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Last but not least I want to thank my family and friends for their support.

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1. Introduction

The study of the relationship between an animal's body size and the acoustic parameters of its vocalizations is defined as "acoustic allometry" (Fitch 2000, Gingras et al. 2013). The relevance of body size in anatomy, physiology, ecology and social behavior is well known. For example, in many species body size plays a crucial role in obtaining mates and/or territory defense and thus drives selection (Fitch & Hauser 2002, Modig 1996, Ryan 1980, Schmidt-Nielsen 1984, Wagner 1992). Body size also has consequences for the vocalizations an animal produces. This is because the size of an animal's vocal organs (an important factor in determining the acoustic parameters of vocalization) is tightly correlated with the size of its body. The importance of body size in evolution and its relationship to vocalization gives acoustic allometry the potential to answer questions about the evolution of vocalization (Gingras et al. 2013).

In his "motivation-structural rules" hypothesis, Morten (1977) states that mammals and birds give low frequency, atonal calls in aggressive situations, and high frequency, tonal calls in nonaggressive or fearful situations. Because Morton also argues that larger animals are dominant over smaller ones, his hypothesis relies in part on the assumption that vocalization frequency is negatively correlated with body size. Hauser (1993) found support for this assumption in a sample of primates (36 species; 11 families), demonstrating a strong negative correlation between mean body mass and repertoire frequency (an ambiguous term used by Hauser to denote F_0, F_{dom}, or a combined average). This correlation was maintained when minimum or maximum frequency was used instead of mean frequency, but was strongest for mean frequency. Despite the fact that his sample was limited to one mammalian order (i.e. primates), Hauser concluded that larger species tend to make lower frequency vocalizations than smaller species. Hauser (1993) also found that despite the fact that body size is a good predictor of vocalization frequencies across genera, predictions within genera (in his case *Macaca*) were considerably weaker. This raises the possibility that taxonomically restricted data sets give rise to weaker acoustic correlations with body size than more diverse dataset.

Why should body size be negatively correlated with vocalization frequencies? What are the anatomical and physical principles behind this relationship? The "source-filter" theory links the anatomy of vocal production with its acoustic consequences.

This theory is widely applicable to vocalizing animals (e.g., mammals as well as birds; Fitch 1997, Taylor & Reby 2010) and therefore provides a useful framework for comparative studies. According to the source-filter theory, the vocal production system is divided into two separate areas: the source, which consists primarily of the vocal folds in the larynx; and the filter, which consists of all the air cavities between the larynx and the mouth and nostrils (i.e. the supralarygeal vocal tract). Typically, air coming from the lungs flows through the opening between the vocal folds (the glottis) causing them to vibrate in a passive and sustained fashion (see "myoelastic-aerodynamic" theory; Titze, 1994). These vibrations create acoustic energy across a wide range of frequencies. When vocal fold vibration is periodic, harmonic vibration modes give rise to sounds that are rich in harmonic spectra. F_0 is the lowest frequency of such spectra and is primarily determined by the length and mass of the vocal folds, as well as the tension across them (Taylor & Reby 2010). The acoustic vibrations produced by the vocal folds travel through the supralaryngeal vocal tract, which acts as a filter that attenuates the amplitude of some frequencies and passes others (which ones depends on the shape of the vocal tract, which can be manipulated by, e.g., moving your tongue). The spectral peaks imparted on source spectra by the vocal tract filter are called "formants" (Fitch 1997, Fitch, 2000, Taylor & Reby 2010). Whereas F_0 is primarily determined by the physical characteristics of the source alone, F_{dom} – defined as the frequency with the highest amplitude in the spectrum of a call (Fitch 2002) – is determined by a complex interaction between both source and filter characteristics. Together with the fact that body size is tightly correlated with the dimensions of the vocal system (e.g., vocal fold length and mass, vocal tract length; Fitch 2000, Gingras et al. 2013), the details of source-filter theory offer an explanation of why the vocalizations of larger animals have relatively lower F_{0s} and F_{doms} than the vocalizations of smaller animals.

In this thesis, the relationship between body size and vocalization frequency was investigated in an unprecedented diversity of mammalian species: 2 orders, 18 families, and 90 species, ranging in length from ~15cm to ~230cm, and mass from ~113g to ~200kg. Whereas negative correlations between body size and vocalization frequency have been shown in anurans (Gingras et al. 2013, Ryan 1988), birds (Ryan & Brenowitz 1985), and nonhuman primates (Hauser 1993), much less is known about other vertebrate orders. Hence this thesis provides novel insight into carnivore

bioacoustics and also greatly expands what has been done with primates. I will specifically examine the following four hypotheses:

H_1: The negative correlation between body size and F_0/F_{dom} found by Hauser for primates, will be maintained for carnivores

H_2: Body length will be a better predictor of F_0/F_{dom} than body mass.

H_3: Minimum F_0 will be more strongly correlated with body size than mean F_0

H_4: The correlation between body size and F_0/F_{dom} will be stronger across families than within families.

2. Material and Methods

For this study two mammalian orders were chosen for analysis: primates and carnivores. The carnivores were represented by 43 species from 10 families (out of 16 extant families). The primates were represented by 47 species from 8 families (out of 16 extant families).

2.1 Body Length Data

For each species, head-to-torso body length was obtained from volumes 1 ("Carnivores") and 3 ("Primates") of the recently published "Handbook of the Mammals of the World" (Wilson; 2009, 2013). The two exceptions were the California sea lion (*Zalophus californianus*) and the humans, which were not covered in these volumes and were thus obtained from "The New Encyclopedia of Mammals" MacDonald (2001) and Bogin & Varela-Silva (2010) respectively (see Appendix 1 for further details on the human data). For 29 carnivore species (out of 43) and 18 (out of 46) primate species, minimum and maximum length values were reported in these sources and means were calculated as the averages of these values. For the remaining 14 carnivore species and 27 (of the 29) remaining primate species, minimum and maximum length values were reported separately for males and females. In these cases, means were first calculated as the average of sex specific minimums and maximums and then averaged again to yield an overall value for the species. For the remaining 1 primate species (Black-and-white ruffed lemur, *Varecia variegata*), only mean body length data was available. Wherever possible, separate data for minimums and maximums was retained alongside means to provide range data in plots of body size vs. vocalization frequency (see Results).

2.2 Body Mass Data

Body mass data was also obtained from volumes 1 ("Carnivores") and 3 ("Primates") of the "Handbook of the Mammals of the World" (Wilson; 2009, 2013). Again, two exceptions were the California sea lion (*Zalophus californianus*) and the humans, obtained from "The New Encyclopedia of Mammals" MacDonald (2001) and McDowell et al. (2008) respectively. For 20 (out of 43) carnivore species and 8 (out

of 47) primate species, minimum and maximum body mass values were reported and means were calculated as the averages of these values. For 22 (of the 23) remaining carnivore species and 37 (of the 39) remaining primate species, mass data was available for males and females separately. In these cases, the mean male and female values were again averaged to yield an overall value for the species. For the remaining 1 carnivore species and the two remaining primate species, only mean body mass data could be obtained. Wherever possible, separate data for minimums and maximums has been retained alongside means for use in plotting (see Results).

2.3 Vocalization Data

Recordings of vocalizations from each carnivore and primate species considered here (except humans) were collected from commercially available CD compilations (Bouchain & Gautier 1995, Dingler & Frommolt 2010, 2011; Emmons et al. 1997; Gautier-Hion, n.d.; Delta Music Inc. 1993; Ludwig 1973; Pott & Roché 1999; Ried & Gillard 1997; Roché 1994) and the "Tierstimmenarchiv" at the German "Museum für Naturkunde" in Berlin. Human vocalization data was calculated based on a corpus of speech collected and described in Han et al. (2011; see Appendix 2 for further information). A total of 759 recordings of carnivore vocalizations and 533 recordings of primate vocalizations were initially obtained, but only a subset was selected for further analysis (see Appendix 3). Recordings were excluded if: (1) the signal-to-noise ratio was too low to permit a meaningful analysis of acoustic parameters; (2) information about the recording indicated that the vocalizing animal was not an adult; (3) it was difficult to distinguish between different species in the recording; or (4) calls from multiple individuals overlapped. Because of the small number of species where both male and female calls were available (or where no gender information was specified), no differentiation between genders was made for the vocalization data. The final vocalization subset consisted of 175 recordings (97 for carnivores and 78 for primates). 45 of these recordings came from CDs (24 for carnivores, 21 for primates), whereas the remaining 130 came from the Tierstimmenarchiv (73 for carnivores, 57 for primates). All recordings were in WAV format (sampling rate = 44100 Hz, bit-depth = 32)

Figure 1 shows the time-domain signal and spectrogram of part of a recording from the final subset (top panel). As can be seen by eye and could be heard by ear, the

recording consists of two temporally contiguous bouts of vocalization with different acoustic structure. To simplify the following acoustic analyses, each bout (or "call") was cut out and saved by itself (Figure 1, bottom panels). If two calls had similar acoustic structure, they were saved together in one wav-file. This procedure resulted in 1-5 calls for each species.

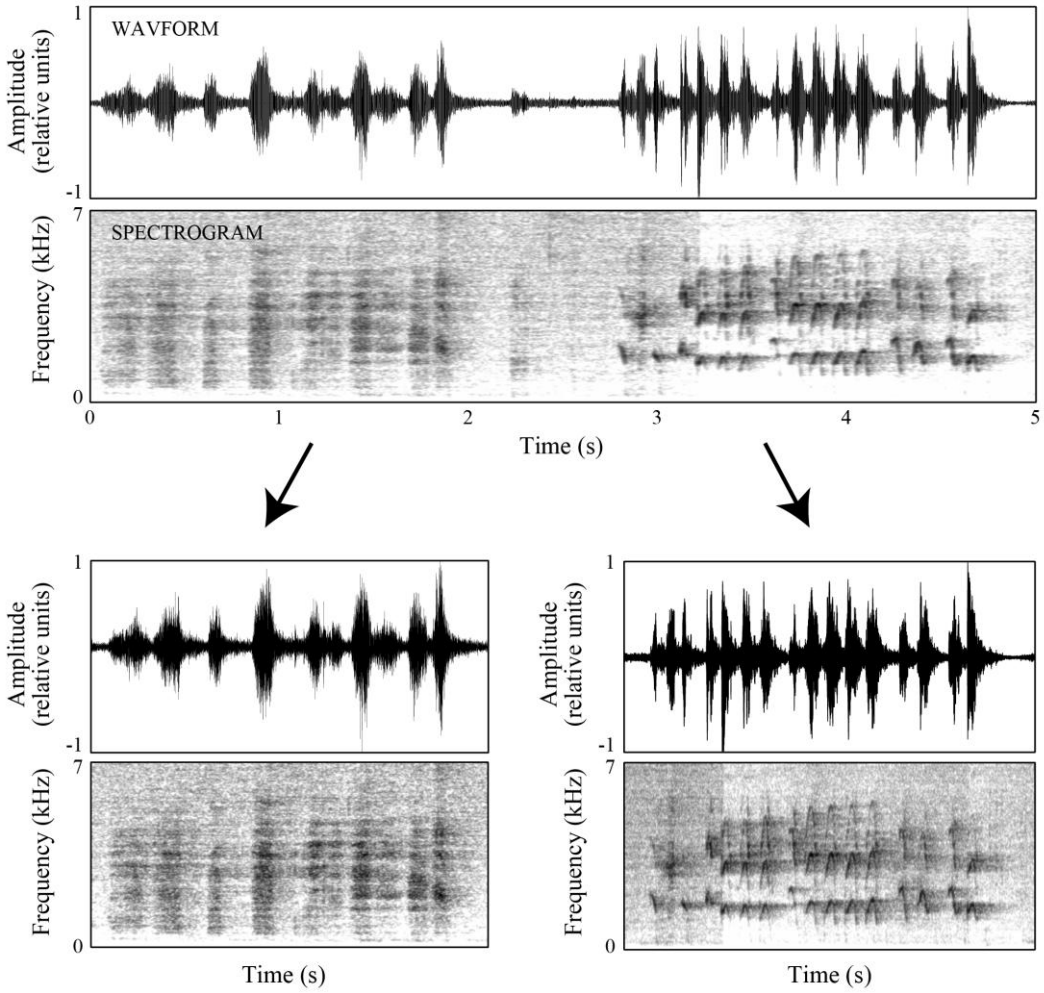

Figure 1. Example of how recordings were cut into calls. Each panel shows the time-domain signal and spectrogram of part of a recording (a Red panda; *Ailurus fulgens*; Dingler & Frommolt, 2011). The top panel shows a continuous part of the original recording that was separated into two calls (bottom panels) for acoustic analysis in this study.

