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Appendix B from S. Lingle and T. Riede, "Deer Mothers Are Sensitive to Infant Distress Vocalizations of Diverse Mammalian Species"

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Acoustic Characteristics of Call Stimuli Relative to Female Response

Introduction

We identified characteristics of the fundamental frequency (F0), the temporal pattern (call duration, number of parts per call), the energy distribution, and the presence of certain nonlinear phenomena for the distress vocalization playback stimuli used in this study. These results can be used to compare and contrast acoustic characteristics of the different stimuli, including comparisons between traits of manipulated calls and traits of the corresponding unmanipulated calls (e.g., marmot and eland). We also used data on acoustic characteristics to test the relationship between acoustic traits and female response.

Methods

Acoustic Analysis

We used Praat (Boersma and Weenink 2011) to analyze several acoustic variables, including the mean F0, minimum F0, maximum F0, range F0/mean F0 (an index of the degree of frequency modulation that is independent of the mean in a call), call duration, number of parts per call, and dominant harmonics. Additional details of methods used to analyze these traits are available elsewhere (Lingle et al. 2012; Teichroeb et al. 2013). We identified the dominant harmonics as an indication of the distribution of energy across different frequencies. First, we identified the "maximum dominant harmonic," usually called the "dominant frequency," which was the harmonic having the maximum amplitude. We also identified the three harmonics having the highest amplitude (one of which was the maximum dominant harmonic) and ranked these harmonics by their frequency.

Four categorical variables were included in the analysis: tonality, the frequency modulation pattern of each call, the presence of certain nonlinear phenomena, and a rating of whether or not "noisy features" (i.e., subharmonics or deterministic chaos) were present in the call overall. Tonality was identified as "tonal" when clearly defined harmonics were visible throughout the call; a "mixed" structure referred to calls that had harmonics that were visible for all or part of the call, with some sections having subharmonics or deterministic chaos that made it difficult or impossible to track the F0 during those sections. Sounds might have been scored as "noisy" if an F0 was not evident throughout the call; that category did not apply to any of the distress vocalizations but would apply to sounds such as the alarm snort (fig. A1*M*). The frequency modulation pattern referred to the overall direction of the F0 contour and was scored on the basis of visual assessment and measurement of a pitch contour extracted and examined within Praat (specific categories and their definitions are available in table B1).

For nonlinear phenomena, we identified whether a call had subharmonics, frequency jumps, or deterministic chaos at any part of the call, regardless of the duration of the feature. To characterize noise for the call overall, we made a binary classification and distinguished calls that were entirely tonal from calls that had either well-defined subharmonics lasting more than 10 ms or sections of deterministic chaos. We left this as a binary classification because such features were uncommon in the sample of distress vocalizations.

Data Analysis

We used a logistic regression to relate acoustic traits of distress vocalization playback stimuli to variation in female response. Characteristics of F0, dominant harmonics, and call duration were tested as second-order polynomials because intermediate values were expected to elicit the strongest response. For dominant harmonics, we tested the relationships of the maximum dominant harmonic and also a principal component formed from the combination of the three dominant harmonics to female response.

Results

The majority of distress vocalizations used in this study were highly tonal, with few cases of nonlinear phenomena such as subharmonics or deterministic chaos. Only the Australian sea lion, human, and dog had sections of deterministic chaos (one human, one dog) or sections with subharmonics exceeding 10 ms (one human, sea lion). Fleeting occurrences (<10 ms) of weak subharmonics were identified in calls of a few other species (ungulates, marmot, bat). As expected, the frequency of dominant harmonics for calls having an F0 manipulated by overriding the sampling frequency (RS) differed from the original call much more than the frequency of dominant harmonics for calls with the F0 manipulated by multiplying the F0 contour by a certain factor (F0S in table B1).

The mean F0 and maximum F0 had a significant curvilinear relationship with the female's response (fig. 3; table B2). Each of these variables was significant when entered alone but not when both variables were included together, since they were highly correlated ($r^2 = 0.99$). The female's distance to the speaker at the start of the trial was not significantly related to her response, regardless of whether it was entered as the sole variable (table B2) or included with mean F0. There was a nonsignificant trend for females to respond more strongly when call duration was at an intermediate value (table B2). There was no indication of a relationship between characteristics of energy distribution or the presence of noise and female response (table B2).

