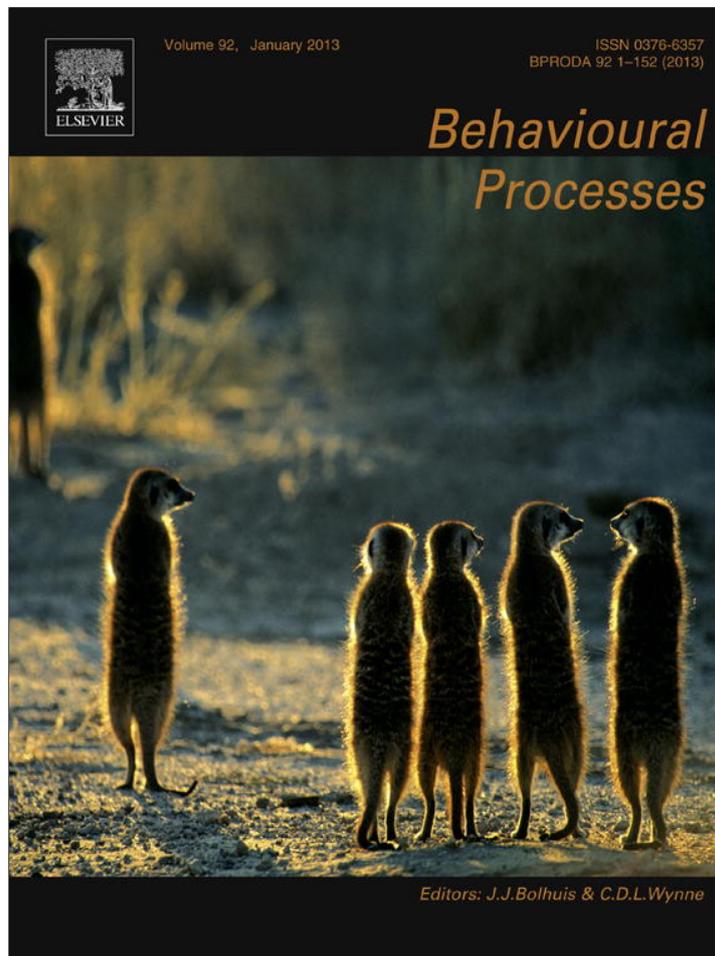


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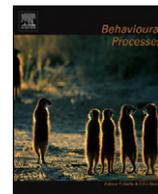
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Fundamental frequency is key to response of female deer to juvenile distress calls

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ABSTRACT

Considerable attention is currently devoted to understanding acoustic mechanisms underlying animal responses to heterospecific vocalizations. A further complication ensues when the response of two species is asymmetrical. For example, white-tailed deer females approach a speaker only when it plays distress calls of conspecific fawns. Mule deer females approach when hearing distress calls of either white-tailed deer or mule deer. We hypothesized that selective species such as white-tailed deer respond to traits distinctive of their species and less-discriminating species such as mule deer respond to traits shared across species. Through an acoustic analysis of neonatal distress calls of six ungulate species, we found that mean and maximum fundamental frequency (F0) enabled the greatest statistical discrimination, and the pattern of frequency modulation (FM) was shared across species. Contrary to our initial hypothesis, playback experiments revealed that females of the two species respond similarly to manipulation of F0 and FM. F0 was critical to the response of females from both species, which tolerated the same relative F0 variation (approx. 0.6–1.4× the mean F0 for conspecific fawns). This discovery suggests that mule deer females only appear less discriminating because they are tuned to the higher F0 of mule deer distress calls (964 Hz vs. 546 Hz), resulting in a larger absolute response range that encompasses the F0 produced by white-tailed deer fawns. We propose that animals will have larger absolute response ranges, and therefore appear to be less discriminating, when they belong to a species that produces higher F0 calls.