2.4 Call Analysis

For each call I attempted to extract a dominant frequency (F_{dom}) and, if present, a fundamental frequency (F_0) using Praat (Version 5.3.48, Boersma & Weenik, 2013).

The first step in this analysis was to visually inspect the spectrogram to determine if a call possessed harmonics. This involved adjusting the spectrogram settings in Praat for each call (i.e., "View range", "Window length", and "Dynamic range"). After visual inspection, F_{dom} was measured by selecting the whole call in the time domain, calculating a spectrum using the "View spectral slice" function in Praat, and recording the frequency with the highest amplitude (Figure 2A). In a few cases the background noise in a recording was more powerful than the call itself (i.e., exhibiting a higher peak in the spectrum), but was nonetheless sufficiently different in terms of spectra to be excluded. In these cases, the highest peak corresponding to the call was selected rather than the highest overall peak. If a call possessed visible harmonics, further steps were taken to calculate an F_0 value. This was done by first adjusting the pitch settings in Praat (e.g., "Pitch range") until the pitch contour drawn by Praat matched with the F_0 identified visually in the spectrogram (Figure 2B), and second, selecting the whole call and using the functions "Get pitch", "Get minimum pitch" and "Get maximum pitch" to extract mean, minimum (min), and maximum (max) F_0 values respectively. In some cases (~2% of those calls that possessed visible harmonics), the F_0 contour drawn by Praat could not be made to fit with the visually identified F_0. In these cases F_0 measurement was done manually by magnifying the relevant part of the time-domain signal, measuring the average fundamental repetition period, and calculating the frequency as the inverse of this period.

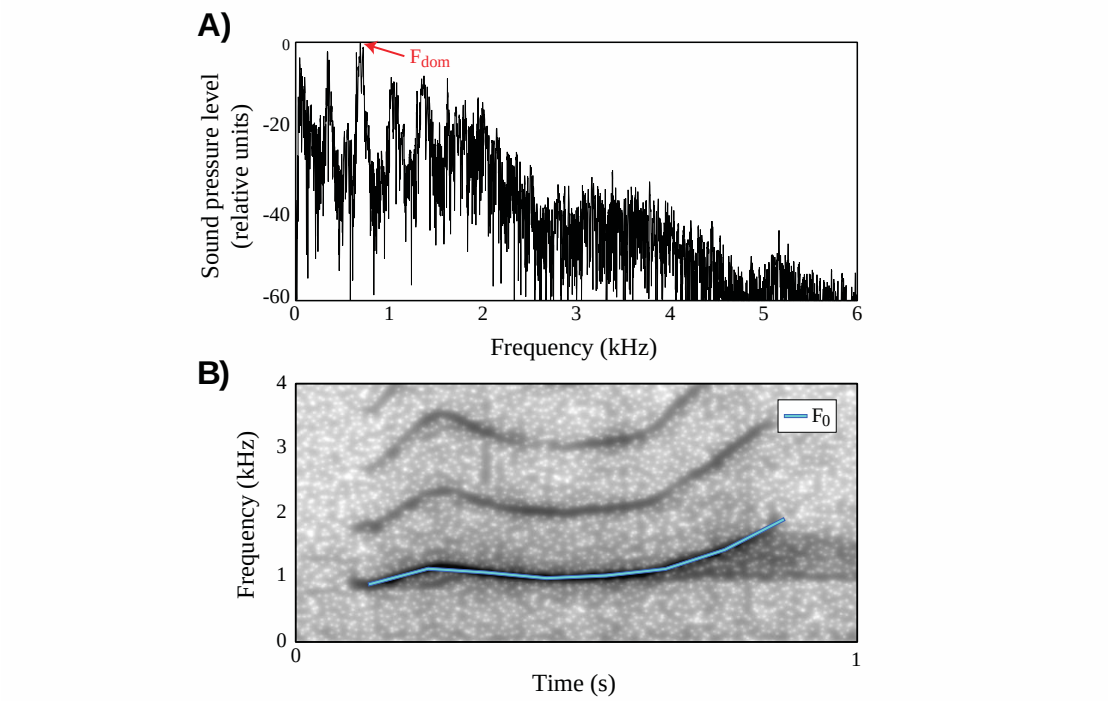

Figure 2. Measurement of dominant and fundamental frequency. (A) The spectrum of a Lar gibbon (*Hylobates lar*; Tierstimmenarchiv) call with a red arrow pointing to the dominant frequency (F_{dom}; in this case the peak with the highest amplitude in the spectrum). (B) The spectrogram of an ocelot (*Leopardus pardalis*; Tierstimmenarchiv) call with visible harmonics (horizontal dark bands) and a clear fundamental frequency (F_0). The blue line shows the F_0 contour drawn by Praat after adjustment of the pitch settings.

All measured data were collected in an Excel spreadsheet and mean values for F_{dom} and F_0 were calculated across calls for each species. F_{dom} was present and measurable in all 97 carnivore recordings and all 78 primate recordings. F_0 was present and measurable in 73% of the carnivore recordings (71/97) and 67% of the primate recordings (52/78). It is important to note that the proportion of calls with measureable F_{0s} in this sample does not necessarily correspond to the real proportions of vocalizations with F_{0s} in the vocal repertoires of carnivores and primates.

2.5 Comparisons, Statistics, and Plotting

The following six relationships for carnivores and primates were examined: (1) mean body length vs. mean F_0; (2) mean body mass vs. mean F_0; (3) mean body length vs. min F_0; (4) mean body mass vs. min F_0; (5) mean body length vs. mean F_{dom}; and (6) mean body mass vs. mean F_{dom}. Before any comparisons, however, the distributions

for each of the examined variables were checked for normality using one-sample Kolmogorov-Smirnov tests in SPSS (Version 20.0; IBM Corporation, 2011). As some of the variables were not normally distributed, while others varied over 1-2 orders of magnitude, all variables were log-transformed ($\log_{10}$ [x]) prior to comparisons. Relationships were assessed by calculating linear regressions (after log-transformations), Pearson's r, and the coefficient of determination (r^2) in SPSS. Plots of log body size data vs. log acoustical data were made for carnivores and primates separately using Matlab (Version 2012a; The Mathworks Inc., 2012). Although a plot for each of the 12 comparisons (6 for carnivores, 6 for primates) was generated, only a subset is shown in the results (other plots are shown in Appendices 2 and 3).

2.6 Comparison of Correlations Within and Across Families

For each order, carnivores and primates, the two families represented by the most species in our sample were chosen for an analysis of correlation strength within families compared to across families. For carnivores, these families were Canidae (n= 7 for F_0; n= 9 for F_{dom}) and Felidae (n= 15 for F_0; n= 15 for F_{dom}), and for primates, were Callitrichidae (n= 10 for F_0; n= 10 for F_{dom}) and Cercopithecidae (n= 12 for F_0; n= 17 for F_{dom}). For each of these families, acoustic correlations with body size for the n species within the family were compared to the correlation for a random selection of n species from all other families. In order to reduce the chance that the random selection resulted in a biased sample, the "other families" calculations were always repeated 20 times to obtain an average correlation value for comparison to the within family correlation.

3. Results

The analyses revealed negative correlations between body size and acoustic parameters for all comparisons (ps < 0.001; Table 1). Overall, correlations were stronger for primates than for carnivores, indicating a closer relationship between body size and vocalization frequency in primates than in carnivores. Correlations were also generally stronger for comparisons that used body length rather than body mass. The only exceptions were the comparisons of body size and F_0 (mean and min) for carnivores. But even in these cases, the differences in Pearson's r were small (0.004 and 0.041 respectively; see Table 1). Accordingly, the body size comparisons presented in this section focus on body length rather than mass (see Appendix 4 for body mass vs. F_0/F_{dom} plots). Finally, in almost all cases, comparisons using min F_0 resulted in stronger correlations than mean F_0 (the only exception was the comparison with body mass in primates, where Pearson's r for body mass vs. mean F_0 was 0.003 higher than for body mass vs. min F_0). Accordingly, the F_0 comparisons presented in this section focus on min F_0 rather than mean F_0 (see Appendix 5 for mean F_0 plots).

Table 1. Pearson's r and the coefficient of determination (r^2) for all log body size and log frequency comparisons in (A) carnivores and (B) primates. P-values for all comparisons were < 0.001.

A)

Carnivores	**Pearson's r**	**r squared (r^2)**
mean F_{dom}/ length	- 0.632	0.399
mean F_{dom}/ mass	- 0.606	0.367
min F_0/ length	- 0.639	0.409
min F_0/ mass	- 0.68	0.462
mean F_0/ length	- 0.625	0.39
mean F_0/ mass	- 0.629	0.395

B)

Primates	**Pearson's r**	**r squared (r^2)**
mean F_{dom}/ length	- 0.725	0.526
mean F_{dom}/ mass	- 0.708	0.502
min F_0/ length	- 0.745	0.555
min F_0/ mass	- 0.739	0.546
mean F_0/ length	- 0.742	0.551
mean F_0/ mass	- 0.742	0.511

3.1 Body Size and Vocalization Frequency in Carnivores

Figure 3 shows the relationship between mean body length and mean F_{dom} for carnivores. Pearson's r = -0.632 and r^2 = 0.399, showing that as body length increases, F_{dom} generally decreases and that variation in body length accounts for ~40% of the variance in F_{dom}. The smallest species in our sample of carnivores belonged to the families Mustelidae and Herpestidae. The least weasel (*Mustela nivalis*; Mustelidae) is the smallest carnivore species, with a mean body length of only 18.7 cm. In our sample, it had a F_{dom} of 3000 Hz. The next smallest carnivore in our sample, the common dwarf mongoose (*Helogale parvula*; Herperstidae; mean body length= 20.02 cm), had an even higher F_{dom} (8778 Hz; the highest among our carnivores). Of the Mustelids and Herpestids, the stoat (*Mustela erminea*; Mustelidae) had the lowest F_{dom} (575 Hz) relative to its body length (26.5 cm) and was thus an outlier compared to the other species in these families (see Figure 3). All of the Procyonids, e.g., the kinkajou (*Potos flavus*), were above the regression line and therefore all had higher F_{doms} than predicted based on body length. Canines and Felids were represented by the most species (n = 9 and 15 respectively) in our sample and are widely scattered throughout Figure 3. Ursids are among the largest carnivore species, and the polar bear (*Ursus maritimus*) was the largest species in the sample (230 cm; F_{dom} = 303 Hz). The polar bear did not, however, have the lowest F_{dom}, which belonged to the slightly smaller lion (*Pathera leo*; Felidae; 193 cm; F_{dom} of 158.5 Hz). The families of Ailuridae, Hyaenidae, Otariidae and Viverridae are each represented by only one species. Thus, the data included for these families here can only give a general impression of where other family members might be located. This is particularly true for the Otariids and the Viverrids, represented here by the California sea lion (*Zalophus californianus*) and the binturong (*Arctictis binturong*), as both of these families contain a diverse array of species (15 and 38 respectively). Hyaenidae, represented here by the striped hyena (*Hyaena hyaena*), is currently comprised of only four, largely similar, species, suggesting that the present data are likely to be more representative. Finally, Ailuridae is comprised of just one species (the red panda; *Ailurus fulgens*), which is thus necessarily included here.