Discussion

Mean F0 (and maximum F0) had a significant relationship with a female's response to infant distress vocalizations, regardless of whether the calls were emitted by mule deer or by other species. Other acoustic variables were not significantly related to variation in the responses of females. Considerable variation was present in the frequency of dominant harmonics (table B1), so this variable appears relatively unimportant for a response to infant distress vocalizations. In the case of call duration and noise, the lack of an effect may be due to the absence of sufficient variation in these traits. We detected a trend for calls of intermediate duration to elicit a stronger response: a stronger effect may be detected if calls that were much shorter or longer were included.

We similarly suspect that the lack of a relationship between noise and female response was because the sample lacked much variation in this trait. The juvenile distress vocalizations were overwhelmingly tonal. Substantial segments of noise associated with subharmonics or sections of deterministic chaos were present only in recordings of one individual each belonging to three species: an Australian sea lion, a dog, and a human infant. We suspect that deer did not approach when hearing alarm snorts or coyote barks because of the harsh and perhaps repellent quality of broadband noise (Morton 1977). Manipulations of distress vocalizations to introduce these forms of noise can be used to determine how these traits influence a female's response.

Mule deer females appeared to respond more weakly to the dog vocalizations and to some of the marmot F0-shift vocalizations than to other types of calls (fig. 2*A*, 2*B*; tables 1, B3). Females displayed clear alert behavior to these calls, and we do not have insight into why the responses were weaker. A sample of recordings in which a larger number of individuals of different species are recorded in similar contexts is needed to determine whether this variation is representative of the response to calls of any particular species. An answer to this question may help us to understand variation in the intensity of a female's response. However, variation in the response of females to different stimuli does not negate the main finding that sufficient commonality is present in distress vocalizations produced by infants of different species for the deer to respond to cries emitted by taxonomically and ecologically diverse species.

Table B1. Acoustic characteristics of distress vocalization stimuli used in playback experiments

Species, call type[a]	*n*	Tonality[b]	Frequency modulation pattern[c]	Call duration (s)	Duty cycle (sound/20 s)	Fundamental frequency (Hz)				Dominant harmonics (Hz)[d]				NLP[e]
						Mean	Min	Max	Range/mean	Max DH	Low DH	Mid DH	High DH	
Mule deer original	5	T	Chevron, chevron/descend, flat/descend	.650	5.20	933	605	1,041	.47	3,736	2,154	3,748	5,435	None
Eland original	3	T	Chevron, chevron/descend, flat/descend	1.677	6.15	172	131	185	.31	2,089	1,261	2,358	2,834	None
Eland F0S	3	T	Chevron, chevron/descend, flat/descend	1.677	6.15	916	748	1,055	.33	2,394	1,384	2,364	3,362	None
Eland RS	3	T	Chevron, chevron/descend, flat/descend	.693	5.54	465	364	496	.28	4,383	2,877	5,185	6,945	None
Marmot original	2	T	Chevron, chevron/descend	.570	4.56	1,731	935	2,092	.65	2,686	2,358	4,161	6,763	SH, FJ
Marmot F0S	2	T	Chevron, chevron/descend	.570	4.56	779	436	943	.63	2,214	1,829	2,738	3,652	SH, FJ
Marmot RS	2	T	Chevron, chevron/descend	1.187	5.94	821	470	517	.60	1,258	1,095	1,975	2,867	SH, FJ
Bat RS	2	T	Descend	.335	2.68	849	804	953	.17	2,454	1,381	2,434	3,352	SH
Fur seal original	1	T	Chevron/ascend	1.390	8.34	589	369	668	.51	1,977	656	1,977	2,638	None
Sea lion original	1	M	Chevron	.960	5.76	519	441	592	.29	1,158	1,158	2,316	2,896	SH, DC
Human original	3	T, M	Chevron, ascend, undulating	1.138	6.88	489	369	546	.36	1,065	812	1,435	3,585	SH, DC
Cat original	2	T	Chevron, chevron/ascend	.626	5.01	1,124	756	1,331	.51	2,901	1,548	3,019	5,632	SH, FJ
Cat F0S	2	T	Chevron, chevron/ascend	.626	5.01	838	609	976	.44	2,847	1,963	3,467	5,047	SH, FJ
Dog original	3	T, M	Chevron, descend or flat/ascend	.503	4.02	1,210	935	1,349	.34	2,150	1,357	2,623	4,402	SH, DC, FJ
Dog F0S	3	T, M	Chevron, descend or flat/ascend	.503	4.02	808	660	902	.30	2,256	1,124	1,998	3,189	SH, DC, FJ