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1. Introduction

The ability to recognize and respond to alarm calls produced by other species is usually considered adaptive for it can lead to early detection of predators and enable an individual to move to a safe location (Caro, 2005; Magrath et al., 2009; Fallow et al., 2011). A response to mobbing calls of heterospecifics can result in the eviction of a predator from a common nesting area (Caro, 2005), although the reasons why particular individuals accept the risk inherent in such close interactions with predators requires a more nuanced understanding of the fitness consequences of cooperation (Krams and Krama, 2002; Grabowska-Zhang et al., 2012). In contrast to alarm or mobbing calls, distress calls are produced when a particular prey individual is attacked or captured by a predator (Caro, 2005). Animals from certain species, for example, white-tailed deer (*Odocoileus virginianus*), respond selectively to distress calls, only approaching when hearing a call produced by its own species (Lingle et al., 2007b). Animals from other species,

including the closely related mule deer (*Odocoileus hemionus*), are less discriminating. Mule deer females will approach a speaker when hearing distress calls of mule deer or white-tailed deer (Lingle et al., 2007b), and will defend unrelated conspecific fawns and even white-tailed deer fawns in addition to their own offspring (Lingle et al., 2005). The adaptive value of defending unrelated conspecific and heterospecific individuals remains unclear (Lingle et al., 2007b), as well as the acoustic mechanisms that facilitate the listener's response to conspecific and heterospecific distress calls.

Considerable attention is currently devoted to the question of acoustic mechanisms underlying the response of animals to heterospecific alarm calls (Johnson et al., 2003; Magrath et al., 2009; Fallow et al., 2011) and mobbing calls (Randler and Förschler, 2011; Randler, 2012). An unexamined complication ensues when the response of two species to each other's calls is asymmetrical. That is, why would an animal from one species but not the other approach when hearing distress calls of the other species? One possibility is that each species learns to recognize the calls of the other species (Magrath et al., 2009), with an adaptive advantage to one species in responding to heterospecific calls that does not apply to the other. Another possibility is that the response to heterospecific calls is an extension of an animal's response to conspecific calls so that each species responds to heterospecific calls that are acoustically

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similar (Johnson et al., 2003; Fallow et al., 2011; Randler, 2012). If the species are tuned and respond to the same acoustic traits, their response to each other's calls would be expected to be symmetrical. If the species are tuned to different acoustic traits, their response could be asymmetrical.

Mule deer and white-tailed deer coexist in much of western North America. Mule deer females are more aggressive than white-tailed deer to predators (Lingle and Pellis, 2002; Lingle et al., 2005), even though adults and newborns of the two species are identical in body mass when measured at the same location (Mackie, 1964; Wishart, 1986; this study). Fawns often emit loud distress calls when attacked and these vocalizations are the main stimuli attracting females to a fawn that is in trouble. Previous work revealed that distress calls of mule deer newborns have a fundamental frequency (F0, perceived as the pitch of a voice) that is about twice as high as the F0 of distress calls of white-tailed deer newborns (Lingle et al., 2007a). Despite the large difference in F0, mule deer females respond vigorously to distress calls of both species (Lingle et al., 2007b). White-tailed deer females approach a speaker only when hearing calls of white-tailed deer fawns. These playback results suggest that certain acoustic traits are present in neonatal distress calls that enable white-tailed deer females to restrict their response to calls of their own species, but cause mule deer to respond to calls of both species.

We therefore hypothesized that white-tailed deer and other selective species respond to acoustic traits of distress calls that are “distinctive” of their own species, whereas mule deer and other less discriminating (more altruistic) species respond to acoustic traits “shared” across species. The test of this hypothesis requires two steps: (1) an acoustic analysis of distress calls of various species to identify distinctive and shared acoustic features and (2) a test of the salience of these acoustic features through playback experiments.

Acoustic traits that have been proposed to be responsible for the profound effect of infant vocalizations on a caregiver's response include F0 characteristics and modulation in F0 (frequency modulation or FM) (Aubin, 1987, 1989; Charrier et al., 2002; Lingle et al., 2012), harmonic structure (Aubin and Bremond, 1992; Charrier et al., 2002), and the presence or absence of nonlinear phenomena (e.g., Blumstein et al., 2008). F0 has been found to be one of the most useful traits for statistical discrimination of infant distress vocalizations made by different individuals (Blumstein et al., 2008; Charrier et al., 2002; Sousa-Lima et al., 2002; Lingle et al., 2012) and by different species, including white-tailed deer and mule deer (Lingle et al., 2007a). However, F0 has not specifically been manipulated in distress calls to determine the tolerance of caregivers for variation in this trait. Playback experiments suggest that FM and harmonic structure are critical to the response of seal mothers to the contact calls of their pups (Charrier et al., 2002) and to the response of adult starlings to distress calls of other adults (Aubin, 1987, 1989; Aubin and Bremond, 1992). The salience of vocal tract resonance frequencies has not been tested for the vocalizations of newborns but these certainly play an important role in the vocal communication of adults (Charlton et al., 2007; Taylor and Reby, 2010). Nonlinear phenomena have been proposed to reflect higher stages of distress and therefore lead to a heightened response by receivers (Riede et al., 2007), although the importance of these traits may depend on the taxonomic group (Blumstein and Chi, 2012; Lingle et al., 2012).