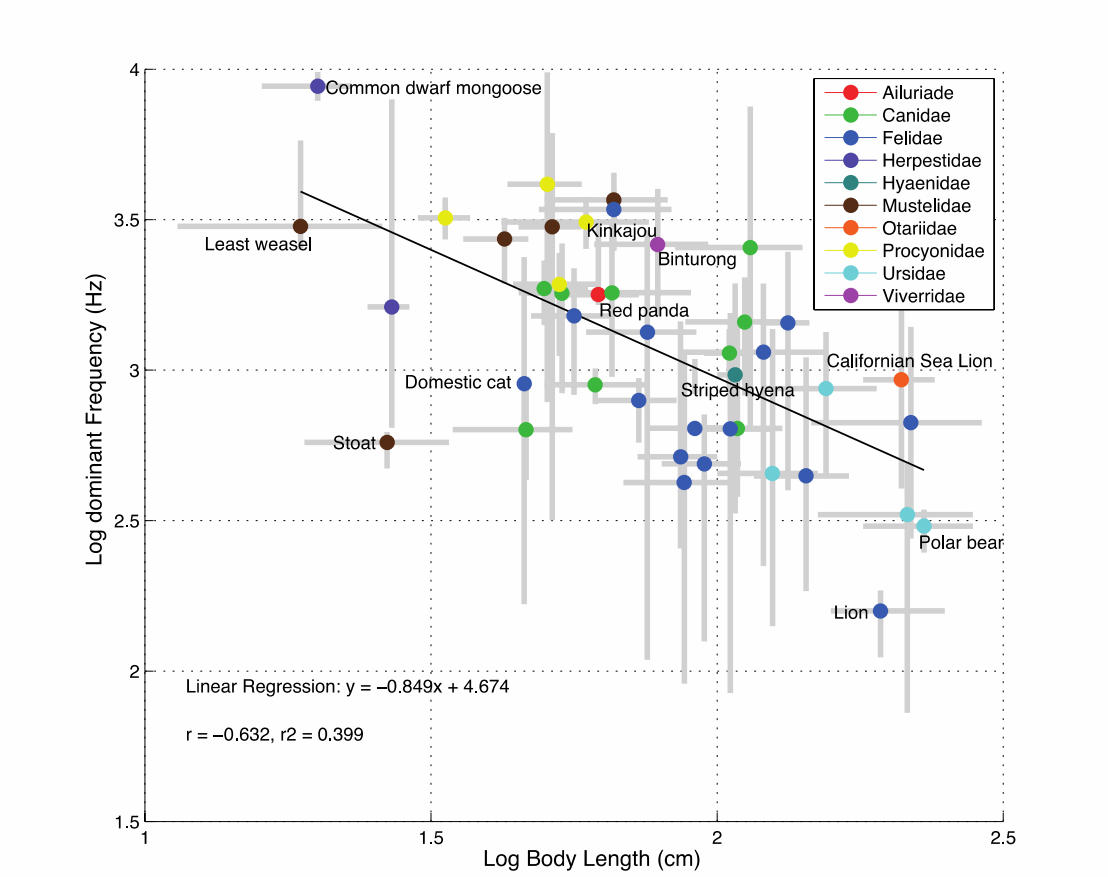

Figure 3. Log body length vs. log dominant frequency for carnivores. Each data point represents the mean body length and dominant frequency for one species in our sample. Species of the same family have the same color. Vertical gray bars represent ranges for dominant frequency (minimum to maximum; where available), and horizontal gray bars represent ranges for body length (minimum to maximum; where available). The regression line is drawn in black and the formula is given at the lower left along with Pearson's r and the coefficient of determination. Common names are given for species referred to in the text.

Figure 4 shows the relationship between mean body length and min F_0 for carnivores. Pearson's r = -0.639, r^2 = 0.409, showing essentially the same relationship as observed for F_{dom}, but marginally better. Major differences from the body length vs. F_{dom} comparison (see Figure 3) include that the Canids were mostly above the regression line (except for the bat-eared fox [*Otocyon megalotis*], for which we obtained an exceptionally low min F_0 of 39.5 Hz, despite its being among the smaller Canids in our sample [53.58 cm]), and the felids were mostly distributed on or below the regression line (possibly due to a specialized mechanism that allows this clade to purr at very low frequencies; see Section 4.4). The Felid with the highest min F_0 was the jaguarundi (*Puma yagouaroundi*; 1938 Hz), and the Felid with the lowest min F_0

was the jaguar (*Panthera onca*; 30.71 Hz). The jaguar min F_0 was even lower than the Bengal tiger (*Panthera tigris tigris*; 63.58 Hz), which was the largest Felid species (218 cm) with a measurable min F_0. These large differences between Felids might be attributable to the fact that our sample of vocalizations included low purrs for some species (e.g., the jaguar and tiger) but not others (e.g., the jaguarondi).

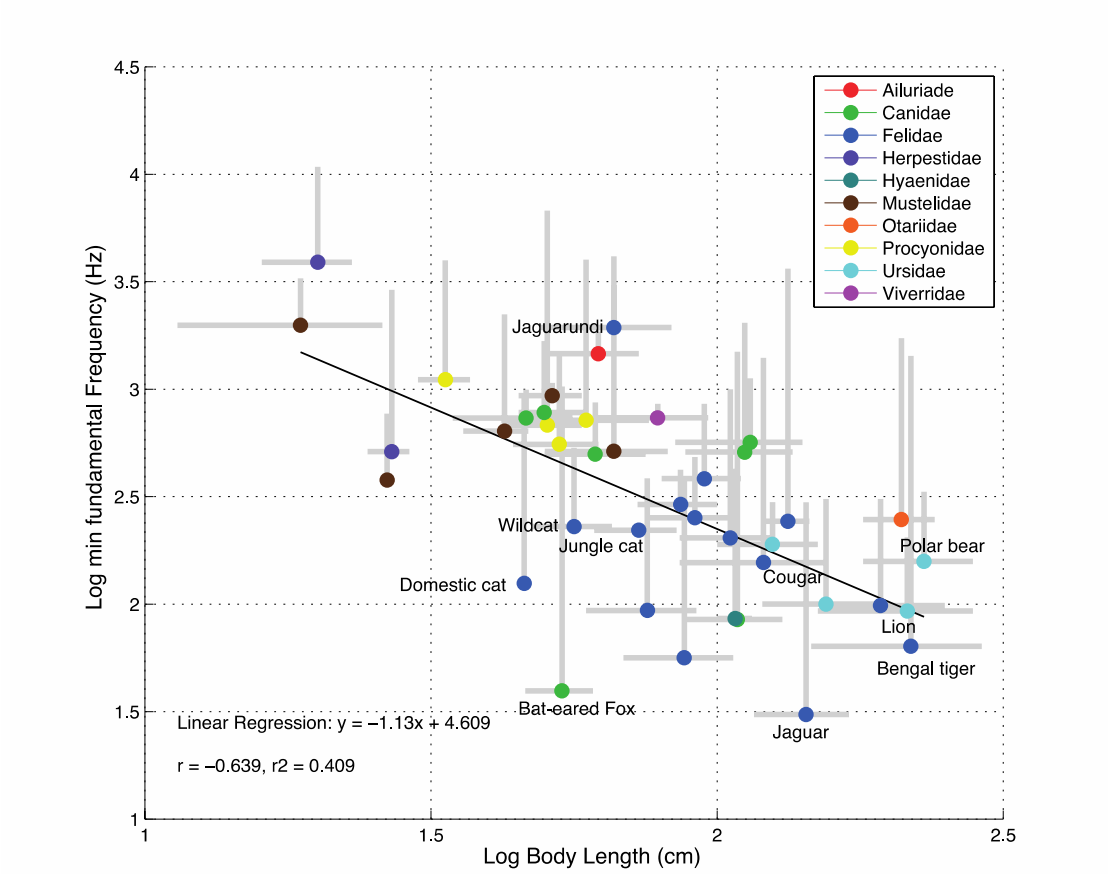

Figure 4. Log body length vs. log minimum fundamental frequency for carnivores. Format is the same as Figure 3.

3.2 Body Size and Vocalization Frequency in Primates

Figure 5 shows the relationship between mean body length and F_{dom} in primates. Pearson's r = -0.725 and r^2 = 0.526, showing that as with carnivores, body length increases as F_{dom} decreases. However, the relationship was stronger for primates, with variation in body length accounting for ~53% of the variance in F_{dom}. The smallest primate species in our sample belonged to the families Callitrichidae and Cercopithecidae (these families were also the best represented here; n = 10 and 17

respectively). The Pygmy marmoset (*Cebuella pygmaea*) was the smallest primate in our sample (14cm) and had a F_{dom} of 8804.6 Hz. The slightly larger silvery marmoset (*Mico argentatus*) was the fourth smallest primate (21 cm) overall, but had the highest F_{dom} (10506 Hz). The members of the family Cebidae were all above the regression line and therefore had higher F_{doms} than predicted based on body length. Within the Cebidae family, the squirrel monkey (*Saimiri sciureus*) was the smallest (30.25 cm) and also had the highest F_{dom} (7819.65 Hz). Members of the family Lemuridae are widely scattered throughout Figure 5 and exhibited considerable variation in F_{dom}. The mongoose lemur (*Eulemur mongoz*) had the lowest F_{dom} (278 Hz) relative to body length (32.5 cm), whereas the ring-tailed lemur (*Lemur catta*) had the highest F_{dom} (7322.25 Hz) relative to body length (42.5 cm). Members of the family Hominidae are the largest primates, and the western gorilla (*Gorilla gorilla*) was the largest species in the sample (105 cm). It did not, however, have the lowest F_{dom}, which belonged to the much smaller black howler monkey (*Alouatta caraya*; Atelidae; F_{dom} = 273.77 Hz, 56.25 cm).

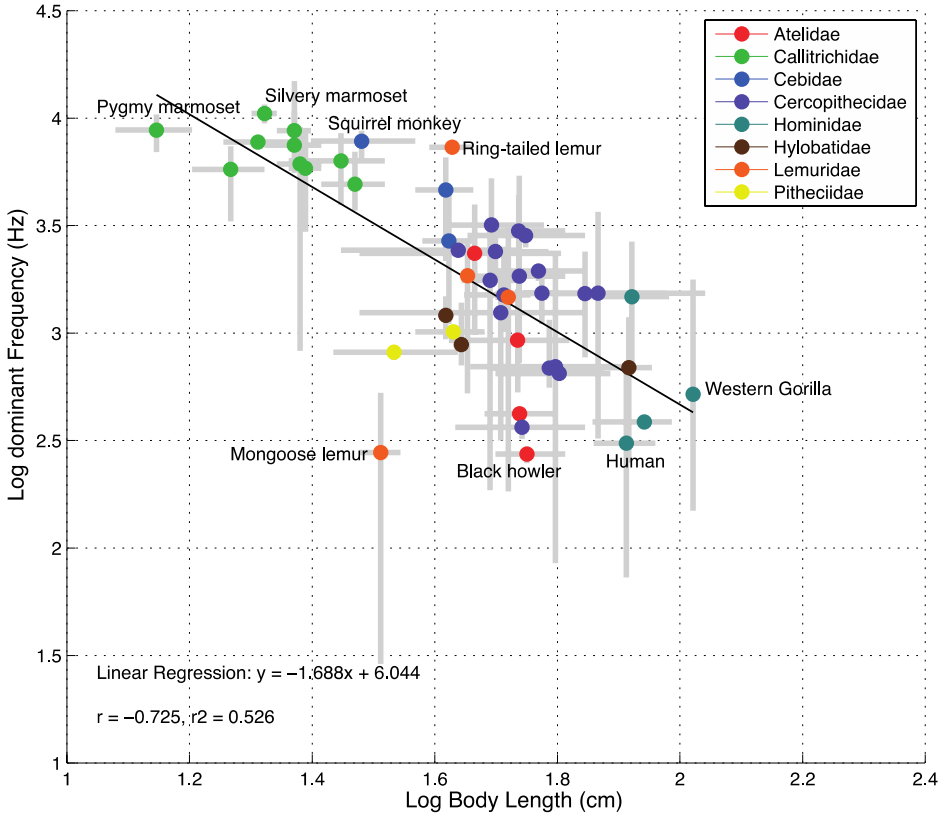

Figure 5. Log body length vs. log dominant frequency in primates. Format is the same as Figure 3.