Note: Mean values shown for continuous traits. All calls consisted of a single pulse of sound. n = number of individuals for which calls were available. F0 = fundamental frequency.

[a]Original calls did not have the F0 manipulated, although the calls were put through the “Manipulation Editor” function of Praat. F0S = F0 manipulated by multiplying the F0 by a particular value (F0-shift); RS = F0 manipulated by overriding the sampling frequency.

[b]T = tonal, with clearly defined harmonics; M = mixed, that is, primarily tonal calls with sections of deterministic chaos or subharmonics that made it difficult or impossible to track the F0 in those sections; T, M = calls of both forms were observed.

[c]Overall direction of frequency modulation from start to end of call, based largely on visual assessment of, and measurements from, a pitch contour extracted and examined within Praat. Chevron = F0 (and other harmonics) rises and then falls, so the maximum F0 usually falls within the middle half of the call duration. Descend or ascend = F0 consistently descends or ascends, respectively, throughout the call. Flat = F0 does not vary by more than 10% of the mean F0 during the call, as shown by the “Range/mean” column. Undulating = F0 undulates by more than 10% of the mean but does not change in a consistent direction throughout the call. A comma (e.g., chevron, descend) indicates that different patterns were observed for different calls. A slash indicates that the pattern is intermediate between two forms. Chevron/descend or chevron/ascend = F0 rises and then falls to an F0 that is more than 20% lower or higher, respectively, at the end of the call than that at the start. Flat/descend = F0 remains stable for much of the call, followed by a period in which it descends.

[d]Max DH = the harmonic having the maximum amplitude. Low DH, Mid DH, and High DH = the three harmonics having the highest amplitudes, organized by frequency.

[e]NLP = nonlinear phenomena, including the presence of subharmonics (SH), deterministic chaos (DC), frequency jumps (FJ), or the absence of these traits (None).

Table B2. Relationship between acoustic characteristics of juvenile distress vocalization and the probability that a female showed a moderate-to-strong response to calls of species other than mule deer and to mule deer calls

Variable	Estimate	SEM	Lower 95% CI	Upper 95% CI	Wald χ^2	*P*
Calls of other species:						
Distance to speaker	.19	.23	−.26	.67	.68	.41
No. females in group	−.16	.18	−.55	.17	.84	.36
Mean F0	.41	1.02	−2.57	2.52	.16	.69
Mean F0 × mean F0	**8.88**	**2.88**	**3.64**	**15.1**	**9.52**	**.002**
Max F0	.32	.83	−1.30	2.03	.15	.70
Max F0 × max F0	**6.04**	**2.02**	**2.32**	**10.35**	**8.95**	**.003**
Range F0/mean F0	.32	1.91	−3.42	4.19	.03	.87
Range F0/mean F0 × range F0/mean F0	7.61	8.09	−8.26	23.77	.89	.35
Call duration	−.65	.74	−2.16	.80	.77	.38
Call duration × call duration	1.30	.89	−.36	3.19	2.14	.14
Max dom harm[a]	.13	.35	−.55	.84	.14	.71
Max dom harm × max dom harm[a]	−.02	.19	−.43	.35	.013	.91
Dom harm PC	.34	.29	−.21	.95	1.37	.24
Dom harm PC × dom harm PC	.001	.11	−.22	.22	.0001	.99
Noise[b]	.06	.29	−.51	.66	.038	.85
Mule deer calls:						
Distance to speaker	−.02	.21	−.43	.39	.0095	.92
Mean F0	.21	.89	−2.01	1.60	.05	.82
Mean F0 × mean F0	**9.88**	**3.06**	**4.88**	**17.20**	**10.38**	**.001**