We included six species of ungulates in the acoustic analysis because anecdotal observations suggested that mule deer respond to distress calls made by juveniles from species other than white-tailed deer (Lingle, unpublished data). Species included in the analysis were eland (*Taurotragus oryx*), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), mule deer, white-tailed deer and pronghorn (*Antilocapra americana*), species that vary in body size from 31 kg to 3 kg at birth. These species have different lifestyles

(hider vs. follower), habitats (closed and open habitats) and taxonomical position (Cervidae, Bovidae and Antilocapridae) within the order Artiodactyla.

The acoustic results revealed that a basic pattern of FM was shared among the six species while the mean and maximum F0 enabled the greatest statistical discrimination of the six species. However, the fact that a trait occurs reliably in the calls of a particular species or in the calls of different species does not mean it is relevant to the response of receivers (Gerhardt and Bee, 2007). To determine whether the particular distinctive or shared traits we identified were salient to caregivers, we conducted playback experiments with manipulated distress calls to test the specific predictions that (1) the selective white-tailed deer would be less tolerant of shifts in F0 (the distinctive trait) than mule deer, and (2) the less discriminating (more altruistic) mule deer would approach the speaker only if the shared pattern of FM was present, but not to calls once the FM was removed.

2. Methods

2.1. Acoustic analysis

2.1.1. Recording of vocalizations

White-tailed deer and mule deer juveniles were recorded at the McIntyre Ranch (Alberta, Canada) between 2002 and 2004 for a previous study (Lingle et al., 2007a). Free-ranging pronghorn fawns were recorded at the Montana Bison Refuge (Montana, USA) in 2007. Captive eland were recorded in 2007 and 2008 at an eland farm at Lany, the Czech University of Life Sciences, and captive red deer fawns were recorded in 2007 at the Experimental Deer Farm, Institute of Animal Science (Prague, Czech Republic). Captive reindeer and additional pronghorn fawns were recorded in 2011 at the Assiniboine Park Zoo (Winnipeg, MB, Canada). Sound recording was either conducted or coordinated by S.L. and R.K. to ensure that equipment and procedures were comparable regardless of location or species. Juvenile ungulates were captured by hand or with small pole nets. One person manually restrained the animal, while another sexed and weighed it and attached an ear-tag. A third person stood 4 m from the animal to record vocalizations. Animals were released after these procedures. Free-ranging animals (mule deer, white-tailed deer, pronghorn) were monitored to ensure they were safely bedded and checked later in the day and the following day to confirm they were reunited with their mothers. Protocols for capture and handling procedures were approved by the Canadian Council on Animal Care (University of Lethbridge protocol #0707; University of Winnipeg protocol #117) and the Central Commission for Animal Welfare, Czech Republic (Czech University of Life Sciences, protocol #0308).

From 2002 to 2004, recordings were made with a Sony WM-DC6 or a Marantz PMD222 tape recorder and a Sennheiser directional microphone (ME 66) with windscreen. These analogue recordings were digitized with 16-bit accuracy at a sampling rate of 44.1 kHz. From 2007 to 2011, digital Marantz PMD660 and PMD671 recorders (44.1 kHz sampling rate) with a ME 80 or ME 66 Sennheiser microphone were used.

2.1.2. Acoustic analysis

Six calls from each of six pronghorn, nine reindeer, ten white-tailed deer, ten eland, ten mule deer, and ten red deer juveniles were analysed. Calls were selected for analysis from recorded calls using a random numbers table as long as they had an adequate signal to noise ratio. Calls made when an animal was ear-tagged were not used because the click of the tagging pliers interfered with the animal's vocalization. The sample for each species was split relatively equally between male and female individuals. Calls