Figure 6 shows the relationship between mean body length and min F_0 for primates. Pearson's r = -0.745, r^2 = 0.555, showing essentially the same relationship as observed for F_{dom}, but (as with carnivores) slightly better. Members of the family Cercopithecidae are fairly scattered throughout Figure 6. Even though many of the Cercopithecids were of a similar size, they exhibited considerable differences in min F_0. For example, while both De Brazza's monkey (*Cercopithecus neglectus*) and the Diana monkey (*Cercopithecus diana*) had a body length of ~49 cm, their min F_{0s} were 92 Hz and 2444 Hz respectively. This difference may be explained in part as a limitation of the vocalization database, which only included low grunts and clicks for De Brazza's monkey and high screams for the Diana monkey. Despite being the largest species with a measureable F_0 in our sample, the Chimpanzee (*Pan troglodytes*; 83.5 cm; 956 Hz) was not among the primates with the lowest min F_0 values. Instead, the lowest min F_{0s} in our sample belonged to smaller species, such as the Drill (*Mandrillus leucophaeus*; Cercopithecidae; 62.63 cm; 87 Hz) and other Cercopithecidae. The only other Hominid with a measurable F_0 was the human (*Homo sapiens;* 81.75 cm; 180 Hz), which despite being comparable in size to the chimpanzee, had a much lower min F_0. Although chimpanzees may in fact have higher F_{0s} than humans, the magnitude of this difference (776 Hz) suggests another potential limitation of our vocalization database. The siamang (*Symphalangus syndactylus*; Hylobatidae) was also among the largest primates in our sample (82.5 cm; nearly twice as long as the other Hylobatidae examined here) and also had a low min F_0. The red-bellied titi (*Callicebus moloch*) has a low min F_0 (198 Hz) relative to its body length (34 cm) and thus is an outlier compared to the other species within the dataset.

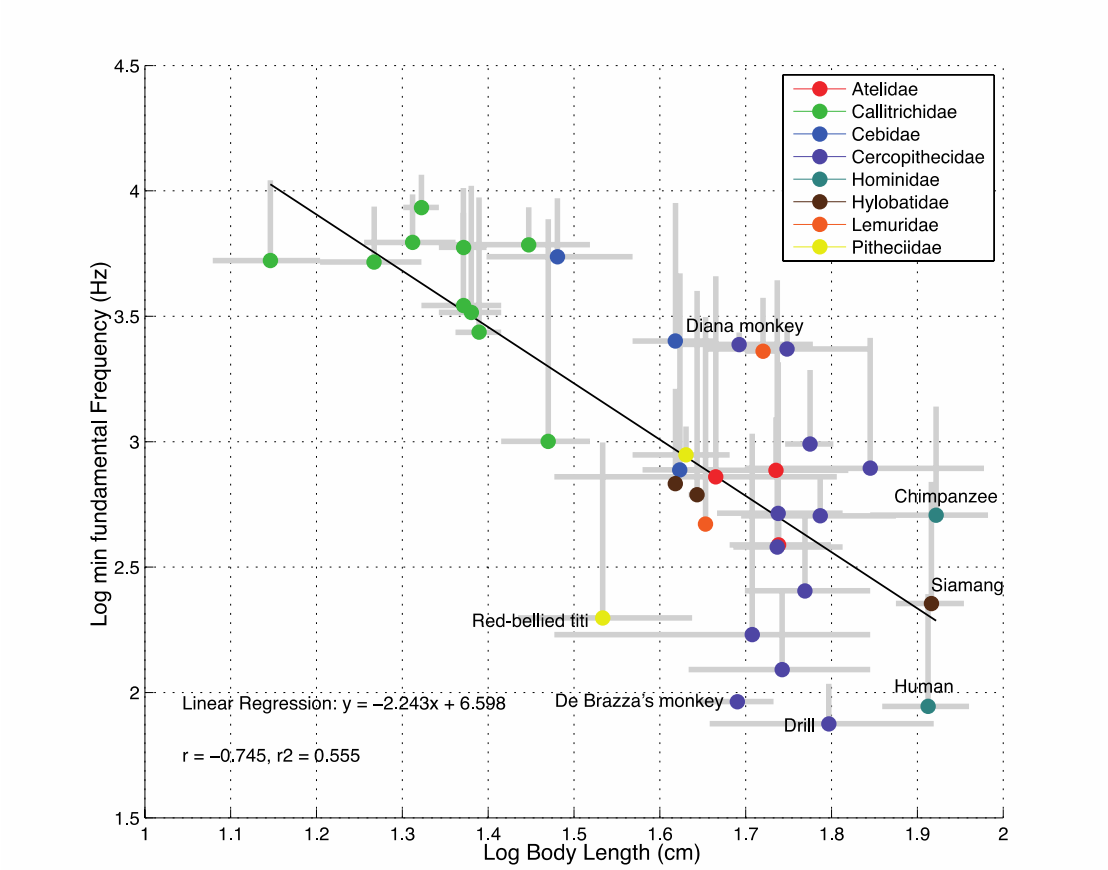

Figure 6. Log body length vs. minimum fundamental frequency for primates. Format is the same as Figure 3.

3.3 Comparison of Correlations Within and Across Families

Table 2A shows the correlations within and across families for Canids and Felids. For all of the families considered, correlations across families were stronger than correlations within. This was particularly true for Canids, where the average Pearson's r values for the across family comparisons (-0.65 for length vs. F_{dom} and -0.71 for length vs. min F_0) were considerably larger than the almost non-existent Pearson's r values for within family comparisons (-0.092 for length vs. F_{dom} and -0.076 min F_0). The story is similar for the Felids, but with much smaller differences between within and across family comparisons. None of the within family correlations attained statistical significance at $p < 0.05$, probably reflecting a combination of weak relationships and small sample sizes. Some of the across family comparisons, however, did reach significant at $p < 0.05$, particular when the sample size was relatively large (see Felids in Table 2A).

Table 2B shows the correlation within and across families for Callitrichids and Cercopithecids. Overall, the correlations across families were stronger than the correlations within families. The differences in across vs. within family comparisons were larger for Cercopithecidae than Callitrichids. For Cercopithecidae, the average Pearson's r values for the across family comparisons (-0.53 for length vs. F_{dom} and -0.75 for length vs. min F_0) were considerably larger than those for the within family comparisons (-0.39 for length vs. F_{dom} and 0.054 for length vs. min F_0). These large differences can be explained by the fact that Cercopithecidae had a lot of variation in min F_0 that was not related to body size (see Figure 6). Callitrichids, on the other hand, had much smaller differences between within and across family comparisons. Accordingly, most of the variation in F_0 among Callitrichids was related to differences in body size (see Table 2B and Figure 6). The across family correlations for body length vs. min F_0 attained significance at $p < 0.05$ for both families.

Table 2. Statistics for the within and across families comparisons. Pearson's r, r^2 and the p-value are given for mean body length vs. min F_0 and mean body length vs. F_{dom} within and across families for the (A) carnivores (Canidae and Felidae), and (B) primates (Callitrichidae and Cercopithecidae). See section 2.6 for further description of how the within and across family statistics were calculated.

A)

		Canidae		**Felidae**	
Carnivores		**(**n= 7 for F_0, n = 9 for F_{dom})		**(**n= 15 for F_0, n= 15 for F_{dom})	
		Within family	**Across family**	**Within family**	**Across family**
Length vs. F_{dom}	**Pearson's r**	-0.092	-0.653	-0.515	-0.607
	r^2	0.009	0.469	0.265	0.408
	p	0.813	0.116	0.049	0.078
Length vs. min F_0	**Pearson's r**	-0.076	-0.710	-0.428	-0.633
	r^2	0.006	0.527	0.183	0.416
	p	0.872	0.101	0.111	0.027

B)

Primates		**Callitrichidae** ($n = 10$ for F_0, $n = 10$ for F_{dom})		**Cercopithecidae** ($n = 12$ for F_0, $n = 17$ for F_{dom})	
		Within family	**Across family**	**Within family**	**Across family**
Length vs. F_{dom}	**Pearson's r**	-0.52	-0.68	-0.389	-0.531
	r^2	0.271	0.552	0.151	0.346
	p	0.123	0.139	0.123	0.145
Length vs. min F_0	**Pearson's r**	-0.5	-0.739	0.054	-0.747
	r^2	0.25	0.562	0.003	0.568
	p	0.141	0.032	0.868	0.013

4. Discussion

4.1 Summary

In many species, body size plays a crucial role in mate choice (Wagner 1992), reproductive success and territory defense (Modig 1996). Therefore, the ability to make predictions about body size using auditory cues provides an animal with evolutionary advantages in selecting good mates and reducing the risks of combat (Fitch & Hauser 2002, Morton 1977). The aim of this thesis was to investigate the relationship between body size and specific acoustic properties of vocalization. Negative correlations between body length/mass and F_0/F_{dom} were found for samples of 47 primate species and 43 carnivore species. These correlations were generally strong, ranging from -0.71 to -0.76 in primates and -0.61 to -0.68 in carnivores ($ps < 0.001$; see Table 1). Body length was a better predictor of min F_0 and F_{dom} in primates and F_{dom} in carnivores (see Table 1). In comparisons between body size and fundamental frequency, min F_0 was always a better predictor than mean F_0 (see Table 1). Finally, for a sample of four biological families (Canidae Fieldae, Callitrichidae, and Cercopithecidae) correlations between body size and acoustic parameters were always stronger across families than within families (see Table 2).

4.2 Limitations

There are a variety of factors that may have limited the accuracy of the data collected to represent body size and the acoustic parameters of vocalization. First, the measurements of body length might not have been performed in a consistent fashion across the studies used as source material for the "Handbook of the Mammals of the World", despite the fact that body length was always reported as "head-body length" in the encyclopedia. Second, many of the measurements are likely to have come from samples that were not representative of the corresponding populations (e.g., because they were zoo animals, or because the sample sizes were too small). Third, sex differentiation was neglected, despite the fact that a number of species are known to exhibit sexual dimorphism in vocal behavior (e.g., members of the genus *Alouatta*). Four, only a limited number of vocalization recordings were available, and in many cases are unlikely to have covered the actual vocal ranges of each species. Five, some families were over-represented in our sample (e.g., Felidae and Callitrichidae)

whereas others were under-represented (e.g., Viverridae and Pithicidae) or not included (e.g., Phocidae and Galigadae). Given such potentially flawed data, the fact that we were able to consistently demonstrate strong and significant correlations reflects the strength of the underlying relationships.

