behav.* 69, 353-361.
- S41. Wong, J., Stewart, P.D., and Macdonald, D.W. (1999). Vocal repertoire in the European badger (*Meles meles*): Structure, context, and function. *J. Mammal.* 80, 570-588.
- S42. Floody, O.R., and Pfaff, D.W. (1977). Communication among hamsters by high-frequency acoustic signals: I. Physical characteristics of hamster calls. *Journal of Comparative and Physiological Psychology* 91, 794-806.
- S43. Zimmermann, E., and Lerch, C. (1993). The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*, Prosimii, Primates) and sources of its variation. *Ethology* 93, 211-224.
- S44. Zimmermann, E., Vorobieva, E., Wrogemann, D., and Hafen, T. (2000). Use of vocal fingerprinting for specific discrimination of gray (*Microcebus murinus*) and rufous mouse lemurs (*Microcebus rufus*). *Int. J. Primatol.* 21, 837-852.
- S45. Furrer, R.D., and Manser, M.B. (2009). Banded mongoose recruitment calls convey information about risk and not stimulus type. *Anim. Behav.* 78, 195-201.
- S46. Gourbal, B.E.F., Barthelemy, M., Petit, G., and Gabrion, C. (2004). Spectrographic analysis of the ultrasonic vocalisations of adult male and female BALB/c mice. *Naturwissenschaften* 91, 1-5.
- S47. Charrier, I., and Harcourt, R. (2006). Individual vocal identity in mother and pup Australian sea lions (*Neophoca cinerea*). *J. Mammal.* 87, 929-938.
- S48. Charrier, I., Aubin, T., and Mathevon, N. (2010). Mother-calf vocal communication in Atlantic walrus: a first field experimental study. *Animal Cognition* 13, 471-482.

- S49. Frey, R., Gebler, A., and Fritsch, G. (2006). Arctic roars - laryngeal anatomy and vocalization of the muskox (*Ovibos moschatus* Zimmermann, 1780, *Bovidae*). *J. Zool.* 268, 433-448.
- S50. Walser, E., and Hague, P. (1980). Variations in the structure of bleats from sheep of four different breeds. *Behaviour* 75, 22-35.
- S51. Pfefferle, D., and Fischer, J. (2006). Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. *Anim. Behav.* 72, 43-51.
- S52. Rendall, D., Kollias, S., and Ney, C. (2005). Pitch (Fo) and formant profiles of human vowels and vowel-like baboon grunts: The role of vocalizer body size and voice-acoustic allometry. *J. Acoust. Soc. Am.* 117, 944-955.
- S53. Keesom, S.M., Rendon, N.M., Demas, G.E., and Hurley, L.M. (2015). Vocal behaviour during aggressive encounters between Siberian hamsters, *Phodopus sungorus*. *Anim. Behav.* 102, 85-93.
- S54. Koren, L., and Geffen, E. (2009). Complex call in male rock hyrax (*Procavia capensis*): a multi-information distributing channel. *Behav. Ecol. Sociobiol.* 63, 581-590.
- S55. Patel, E., and Owren, M. (2012). Silky sifaka (*Propithecus candidus*) "zzuss" vocalizations: Sexual dimorphism, individuality, and function in the alarm call of a monomorphic lemur. *The Journal of the Acoustical Society of America* 132, 1799-1810.
- S56. Jones, G. (1999). Scaling of echolocation call parameters in bats. *J. Exp. Biol.* 202, 3359-3367.
- S57. Leuchtenberger, C., Sousa-Lima, R., Duplaix, N., Magnusson, W.E., and Mourão, G. (2014). Vocal repertoire of the social giant otter. *The Journal of the Acoustical Society of America* 136, 2861-2875.
- S58. Nelson, J.E. (1964). Vocal communication in Australian flying foxes (*Pteropodidae*; *Megachiroptera*). *Ethology* 21, 857-870.
- S59. Jourdan, D., Ardid, D., Chapuy, E., Le Bars, D., and Eschali r, A. (1997). Audible and ultrasonic vocalization elicited by a nociceptive stimulus in rat: relationship with respiration. *Journal of Pharmacological and Toxicological Methods* 38, 109-116.
- S60. Winter, P., Ploog, D., and Latta, J. (1966). Vocal repertoire of the squirrel monkey (*Saimiri sciureus*), its analysis and significance. *Exp Brain Res* 1, 359-384.
- S61. Townsend, S.W., Z ttl, M., and Manser, M.B. (2011). All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behav. Ecol. Sociobiol.* 65, 1927-1934.
- S62. Schrader, L., and Todt, D. (1998). Vocal quality is correlated with levels of stress hormones in domestic pigs. *Ethology* 104, 859-876.
- S63. Brand, L.R. (1976). The vocal repertoire of chipmunks (genus *Eutamias*) in California. *Anim. Behav.* 24, 319-335.
- S64. Bergman, T.J. (2013). Speech-like vocalized lip-smacking in geladas. *Current biology : CB* 23, R268-R269.
- S65. Binz, H., and Zimmermann, E. (1989). The vocal repertoire of adult tree shrews (*Tupaia belangeri*). *Behaviour* 109, 142-162.
- S66. Gamba, M., and Giacoma, C. (2006). Vocal tract modeling in a prosimian primate: the black and white ruffed lemur. *Acta Acustica United With Acustica* 92, 749-755.
- S67. Newton-Fisher, N., Harris, S., White, P., and Jones, G. (1993). Structure and function of red fox *Vulpes vulpes* vocalisations. *Bioacoustics* 5, 1-31.