were analysed with PRAAT 5.2 (Boersma and Weenink, 2011). Calls from eland and reindeer ($F_0 \sim 0.15$ kHz) were bandpass-filtered between 0.1 and 20 kHz. Calls from pronghorn, white-tailed deer, red deer and mule deer fawns ($F_0 > 0.3$ kHz) were bandpass filtered between 0.2 and 20 kHz. We measured 21 acoustic traits: (i) temporal traits (call duration, number of parts per call, time of maximum intensity, time of maximum F_0); (ii) F_0 (mean, maximum and minimum, start and end F_0); (iii) F_0 modulation (end F_0 – start F_0 , range F_0 = maximum – minimum F_0 , range F_0 as a proportion of the mean F_0 = range F_0 /mean F_0 , initial rise or descent during initial 50 ms, the number of inflections or change in $F_0 \geq 50$ Hz, and jitter); (iv) energy distribution: energy quartiles and dominant harmonics; (v) nonlinear parameters (deterministic chaos, subharmonics, biphonation and frequency jumps) (see Appendix A, Bohn et al., 2008; Table A.1 for methods used to analyse each trait).

Acoustic traits related to vocal tract filtering are formants, however, formant measurements were not possible in species having higher F_0 such as mule deer, white-tailed deer and red deer. Formant measurements depend on the presence of sufficient energy in the frequency range where formants can occur. For example, in mule deer and white-tailed deer with vocal tract lengths of 8 and 8.5 cm, respectively (measured in cadavers between glottis and incisors), a first formant around 1100 Hz and a second formant around 3200 Hz are expected. Mule deer distress calls have a F_0 near 1000 Hz and white-tailed deer distress calls a F_0 near 500 Hz. Only one or two harmonics would fall into the expected range of the first formant, which is not sufficient for reliable measurement.

Alternative traits that provide an indication of vocal tract filtering, and can be measured regardless of the animal's F_0 , are dominant harmonics and energy quartiles. Before measuring these traits, calls were sampled at 20 kHz and a spectrum (512-point FFT) was calculated for a 100 ms segment positioned in the middle of the call. Dominant harmonics were identified as the frequencies of the three harmonics with the highest amplitudes in a spectrum and were ranked according to their frequency (Lingle et al., 2007a). Energy quartiles (Schrader and Hammerschmidt, 1997) were identified as the frequency values that correspond to one-fourth, one-half and three-fourths of spectral energy.

2.1.3. Statistical analysis of acoustic data

An average value for each acoustic trait for each individual was included in the statistical analysis. Before using parametric tests, data were tested for homoscedasticity and normality. Log10 transformations were applied to the following variables to improve the equality of variances among groups or the normality of the distribution: call duration; mean, minimum, maximum and range F_0 ; initial ascent or descent; and jitter. A power transformation was applied to the start-end F_0 . We used one-way ANOVA to compare acoustic traits among the six species, followed by Tukey–Kramer tests for pairwise comparisons. We used the non-parametric median test to compare the number of inflections. A two-tailed P -value of 0.05 was considered statistically significant. Statistical tests were performed with JMP 7.0 (SAS Institute 2007).

We used a descriptive discriminant analysis (Huberty and Olejnik, 2006) to assess the relative importance of selected acoustic traits in the statistical distinction of calls made by the six species. The ANOVA results were used to aid selection of variables representing each category (temporal patterning, fundamental frequency, frequency modulation, and energy distribution), with a forward stepwise approach used in the discriminant analysis to evaluate the relative strength of similar traits that were highly correlated (e.g., mean vs. max F_0). Variables were standardized to eliminate dimensions before running the discriminant analysis. Using this approach, the following variables were selected for the discriminant analysis: (a) call duration; (b) mean F_0 ; (c) range/proportion of mean F_0 ; and (d) 2nd energy quartile.

Range/proportion of mean F_0 was selected over range F_0 because it gives an index of frequency modulation that is independent of the mean. The 2nd energy quartile was highly correlated with and had a similar effect to the other quartiles. These variables were retained in the discriminant analysis results even if they contributed little to the discrimination of species so that their contribution relative to other traits could be evaluated.

2.2. Playback experiments

2.2.1. Preparation of call stimuli

Playback stimuli were prepared from five white-tailed deer and five mule deer fawns. Eight calls (average duration 0.5 s) were assembled into one 20-s clip.