4.3 Phylogenetic Diversity and Prediction

Morton (1977) and Hauser (1993) argue that the relationship between body size and acoustic parameters can be understood in terms of the physics of vocal production. Assuming that the size of an animal's vocal organs is positively correlated with the size of their body, it follows that larger animals (with longer or more massive vocal folds and longer vocal tracts) will be capable of producing vocalizations with lower frequency content. Despite the appeal of this simple and clear hypothesis, it is worth noting that while Hauser (1993) found a strong negative correlation between body mass and frequency in nonhuman primates, McComb (1991) failed to find a similar correlation in red deer, and Pisanski et al. (2014) failed to find it in humans. Thus, while the hypothesis clearly holds for some comparisons it holds less well for others.

One factor in determining the strength of observed relationships between body size and acoustic parameters appears to be the phylogenetic diversity of the sample. When comparisons are made across species, the resulting correlations are typically strong (Ryan & Brenowitz 1985; Hauser, 1993; and Gingras et al. 2013; see also Results). But when comparisons are more specific (e.g., within species), the resulting correlations tend to be much weaker (Hauser 1993). Supporting this possibility, the correlations I observed within families were always smaller than the correlations across families (see Table 2 and Section 4.7 below). Accordingly, a principle of acoustic allometry seems to be that better predictions result from greater phylogenetic diversity.

4.4 Variation in Vocal Anatomy

What accounts for the considerable variation in vocal acoustics not explained by variation in body size? In some species, the anatomical characteristics of vocal organs have been shown to vary somewhat independently of body size (e.g., Howler monkeys). Below, I list a number of modifications in vocal anatomy that are likely to

affect the acoustical parameters of vocalization and may be independent of body size. Modifications to the source (i.e., the vocal folds) are considered first, and modifications of the filter (i.e., the supralaryengeal vocal tract) are considered second.

The vocal folds. Members of the Felid genus *Pathera* (lions, tigers, leopards, and jaguars) have very large vocal folds with "fleshy pads" that play a role in the low-pitched roars (Hast 1989, Peters 2006). Accordingly, many of these species, e.g., the lion, tiger and jaguar, had F_{0s} that fell well below the regression lines (see Figure 4). Other felids, e.g., of the genus *Puma* (cougars and jaguarundis) or *Felis* (wildcats, jungle cats, and domestic cats), lack these morphological specializations and have higher F_{0s} (see Figure 4). Further, Felids possess a mechanism for neurally driven vocal fold vibration at low F_{0s} (e.g., as heard in purring) that may also explain why many of the Felids in our sample had low F_{0s} (Herbst et al. 2012, Frazer Sissom et al. 1991).

The vocal folds are attached to a cartilaginous larynx that is quite flexible. As the larynx is not closely surrounded by bony structures, it is able to move around at the top of the trachea and can grow independently of other body parts (Fitch 2000, Fitch & Hauser 2002). Conspicuous examples of independent laryngeal growth (hypertrophy of the larynx) occur during puberty in male humans and howler monkeys (*Alouatta*). During puberty in these species, the enlargement of the larynx is disproportionately greater relative to that of the body overall (Fitch & Hauser 2002, Kelemen & Sade 1960). In our present sample, humans had the lowest min F_0 of all primates despite being smaller than other Hominids (Figure 6). This aberration might be explained by hypertrophy of the larynx in human males, and may also be a reason why Pisanski et al. (2014) failed to show a correlation between body size and speaking fundamental frequency in humans. Our sample also included two *Alouatta* species: the Venezuelan red howler (*Alouatta seniculus*) and the black howler (*Alouatta caraya*). The black howler had the lowest F_{dom} (273.77 Hz) despite being of average size (56.25 cm; see Figure 5).

The vocal tract. Air sacs opening off the vocal tract are also likely to influence the acoustic parameters of vocalizations. Species belonging to the genera *Cercopithecus* and *Alouatta* possess a "subhyoid air sac" that inflates into a cavity protected by an enlarged hyoid bone. Since the subhyoid air sac inflates into an ossified chamber, it may act as a Helmholtz resonator (Fitch & Hauser 2002, Kelemen & Sade 1960, Taylor & Reby 2010). With the exception of humans, all Hominids possess a

"laryngeal air sac" that can be inflated by air coming from the lungs (Fitch 2000, Fitch & Hauser 2002). The laryngeal air sac is connected to the larynx through a channel that opens directly above the vocal folds. After the air sac is inflated, muscular deflation of the air sac could also affect the acoustic parameters of source vibration by altering local air pressure (Fitch 2000, Fitch & Hauser 2002). Thus, many of the primates in our sample are known to possess air sacs that could influence their acoustic parameters of their calls. Inspection of Figures 5 and 6 shows that many of the Hominids we examined (Orangutan, Western gorilla and Chimpanzee), as well as members of the genera *Cercopithecus* (Greater spot-nosed monkey, Sun-tailed monkey, De Brazza's monkey) and *Alouatta* (Black howler, Venezuelan red howler monkey) had particularly low F_{doms}, F_{0s}, or both.

Structures that can be described as "air sacs" are also found in carnivores. Some members of the family of Ursidae, for example, have "epipharyngeal pouches" that open into the pharyngeal cavity and might function to enlarge the resonating space within the vocal tract (Weissengruber et al. 2001). With the exception of the American black bear (*Ursus americanus*), all of the Ursids examined here had a F_{dom} value clearly below the regression line (see Figure 3), lower than expected based on body size.

Other factors. Peters (2006) highlights the diversity of calls and call types produced by different families of carnivores. This diversity might rely on sound sources other than the vocal folds (e.g., vibrating tissues that lie above the vocal folds in the larynx) and may partially explain why the observed acoustic correlations with body size were smaller for carnivores than for primates. Pinnipeds (Odobenids, Otariids, and Phocids), for example, are known to be capable of simultaneously producing two sounds with independent F_{0s} implicating the possible involvement of two independently vibrating sources (Peters 2006). In accordance with this possibility, two of the California sea lion calls in our sample consisted of portions with overlapping but different F_0 values (see Appendix 6).

Social structure is one potential factor that might drive the evolution of morphological adaptations in vocal organs. Robbins (2000) and Freeberg et al. (2012) argue that high social complexity is often associated with wide vocal repertoires. Robbins also emphasized the fact that carnivores exhibit a diversity of social structures, ranging from mostly solitary (e.g., Felids) to highly social (e.g., Canids). This diversity might

be another reason why smaller acoustic correlations with body size were observed for carnivores than for primates.

4.5 Differences in Correlations between Acoustic Parameters

Why were correlations between body size and F_0 stronger for min F_0 than mean F_0 (see Table 1)? Hauser (1993) examined differences in correlations with body mass between minimum and mean values of a parameter he called "repertoire frequency" (see Section 1), finding a stronger Pearson's r for mean values (r= 0.73) than for min values (r=0.57). This apparent difference between Hauser (1993) and the present study might be explained by the fact that mean and min values for repertoire frequency were presumably calculated over both F_0 and F_{dom} values (at least for some species), whereas the present comparisons of mean and min values were specific to F_0. It is also worth noting that whereas the differences between correlations with mean and min F_0 were quite small in the present study (Pearson's r for min F_0 correlations was only stronger by 0.014 for carnivores and 0.003 for primates), Hauser (1993) found a much larger difference in his study for repertoire frequency (0.24). This suggests that Hauser's inclusion of F_{dom} values in his calculations of repertoire frequency may have strongly influenced his results. One advantage of Hauser (1993) over the present study is that he included a greater diversity of call types (a minimum of five, vocalizations with different structure for each species he examined), analyzing a total of 474 calls. Even though a similar amount of primate calls was examined in the present study (n = 429, see Appendix 3), the overall diversity of the calls was lower, as there was no lower limit on the number of call types for each species. Therefore, it is likely that Hauser's acoustic data more fully represents the range of vocalizations produced by the species he examined.

The present study also showed slightly higher correlations for body length vs. min F_0 than for body length vs. F_{dom} (Pearson's r differed by 0.02 for primates, and 0.007 for carnivores; see Table 1). Despite the very small size of these differences, an explanation based on physical principles can be proposed. The minimum F_0 that an animal is capable of producing is principally constrained by the length and mass of the vocal folds when there is little or no muscular tension (Taylor & Reby 2010). F_{dom} is also physically constrained of course, but many additional factors are involved, including a complex interaction between the frequency of vocal fold vibration and the

shape of the vocal tract (Fitch 2002). Because the length and mass of the vocal folds is likely to be more closely related to body size than, for example, the amount of tension on the vocal folds and/or the shape of the vocal tract, correlations between body size and min F_0 are expected to be higher than correlations between body size and F_{dom}.

Although not considered here, formants are another important acoustic parameter of vocalizations that would be interesting to examine in future acoustic allometry studies. Formants are determined by the shape of the vocal tract, which is also closely connected to the body size. In general, variation in formant frequencies for a given species tends to be smaller than variation in F_0 or F_{dom}. Consequently, formant frequencies are often better predictors of body size than the parameters examined here (Fitch, 1997, Fitch & Hauser 2002). Unfortunately, a thorough analysis of formants was not possible in this data set because many calls lacked the quality to accurately identify formants.

4.6 Body Length versus Body Mass

Body length was a better predictor of min F_0 and F_{dom} in primates and F_{dom} in carnivores (in 3 out of 4 comparisons; see Table 1). This might be due to the fact laryngeal size is likely to be better correlated with body length than mass. The reason is that body mass is highly dependent on factors such as diet and population density, whereas length is less dependent on these factors (at least for animals that have completed developmental growth, like the adults considered here; Robinson & Redford 1986).

4.7 Comparison of Correlations Within and Across Families

Why are acoustic correlations with body size stronger across families than within families? Hauser (1993) found that in most nonhuman primate genera, species tend to have similar body mass and repertoire frequencies. But in some genera, e.g., *Macaca*, repertoire frequencies differed greatly across species, leading to poor acoustic correlations with body size with genera. Generalizing Hauser's findings to higher taxonomical units, I hypothesized that acoustic correlations with body size would be weaker within families than across families. The results of the within and across

family comparisons in Section 3.3 confirmed this hypothesis (see also Table 2). Thus, although F_0/F_{dom} appear to be good predictors of body size across taxonomical units, they may not work as well in samples with limited diversity.

One factor that can contribute to the diversity of vocalization frequencies within a taxonomical unit is if different groups live in different habitats. For example, Brown et al. (1995) argues that Cercopithecids living in different habitats (e.g., savanna and rainforest) have adapted the frequency content of their vocalizations to enable higher fidelity communication. Some species in our sample, like the hamadryas baboon (Papio hamadryas; min F_0 = 1824 Hz), live in semi desert areas or savannas, whereas other species, like the Drill (Mandrillus leucophaeus; min F_0 = 87 Hz), live in rainforests. Brown et al (1995) found that there is greater selection pressure to decrease the distortion of vocalizations in species that live in rainforests than in species that live in the savanna. This might be due to the fact that species that live in rainforests often do not have visual contact and therefore rely to a greater extent on high fidelity vocalizations. This difference in habitat may explain the considerable vocal differences between these two Cercopithidae species (i.e., the hamadryas baboon and the drill).

4.8 Conclusion

The results of this study show strong negative correlations between body size and acoustic parameters for primates and carnivores. These correlations were evident despite limitations on the accuracy of some of the anatomical and acoustic data used to calculate them. The reason these correlations are so robust is that the acoustic parameters of an animal's vocalizations are constrained by the size of its vocal organs, which are in turn tightly correlated with body size. It is thus possible to predict body size through acoustic parameters and vice versa. Acoustic correlations with body size were stronger for primates than carnivores, stronger for body length than body mass (with a few exceptions), and stronger for min F_0 than mean F_0. Further, I found that acoustic correlations with body size were stronger across families than within families. In conclusion, body size and the anatomy of vocal organs constrains vocalization and the evolution of acoustic signalling in carnivores and primates. Further questions concern whether acoustic correlations with body size

will also hold for other mammalian orders, and future work should examine the relationship between body size and the anatomy of vocal organs in more detail.