Note: Mule deer calls had been manipulated so that the mean fundamental frequency (F0) varied from 0.2 to 1.8 times the original stimulus (Teichroeb et al. 2013). The effects of a female's group size (number of females in group) and starting distance to speaker were tested as potentially confounding variables. Logistic regression was used to obtain parameter estimates, standard error of the mean (SEM), confidence intervals (CI), Wald χ^2, and the corresponding *P* value. Values in table show results for each variable tested in a model alone, although second-order polynomials and main effects were included in models for call duration, mean F0, maximum F0 (max F0), range F0/mean F0, maximum dominant harmonic (max dom harm), and dominant harmonic principal component (dom harm PC), because intermediate values were predicted to elicit the strongest response for these variables. Additional analyses examined the effect of distance to speaker, number of females in a group, call duration, dominant harmonics, and noise in models including mean F0 and mean $F0^2$. Rows in boldface identify traits that had a significant relationship to female response. Data underlying this analysis are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.pj891 (Lingle and Riede 2014).

[a] "Max dom harm" refers to the harmonic having the highest amplitude, as identified from a spectral slice showing frequencies between 0 and 10 kHz. "Dom harm PC" refers to a principal component formed from the three harmonics showing the highest amplitude.

[b] "Noise" was scored as a binary variable for calls that were entirely tonal versus calls that had sections with deterministic chaos or subharmonics. To rate a call as noisy, subharmonics were scored as present only if they lasted more than 10 ms. (If shorter, they were still identified as present under nonlinear phenomena; NLP in table B1.)

Table B3. Response of mule deer mothers to infant distress vocalizations of different species, control stimuli, and predator stimuli

				Main subject's response[c]							Behavior of females near speaker[d]		
Stimuli	Call type[a]	Mean F0 (Hz)[b]	*n*	Leave (−1)	No behav response (0)	Alert (1–2)	Weak app (3–4)	Mod app (5–6)	Strong app (7–8)	Max app (9)	Females <10 m × speaker	Defensive behavior	Grunt
Control stimuli:													
Meadowlark	NA	2,209	10	0	8	2	0	0	0	0	0	NA	NA
Meadowlark F0-shift[b]	NA	884	8	0	3	5	0	0	0	0	0	NA	NA
Sine wave	NA	935	6	0	0	6	0	0	0	0	0	NA	NA
White noise, narrow-band	NA	400–1,500	7	1	3	3	0	0	0	0	0	NA	NA
Predator stimuli:													
Coyote bark	NA	NA	7	0	0	7	0	0	0	0	0	NA	NA
Deer alarm snort	NA	NA	7	0	0	7	0	0	0	0	0	NA	NA
Infant vocalizations:													
Mule deer, natural distress call[b]	C	933	6	0	0	0	0	2	0	4	4	3/4	2/3
Mule deer, synthesized distress call	NA	935	8	0	0	0	0	1	1	6	7	4/7	2/8
Eland	C	170	6	0	0	4	2	0	0	0	0	NA	NA
Eland RS[e]	C	453	4	0	0	0	1	0	1	2	2	2/4	3/3
Eland F0-shift[e]	C	912	4	0	0	0	0	0	1	3	3	2/2	2/2
Bighorn	C	384	2	0	0	1	0	1	0	0	0	NA	NA
Pronghorn	C	385	3	0	0	0	0	1	0	2	2	1/2	ND
Fallow deer	C	784	1	0	0	0	0	0	0	1	1	1/1	ND
Red deer	C	794	2	0	0	0	0	1	0	1	2	2/2	1/1
Sika deer	C	1,194	2	0	0	0	0	0	0	2	2	2/2	2/2
Marmot 1 original[b]	C	2,121	4	0	0	4	0	0	0	0	0	NA	NA
Marmot 2 original[b]	C	1,297	1	0	0	0	0	1	0	0	0	NA	NA
Marmot 1 RS[e]	C	792	4	0	0	0	0	0	1	3	4	4/4	4/4
Marmot 1 F0 shift[e]	C	810	4	0	0	1	1	1	0	1	2	1/1	UNK
Subantarctic fur seal	I	589	2	0	0	0	0	0	1	1	2	0/2	UNK
Australian sea lion	I	519	3	0	0	0	0	1	1	0	0	NA	1/2
Domestic cat original	I, O	1,124	4	0	0	1	1	0	1	1	1	0/1	0/1
Domestic cat F0-shift[e]	I, O	838	4	0	0	0	1	0	1	2	2	2/2	2/2
Domestic dog original	I, O	1140	2	0	2	0	0	0	0	0	0	NA	NA
Domestic dog F0-shift[e]	I, O	808	3	0	0	2	0	1	0	0	0	NA	NA
Silver-haired bat RS[e]	I	837	4	0	0	0	0	3	0	1	1	1/1	0/1
Human	O	489	4	0	0	0	0	2	2	0	0	NA	NA