The first group of modified stimuli consisted of calls for which the F_0 was either raised or lowered, which were prepared to test the tolerance of females for variation in F_0 . These stimuli will be labeled as “X- F_0 -call”, where X stands for the factor by which the F_0 was multiplied, which ranged between 0.2 and 2.0 (F_0 reduced when $X < 1.0$ and raised when $X > 1.0$). The F_0 manipulation was performed with PRAAT's Manipulation Editor. We used the “multiply pitch frequencies” function to preserve the relationship between the range of F_0 and the mean F_0 and to maintain positive F_0 values when frequencies were lowered, in contrast to the alternative method of subtracting a fixed value. The Manipulation Editor is designed to treat F_0 and formant features independently which means that not only duration will be kept constant, but also energy distribution. In reality there will be a small associative effect. For comparison with the manipulated stimuli, the original calls were entered into the Manipulation Editor but no change was made to their F_0 . These are referred to as 1.0- F_0 calls or “reference calls”.

The frequency tends to rise and then fall during distress calls of the different species (see Section 3). The second group of modified stimuli consisted of calls from which any modulation in frequency was removed to test whether this rising and falling pattern of frequency modulation (FM) is essential for a female's response. FM was removed using the Synthesizer of Avisoft SASLab Pro software. The F_0 contour was flattened to the average F_0 of the call, maintaining the amplitude contour of the original call. Following manipulation of F_0 or FM, the average amplitude of all playback stimuli was standardized in PRAAT.

2.2.2. Study site and subjects

Playback trials were conducted from June through August 2011 and 2012 on a 125-km² portion of a large cattle ranch in southern Alberta, Canada (49°N, 112°W) dominated by rough fescue (*Festuca* spp.) grassland. Fawns were between one and ten weeks in age when playback tests were conducted. During this time period, fawns spend much of their time in hiding, which means they are bedded in vegetation and separated from their mothers except during brief visits to nurse. Female subjects were confirmed as being mothers by the presence of an active fawn, the presence of an udder or by behavioural characteristics such as being particularly solitary and vigilant. We tested a female when her fawn was bedded apart from her because she was unlikely to know the exact location of her fawn at that time. If a fawn was active with its mother, we waited for the fawn to bed and the female to move away from it before beginning a trial. We avoided testing the same subject more than once by distributing trials widely over the study area and by monitoring ear-tags or physical markings on animals that enabled us to identify individuals.

2.2.3. Playback trials

Observers sat at a location where they were unlikely to be detected by the subjects, 500–1500 m away, using binoculars and high-resolution spotting scopes (Swarovski ST-80 HD with 20–60×

zoom lens) for observation. Another person carried a Mipro MA 101 speaker (45 W, 60 Hz to 15 kHz frequency range, DC operated) into place, taking great care not to alert deer to his or her presence. Trials were not conducted if the subject alerted to this person. Observers gave directions over a two-way radio to guide the speaker person into place, with the speaker person using headphones and responding only by clicking the radio to avoid alerting the subject. The speaker person was guided along a route that kept him or her out of the deer's line of sight. The speaker person slowly crawled when moving the speaker within the subject's line of sight. Once the speaker was in place, this person moved to a hiding location, often on the back of a hill from where the speaker was located, and remained concealed by topography or vegetation while operating an iPod that was connected by a 25–50-m cable to the speaker. The speaker was placed within 75–200 m of the subject, with a median distance category of 125–150 m. To maximize sound transmission, we attempted to place the speaker upwind of the deer and to conduct trials when it was less than 25 °C. Calls were played at a peak amplitude of 105 dBC SPL, measured 1 m from the speaker, which is similar to the amplitude of natural distress calls (Lingle et al., 2007a). The propagation of sound to the subject was influenced by variation in temperature, terrain, wind direction and distance from the deer. The goal was therefore to ensure that each subject heard the call clearly, as indicated by their alerting and orienting to the calls.

One series of calls was played three times, lasting 60 s. If a subject was still approaching the speaker at the end of the three rounds, we continued to play the calls until the female had stopped her approach for 10 s. If a subject did not show alert behaviour, we tried to move the speaker closer to the animal.