5. Abstract

Acoustic allometry is the study of the relation between an organism's body size and the acoustical parameters of its calling behavior (Fitch 2000, Gingras et al. 2013). A fundamental hypothesis in this field is that body size (indexed by length or mass) is negatively correlated with important acoustical parameters of vocalization (e.g., fundamental frequency [F_0] and dominant frequency [F_{dom}]; Morten, 1977; Hauser, 1993). The aim of this thesis is to examine this correlation across a large variety of primates and carnivores. The sample consists of 43 carnivore species (ranging in size from the least weasel [*Mustela nivalis*] to the polar bear [*Ursus maritimus*]) and 47 primate species (pygmy marmoset [*Cebuella pygmaea*] to western gorilla [*Gorilla gorilla*]), and therefore constitutes the largest and most diverse sample of species ever examined in an acoustic allometry study. Average body size data (head-to-torso length and mass) for each species was compiled from recently published sources (Wilson; 2009, 2013). Vocalizations were compiled from commercially available CDs and the Tierstimmenarchiv in Berlin and analyzed using Praat (Version 5.3.48, Boersma & Weenik, 2013). The negative correlation hypothesis was tested by examining the relationships between: (1) body size and F_0, and (2) body size and F_{dom}. In each case I also asked which representation of body size (length or mass) results in the strongest relationship. Finally, it was also examined whether correlations between body size and acoustic parameters were stronger across or within taxonomical families. The results confirm the negative correlation hypothesis, showing highly significant negative relationships between body size (length and mass) and F_0 and body size and F_{dom} ($p < 0.001$ for all comparisons). In most cases, using length as an index of body size resulted in better correlations than mass (although improvements were only marginal), and correlations were always stronger across families than within. In conclusion, these results provide strong support for the hypothesis that body size is negatively correlated with the fundamental and dominant frequencies of vocalization in a large and diverse sample of mammalian species. Future work will be aimed at understanding the mechanistic basis of this relationship in the sound production mechanisms of the larynx.

6. Zusammenfassung

Akustische Allometrie bezeichnet das Studium des Zusammenhanges zwischen der Körpergröße eines Organismus und dessen akustischen Parametern seines Rufverhaltens (Fitch 2000, Gingras et al. 2013). Eine grundlegende Hypothese dieses Feldes besagt, dass eine negative Korrelation zwischen Körpergröße (Index durch Länge oder Gewicht) und wichtigen akustischen Parametern von Vokalisierungen (bspw. Grundfrequenz [F_0] und dominanten Frequenz [F_{dom}]; Morten, 1977; Hauser, 1993) besteht. Das Ziel dieser Arbeit ist es, diese Korrelation anhand einer Vielzahl von Primaten und Karnivoren zu untersuchen. Die Auswahl besteht aus 43 Karnivoren (die in Bezug auf Körpergröße eine Spanne vom Mauswiesel [*Mustela nivalis*] bis zum Eisbär [*Ursus maritimus*] abdeckt) und 47 Primaten (vom Zwergseidenäffchen [*Cebuella pygmaea*] bis hin zum westlichen Flachlandgorilla [*Gorilla gorilla*]) und ist daher die größte und vielfältigste Auswahl, die je im Bereich der akustischen Allometrie getroffen wurde. Die durchschnittliche Körpergröße (Kopf-Rumpf-Länge) wurde für jede Art aus aktuell veröffentlichten Quellen (Wilson; 2009, 2013) entnommen. Die Vokalisierungen stammen von kommerziell erhältlichen CDs und dem Tierstimmenarchiv in Berlin und wurden mithilfe von Praat (Version 5.3.48, Boersma & Weenik, 2013) analysiert. Für die negative-Korrelations-Hypothese wurden folgende Zusammenhänge getestet: (1) Körpergröße und F_0, und (2) Körpergröße und F_{dom}. Außerdem wurde untersucht, durch welche Konstante (Länge oder Gewicht) Körpergröße einen jeweils stärkeren Zusammenhang aufwies. Abschließend wurde untersucht, ob die Korrelationen zwischen Körpergröße und akustischen Parametern entlang oder innerhalb taxonomischer Familien stärker waren. Die Ergebnisse bestätigen die negative-Korrelations-Hypothese und zeigen hoch signifikante negative Zusammenhänge zwischen Körperlänge und Gewicht und F_0 und F_{dom} für alle Vergleiche ($p < 0.001$). In den meisten Fällen zeigte sich Länge als Index für Körpergröße mit marginal besseren Korrelationen als Gewicht und die Korrelationen waren immer stärker entlang verschiedener Familien, als innerhalb von Familien. Schlussendlich wurde, anhand eines großen und diversen Beispiels von Säugetierarten, eine deutliche Bestätigung für die Hypothese, dass Körpergröße mit akustischen Parametern von Vokalisation negative korreliert ist, gefunden. Um die grundlegenden, mechanischen Zusammenhänge zwischen der Produktion von

Vokalisierungen und dem Larynx vollends zu verstehen, werden zukünftige Forschungen nötig sein.

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Appendix 1. Calculation of Human Body Length (sitting height) Data

Human body length data was based on average standing height and sitting height ratio data published in Bogin & Varela-Silva (2010). Bogin & Varela-Silva report average minimum and maximum standing heights (based on populations of African Efe Pygmies and Dutch Europeans respectively) and average minimum and maximum sitting height ratios (based on populations of Australian Aborigines and Central/South Americans respectively). Head to torso body length was calculated by averaging the minimum and maximum standing heights to obtain a human mean, and then multiplying this value by the mean sitting height ratio (also calculated as the average of minimum and maximum values).

Appendix 2. Calculation of Human Speech Frequency Range for F_0 and F_{dom}

The human speech data was calculated using a subset of the speech sample collected and described in Han et al. (2011). The subset consisted of 10 native speakers of American English and 10 native speakers of Mandarin Chinese, each reading short monologues (5 different monologues were used in each language; each was read by 1 male and 1 female). The default "Pitch Range" setting in Praat was used for the F_0 calculation (75-600Hz). F_{doms} were calculated as the maximum values in the spectrum of each monologue (calculated by applying a hamming window to the time-domain signal and then implementing a discrete Fourier transform using a custom Matlab script).

Appendix 3. Overview of Names, Recordings and Calls

Table to summarize all common names, Latin binomials, number of recordings and number of calls for (A) carnivores and (B) primates.

A)

Carnivores				
Family	**Latin Binomial**	**English Common Name**	**Number of Recordings**	**Number of Calls**
Ailuridae	*Ailurus fulgens*	Red Panda	1	10
Canidae	*Alopex lagopus*	Artic fox	2	10
	Canis lupus	Eurasian wolf	5	25
	Chrysocyon brachyurus	Maned wolf	2	8
	Cuon alpinus	Dhole	2	6
	Lycaon pictus	African hunting dog	2	15
	Otocyon megalotis	Bat-eared fox	1	8
	Vulpes corsac	Corsac fox	3	15
	Vulpes rueppellii	Rüppell's fox	2	10
	Vulpes vulpes	Red fox	2	10
Felidae	*Acinonyx jubatus*	Cheetah	3	15
	Felis catus	Domestic cat	3	22
	Felis chaus	Jungle cat	2	10
	Felis silvestris	Wildcat	2	10
	Laopardus pardalis	Ocelot	2	10
	Leptailurus serval	Serval	2	10
	Lynx canadensis	Canadian lynx	1	5
	Lynx lynx	Eurasian Lynx	2	10
	Neofelis nebulosa	Clouded leopard	4	19
	Panthera leo	Lion	2	10
	Panthera onca	Jaguar	3	15
	Panthera tigris	Bengal tiger	3	13

	Puma concolor	Cougar	3	14
	Puma yagouaroundi	Jaguarundi	2	10
	Uncia uncia	Snow leopard	2	13
Herpestidae	*Helogale parvula*	Common dwarf mongoose	1	5
	Suricata suricatta	Meerkat	3	14
Hyaenidae	*Hyaena hyaena*	Striped hyena	3	15
Mustelidae	*Aonyx cinera*	Oriental small-clawed otter	3	15
	Lutra lutra	European otter	2	14
	Martes martes	European pine marten	2	9
	Mustela erminea	Stoat	1	9
	Mustela nivalis	least weasel	1	10
Otariidae	*Zalophus californianus*	California sea lion	2	15
Procyonidae	*Bassariscus astutus*	ringtail	2	10
	Nasua nasua	South American coati	2	15
	Potos flavus	Kinkajou	2	10
	Procyon lotor	Raccoon	3	15
Ursidae	*Helarctos malayanus*	Sun bear	3	11
	Ursus americanus	American black bear	2	10
	Ursus arctos	Brown bear	2	10
	Ursus maritimus	Polar bear	2	7
Viverridae	*Arctictis binturong*	Binturong	3	15
		total	97	512

B)

Primates				
Family	**Latin Binomial**	**English Common Name**	**Number of Recordings**	**Number of Calls**
Atelidae	*Alouatta carya*	Black howler	1	5
	Alouatta seniculus	Venezuelan red howler	1	5
	Ateles fusciceps	Black-headed spider monkey	1	9
	Ateles paniscus	Red-faced spider monkey	2	10
Callitrichidae	*Callithrix flaviceps*	Buffy headed marmoset	1	10
	Callithrix geoffroyi	White-headed marmoset	1	5
	Callithrix jacchus	Common marmoset	3	15
	Cebuella pygmaea	Pygmy marmoset	1	10
	Leontopithecus chrysomelas	Golden-headed lion tamarin	2	6
	Leontopithecus rosalia	Golden lion tamarin	2	13
	Mico argentatus	Silvery marmoset	2	10
	Saguinus bicolor	Pied tamarin	1	10
	Saguinus imperator	Emperor tamarin	1	10
	Saguinus oedipus	Cotton-top tamarin	2	9
Cebidae	*Cebus apella*	Tufted capuchin	2	10
	Cebus olivaceus	Wedge capped capuchin	2	10
	Saimiri sciureus	Squirrel monkey	2	10
Cercopithecidae	*Cercopithecus diana*	Diana monkey	1	5
	Cercopithecus lhoesti	L'Hoest's monkey	2	6