Note: Entries for response show the number of trials in which a certain response was observed. n = number of trials.

[a]NA = not applicable. C = capture call. I = isolation call. O = distress vocalization made in contexts other than capture or isolation.

[b]Small differences in mean fundamental frequency (F0) from those in table B1 are because table B1 averages results for playback stimuli made from recordings of different individuals. This table averages results for different trials. The difference in mean F0 was large enough for the two marmots to justify presenting their results separately.

[c]See "Behavioral Observations" for description of ordinal scale used to describe the subject's response. app = approach; behav = behavioral; max = maximum; mod = moderate.

[d]Females <10 m × speaker = the number of trials in which at least one female (not necessarily the main subject) came within 10 m of the speaker. Defensive behavior = the number of trials in which at least one female that came within 10 m of the speaker displayed defensive behavior. Grunt = the number of trials in which at least one female that came within 25 m of the speaker was heard to grunt. NA = not applicable; ND = no data recorded; UNK = unknown.

[e]F0-shift = F0 was manipulated by multiplying the original F0 by a certain factor. RS = F0 was shifted by overriding the original sampling frequency.

Table B4. Response of white-tailed deer mothers to infant distress vocalizations of different species and to control stimuli (meadowlark song)

				Main subject's response[b]							Behavior of females near speaker[c]	
Stimuli	Call type[a]	Mean F0 (Hz)	*n*	Leave (−1)	No behav response (0)	Alert (1–2)	Weak app (3–4)	Mod app (5–6)	Strong app (7–8)	Max app (9)	Females <10 m × speaker	Defensive behavior
Meadowlark song	NA	2,209	10	0	9	1	0	0	0	0	0	NA
White-tailed deer	C	504	6	0	0	0	1	2	1	2	2	1
Eland	C	170	2	1	0	1	0	0	0	0	0	NA
Eland F0-shift[d]	C	502	2	0	0	0	0	0	0	2	2	2
Eland RS[d]	C	464	2	0	0	0	0	1	1	0	0	NA
Pronghorn	C	385	2	0	0	0	0	0	1	1	1	1
Marmot original	C	1,601	2	0	0	2	0	0	0	0	0	NA
Marmot 1 F0 shift[d]	C	525	2	0	0	0	0	2	0	0	0	NA
Subantarctic fur seal	I	597	2	0	0	0	0	0	1	1	1	0
Human	O	467	3	1	0	0	1	1	0	0	0	NA

Note: Values represent the number of trials in which a certain response was observed.

[a]NA = not applicable (control stimulus). C = capture call. I = isolation call. O = distress vocalization made in contexts other than capture or isolation.

[b]See "Behavioral Observations" for description of ordinal scale used to describe the subject's response. app = approach; behav = behavioral; max = maximum; mod = moderate.

[c]Females <10 m × speaker = the number of trials in which at least one female (not necessarily the main subject) came within 10 m of the speaker. Defensive behavior = the number of trials in which at least one female that came within 10 m of the speaker displayed defensive behavior. NA = not applicable.

[d]F0-shift = fundamental frequency (F0) was manipulated by multiplying the original F0 by a certain factor. RS = F0 was shifted by overriding the original sampling frequency.