2.2.4. Observation and scoring of responses

The observers recorded the subject's response on audiotape and videotape and monitored the response of other deer that were observed within 200 m of the speaker during the trial. Data were transcribed from audiotape and videotape following a trial. We identified the latency to alert, the general response (approach, remain in place, move away) and, when applicable, the latency to approach once alert. We identified the gait (walk, trot, lope, gallop or stot) and any pauses made during the approach as an indication of the animal's speed. It was common for animals to pick up speed as they came closer to the speaker and presumably heard the sound more clearly. For this reason, we focused the analysis on the distance to which the subject approached the speaker and her behaviour at that time, rather than on her behaviour at the start of the trial. The female's response was scored on an ordinal scale based on her basic response (alert, approach, retreat), her closest distance to the speaker and, for deer arriving within 10 m of the speaker, the tendency to stay near the speaker while the call was still playing. The scale was as follows: 0 = no alert behaviour; 1 = mildly alert: turns head and ears toward speaker briefly or intermittently; 2 = remains alert and oriented to speaker throughout trial following the moment when subject alerts; 3 = approaches speaker but travels <5 m; 4 = travels <25 m towards the speaker but remains >50 m from speaker; 5 = travels >25 m toward speaker but remains >50 m from speaker; 6 = approaches within 50 m; 7 = approaches within 25 m; 8 = approaches within 10 m; 9 = approaches within 10 m and maintains this proximity for >10 s. If deer came within 10 m of the speaker, we identified whether they displayed any form of aggressive behaviour, identified as leaning towards the speaker, typically with ears held to the side and fur flared, twisting or turning while facing the speaker, or hopping around the speaker. We recorded the number of deer of either species that were known to be within 200 m of the speaker at the start of the trial, and the number of those or other deer approaching the speaker within 50 m or 10 m during a trial.

The subject's starting distance from the speaker was determined following a trial using a GPS unit, unless topographical features enabled us to accurately estimate distance using a map, and assigned to a certain category (75–100 m; 100–125 m; 125–150 m; 150–200 m; 200–250 m; 250–300 m). The subject's closest distance to the speaker was determined using the body length of an adult deer (~1 m) to estimate short distances (<10 m) and topographical map or a GPS unit for longer distances.

2.2.5. Statistical analysis of playback data

Non-parametric tests were used to compare the response of females to calls that differed in fundamental frequency, with the frequency manipulation (e.g., 0.6-F0, 1.0-F0) serving as the categorical *x*-variable and the behavioural response as the ordinal *y*-variable. A Kruskal–Wallis test was used to test the response of females to the different manipulations of F0. Mann–Whitney *U* tests were used for unpaired comparisons when only two groups were involved (e.g., reference calls vs. FM-removed calls).

3. Results

3.1. Acoustic analysis

The distress calls of all six species had clearly defined harmonics throughout each call (Fig. 1). Calls were usually continuous, so that breaks rarely occurred within calls. The overall patterns of frequency and amplitude modulation were similar across species, with the frequency and amplitude typically rising for the first half of the call and falling during the remainder of the call (Fig. 1; Table A.2). Calls of pronghorn, white-tailed deer, red deer and mule deer were similar in duration (means, 0.49–0.61 s). Eland calls were much longer (mean = 1.62 s) and reindeer calls shorter (mean = 0.18 s) (Fig. 1a; Appendix A, Table A.2).

Mean and maximum F0 were the most distinctive acoustic traits (Fig. 2a, Table A.2). Eland (mean = 169 Hz) and reindeer (148 Hz) had F0 values that were similar to each other and much lower than the F0 for the other four species. F0 values for pronghorn (385 Hz), white-tailed deer (546 Hz), red deer (747 Hz) and mule deer (964 Hz) differed significantly from those two species and from each other. Species having a higher mean F0 had a greater range in F0 (maximum – minimum F0) than species with a lower mean F0 (Table A.2). Mule deer and red deer had the largest range in F0 relative to their mean F0 (range F0/mean F0), reindeer and pronghorn the least, with eland and white-tailed deer being intermediate between the other groups.

The species differed in patterns of energy distribution, but these differences were smaller than species differences in F0 (Fig. 2b; Table A.2). Eland and reindeer had the lowest quartile frequencies, and these differed significantly from the other four species.

Nonlinear features were rare in the distress calls of the six species (Table A.2). Subharmonics and biphonation were occasionally present, mostly in calls of eland, pronghorn and reindeer. There were few instances of deterministic chaos or frequency jumps.