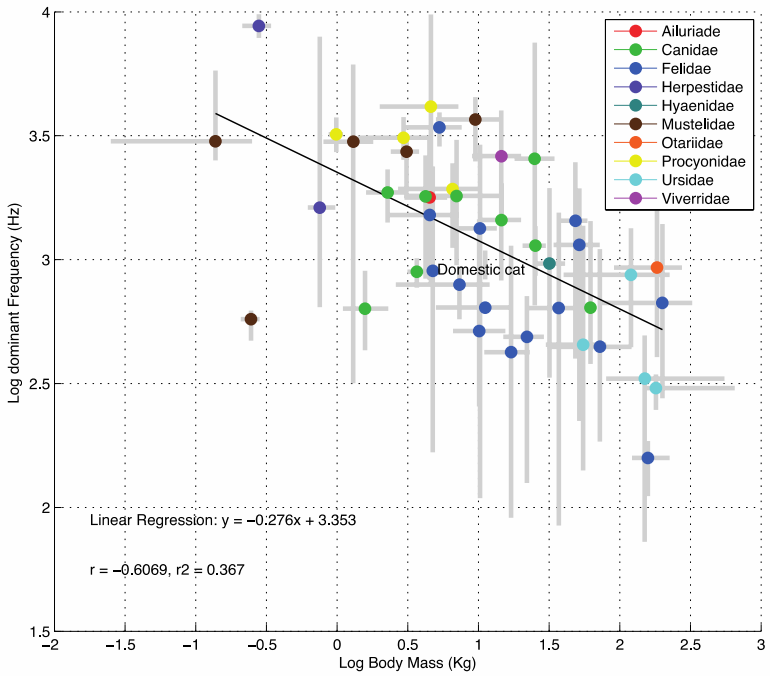
	Cercopithecus neglectus	De Brazza's monkey	2	10
	Cercopithecus nictitans	Greater-spot nosed monkey	1	5
	Cercopithecus solatus	Sun-tailed monkey	1	5
	Cercopithecus wolfi	Wolf's guenon	1	5
	Chlorocebus pygerythrus	Vervet monkey	2	14
	Colobus guereza	Mantled guereza	2	10
	Colobus satanas	Black colobus	1	5
	Macaca arctoides	Stump-tailed macaque	2	9
	Macaca fuscata	Japanese macaque	3	15
	Macaca nigra	Celebes crested macaque	1	5
	Macaca silenus	Lion-tailed macaque	2	10
	Macaca sylvanus	Barbary macaque	2	10
	Mandrillus leucophaeus	Drill	2	10
	Mandrillus sphinx	Mandrill	3	15
	Papio hamadryas	Hamadryas baboon	2	10
Hominidae	*Gorilla gorilla*	Western gorilla	2	10
	Homo sapiens	human		
	Pan troglodytes	Chimpanzee	3	15
	Pongo pygmaeus	Orangutan	2	10
Hylobatidae	*Hylobates lar*	Lar-Gibbon	1	15
	Nomascus concolor	Black crested gibbon	2	10
	Symphalangus syndactylus	Siamang	2	10
Lemuridae	*Eulemur mongoz*	Mongoose lemur	1	5

	Lemur catta	Ring-tailed lemur	1	5
	Varecia rubra	Red-ruffed lemur	3	13
	Varecia variegta	Black-and-white ruffed lemur	2	15
Pitheciidae	*Callicebus moloch*	Red-bellied titi	1	10
	Pithecia monachus	Monk saki	1	5
		total	78	429

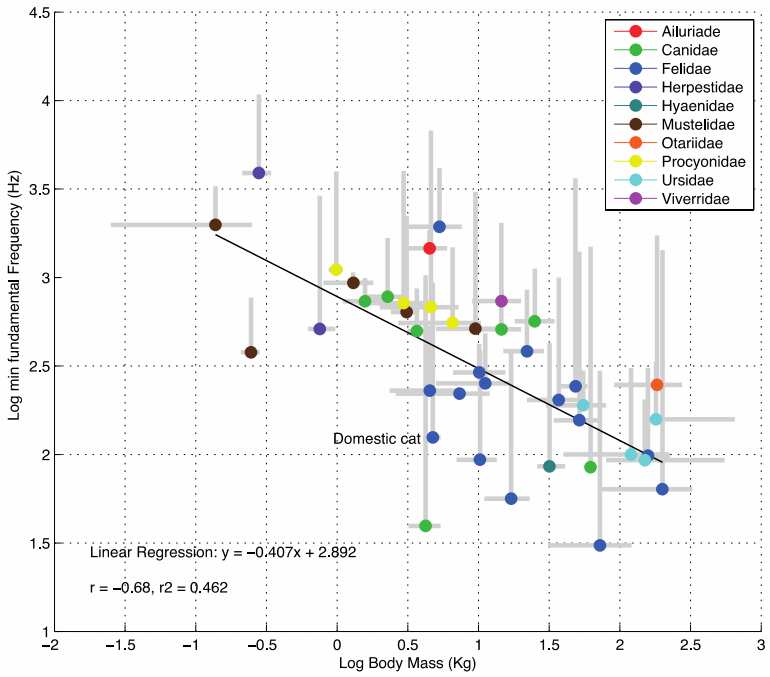
Appendix 4. Plots for Body Mass versus Acoustic Parameters

Body mass versus mean, min F_0 and mean F_{dom} plots (A) Carnivores and (B) Primates.