The results of a discriminant analysis using the variables F0 mean, F0 range/F0 mean, call duration and the 2nd energy quartile, indicated that a combination of these variables was significantly associated with membership in a particular species (Wilk's lambda = 0.0007, approx. $F_{20,00,153.51} = 61.32$, $P < 0.0001$). Two discriminant functions were important in explaining the differences between the species, as revealed by eigenvalues greater than 1.0 (Table 1). The first function accounted for 91% of the variance explained by the four variables, with mean F0 resulting in most of this discrimination (eigenvector = 8.41), followed by call duration (eigenvector = 0.92). Call duration had the largest contribution (eigenvector = 2.65) to the second function. The contribution of

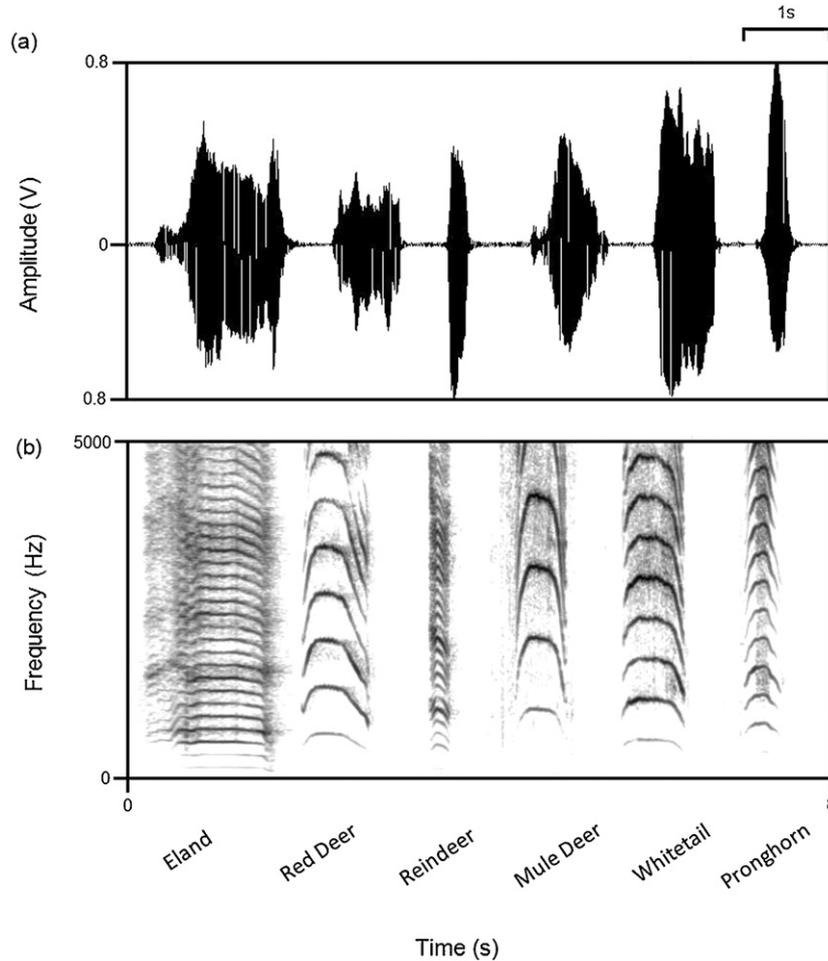


Fig. 1. Representative (a) oscillograms (relative change in output voltage of microphone signal) and (b) spectrograms of a juvenile distress call for six ungulate species. Species are organized according to the average body mass at birth, with the heaviest species on left.

energy quartiles and range F0/mean F0 mean was weak to both functions. The canonical plot of these two functions suggested that mean F0 was effective in discriminating all species other than reindeer and eland; and that call duration was instrumental in distinguishing reindeer from eland. Only one of 55 individuals was misclassified. Because our goal, and the goal of descriptive discriminant analysis, was to describe the nature of differences among the species and not classification (Huberty and Olejnik, 2006), we did not cross-validate the classification results.