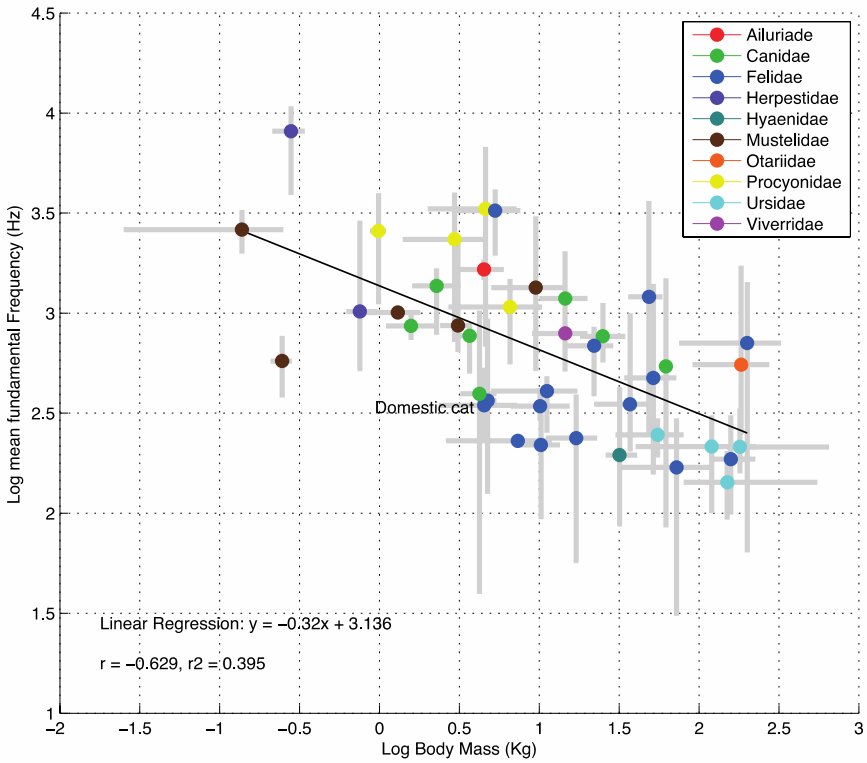
A1) carnivores: body mass vs. F_{dom}



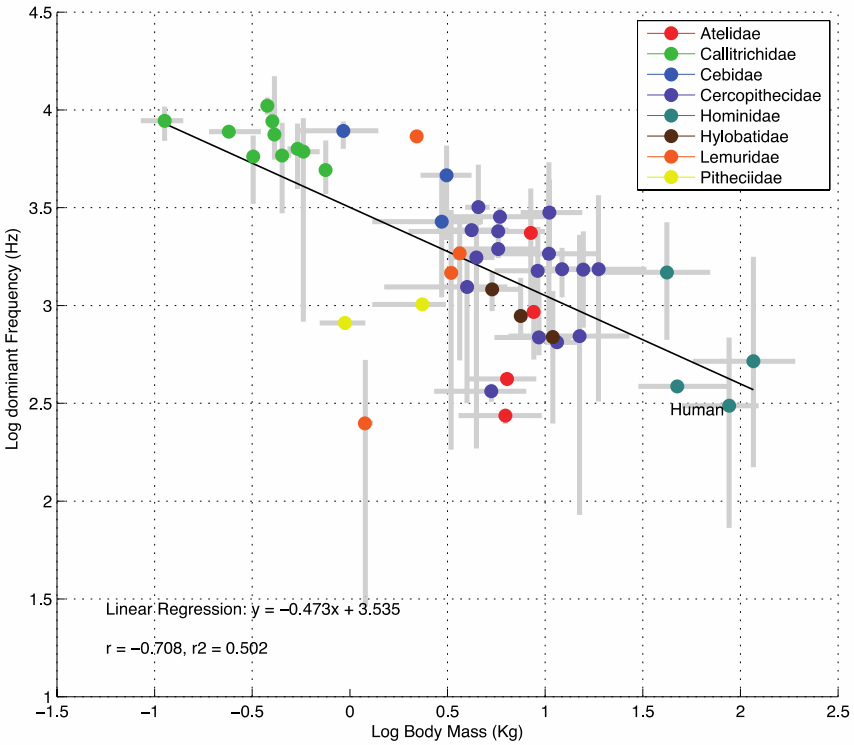
A2) carnivores: body mass vs. min F_0



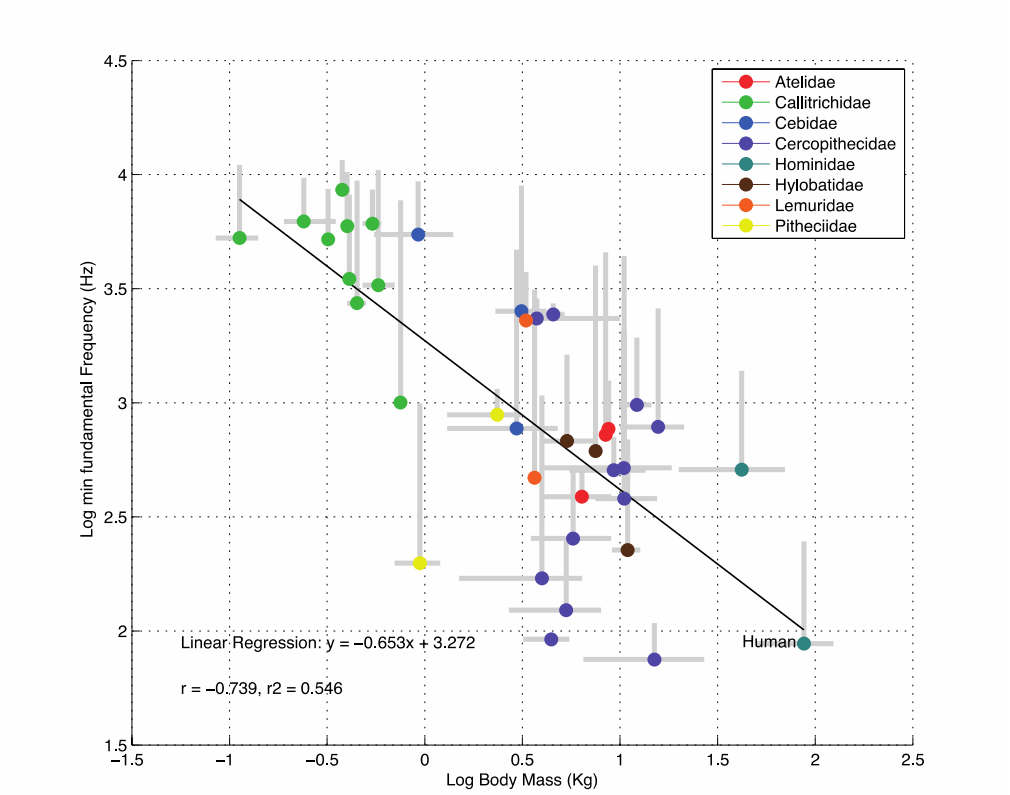
A3) carnivores: body mass vs. mean F_0



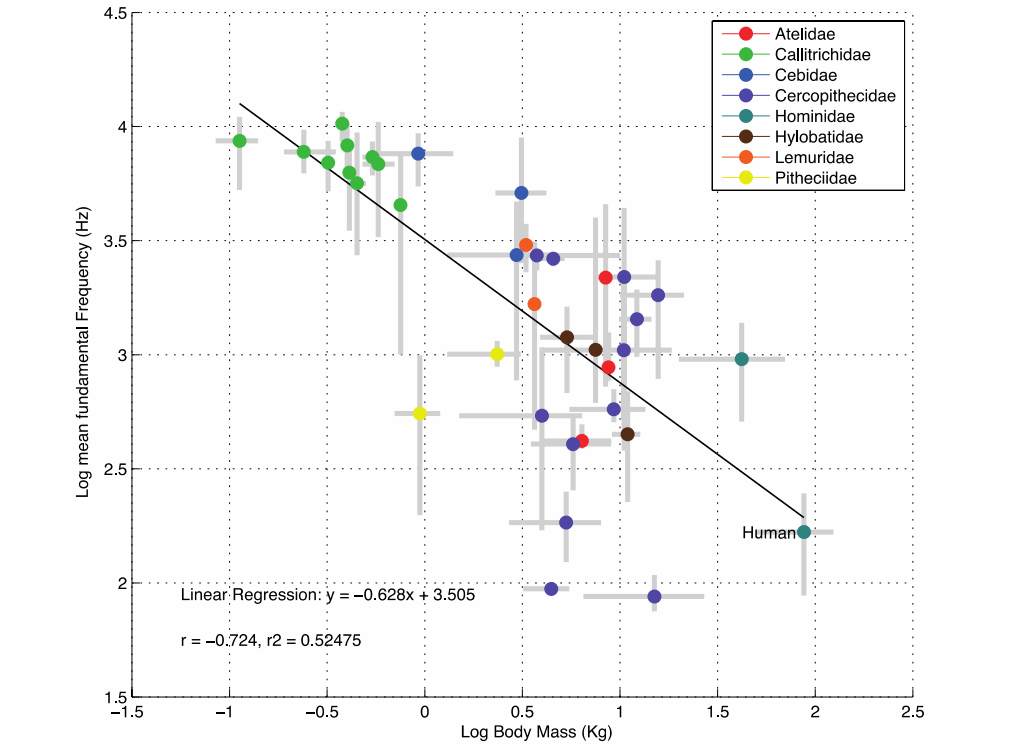
B1) primates: body mass vs. F_{dom}



B2) primates: body mass vs. min F_0



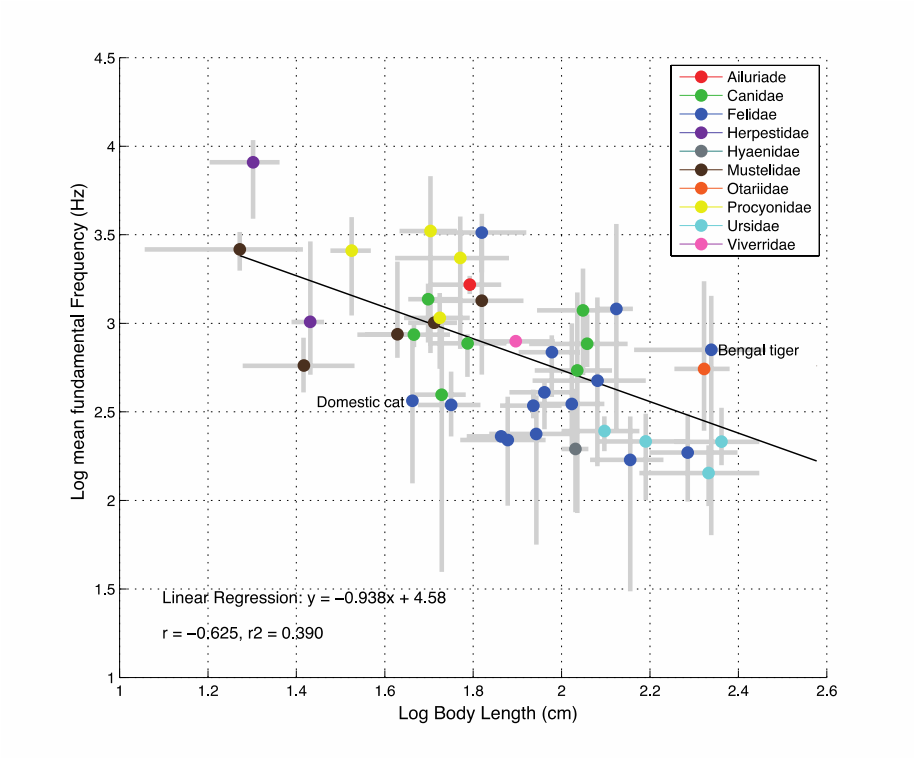
B3) primates: body mass vs. mean F_0



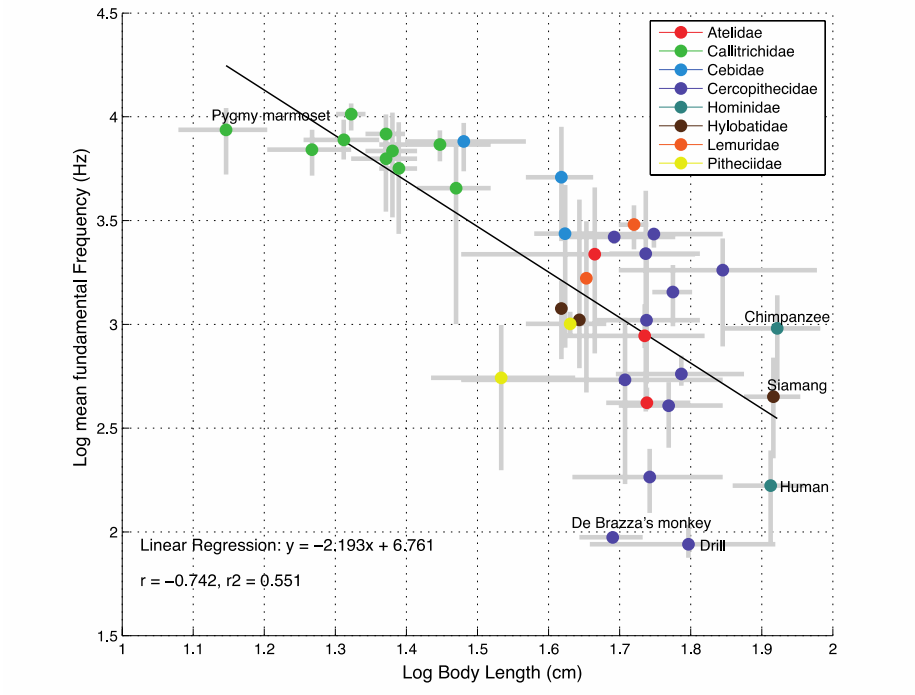
Appendix 5. Plots for Body Length versus Mean F_0

Plots showing Body length versus mean F_0 for (A) carnivores and (B) primates.

A) carnivores: body length versus mean F_0

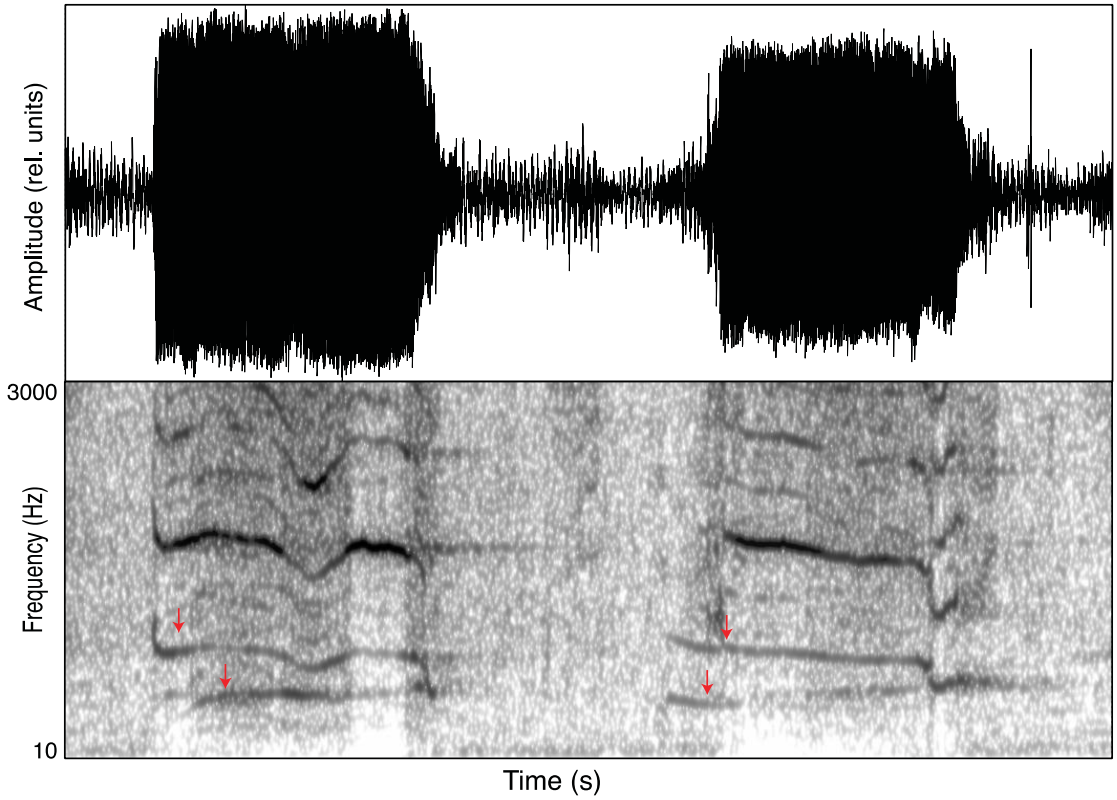


B) primates: body length versus mean F_0



Appendix 6. Two Fundamental Frequencies in California Sea Lion Calls

Top panel showing the time-domain signal of two calls of a California Sea Lion (*Zalophus californianus*). Bottom panel shows the spectrogram. The red arrows show fundamental frequencies (F_0). As can be seen there are two F_{0s} per call.



Curriculum Vitae

Rebecca Ruprecht

Profile

As a communicative and open-minded person, I like social interaction, in particular team work. I strive to bring out the best in myself and those around me. During my study and work experiences I was able to conduct myself in assessing difficult situations and show my ability to stay calm finding the right solutions.

Education

Since 2011 – present attending University of Vienna for the Master in Zoology

Modules	**Subjects**
principles of zoology	taxonomy, evolution, anatomy, zoogeography, behavioral ecology, animal cell biology
practical work	sound signals in animals, performed in the "Tiergarten Schönbrunn" (Vienna Zoo); field trip to the Wadden Sea and the Afred Wegner Institute (AWI) on Sylt
taxonomy and biodiversity	symbiosis, social systems, tropical amphibians
behavioral-, neuro- and cognition biology	bioacoustics, communication, neurobiology, cognition biology, behavioral ecology
marine biology	oceanography, marine ecology, marine biological excursion to the northern Adriatic (Rovinj, Croatia)
Additional qualifications	seminar about communication in science (certified), ecological data interpretation

2006- 2011 University of Salzburg: Title of qualification awarded: Bachelor of Science in "Environmental and Evolutionary Biology"

1997- 2006 Ville-Gymnasium-Erftstadt

Projects

2014 Visited the National Museums Scotland (Edinburgh), as my master thesis is part of a larger collaboration project between the University of Vienna and the museum

2013 Visited the "Tierstimmenarchiv" (Animal Sound Archive) in Berlin; received an introduction to the database, prepared and collected animal sounds

2009 Bachelor's thesis: "Denis Island: How do the Magpie Robins (*Copsychus sechellarum*) behave on feeding platforms?" Related to an internship at the "Green Islands Foundation" on Denis Island (Seychelles)

2008 Bachelor's thesis "Adoption in greylag goose (*Anser anser*) - a pattern of altruism?" Related to a field trip to Neusiedler See/ Seewinkel (Austria)

Working experience

2011- 2013 Taught Austrian pupils on their school trips in Rovinj (Croatia) about marine biological and ecological subjects during the summer (1-3 weeks), organized by **ECONOLOGY GmbH (Salzburg, Austria)**

2010- 2011 helped voluntarily in a nursery home to guide people with dementia (with continued education, certified);

For four months I worked as a cashier at "Karstadt" (department store)