3.2. Playback experiments

3.2.1. Mule deer

Mule deer responded strongly and similarly to 0.6-F0 calls (mean F0 = 580 Hz), 1.0-F0 calls (mean F0 = 930 Hz), and to 1.4-F0 calls (mean F0 = 1238 Hz) (Fig. 3a). They typically trotted or stotted to the speaker, arriving within 10 m of the speaker where they remained until the end of the trial. In 78% of cases, the deer standing within 10 m of the speaker displayed indications of aggressive behaviour. The mule deer's response to the 0.4-F0 calls

did not differ significantly from the 0.6–1.4-F0 stimuli, although there appears to be more variation in the response to 0.4-F0 calls (Fig. 3a). Mule deer responded more weakly to 0.2- and 1.8-F0 calls than to calls falling within the 0.4–1.4-F0 range (Fig. 3a; Kruskal–Wallis test: $H_5 = 21.29, P = 0.0007$). Subjects were only mildly alert to most of the 0.2-F0 calls, with none moving even a few steps closer to the speaker. They usually showed stronger alert behaviour to the 1.8-F0 calls, but did not approach except for in one trial in which a female displayed the maximum response. Differences in response to the F0 manipulations were not due to variation in the starting distance of the subject from the speaker, for this did not differ in a consistent manner across the frequency categories (ANOVA: $F_{5,37} = 0.84, P = 0.53$).

Mule deer responses to manipulated white-tailed deer calls were consistent with their response to the F0 of conspecific calls. Mule deer that were present during trials with white-tailed deer females usually approached when 1.0-F0 to 2.0-F0 (504–1102 Hz, respectively) white-tailed deer calls were played, but not when 0.4 and 0.6-F0 (mean F0 < 300 Hz) white-tailed deer calls were played (Fig. 4a).

Table 1

Relative importance of two discriminant functions (DF) and their component acoustic traits in distinguishing calls of the difference species.

	Eigenvalue	% variance	F0 mean ^a	Call duration	Range F0/mean F0	2nd energy quartile
DF1	89.13	91.00	8.41	0.92	0.32	0.43
DF2	8.09	8.25	-0.57	2.65	0.44	-0.27

^a Similar results were achieved for F0 mean and F0 max.

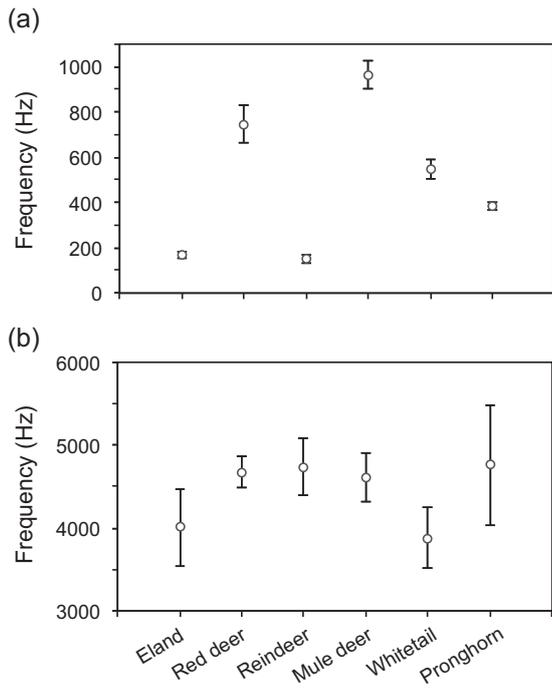


Fig. 2. (a) Average fundamental frequency (F0) and (b) second quartile frequency (i.e., the frequency below or above which 50% of energy is emitted) for juvenile distress calls of six ungulate species (mean \pm SD). Species are organized according to the average body mass at birth, with the heaviest species on left.

Mule deer responded as strongly to FM-removed calls as to reference calls (median, interquartile range: FM-removed, 9.0, 7.75–9, $N=6$; reference, 9.0, 6.0–9.0, $N=9$; Mann–Whitney U test: $U=54.5$, $P=0.39$). They displayed aggressive behaviour in three of four FM-removed trials in which they came within 10 m of the speaker.

3.2.2. White-tailed deer

White-tailed deer females responded strongly and similarly to reference calls (mean 1.0-F0 = 504 Hz) and to calls shifted 40% above or below this range (mean 0.6-F0 = 290 Hz, mean 1.4-F0 = 690) (Fig. 3b). They typically came within 10 m or 25 m to these calls. They did not approach when hearing the 0.2- or 0.4-F0 calls or when hearing 2.0-F0 calls; their response to 0.4-F0 (mean = 206 Hz) and to 2.0-F0 (mean = 1102 Hz) calls differed significantly from their response to calls falling within the 0.6–1.4-F0 range (Fig. 3a; Kruskal–Wallis test: $H_4=16.19$, 5 df, $P=0.006$). In contrast to mule deer, their response to the 0.4-F0 calls was weak and their response to the 1.8-F0 calls was relatively strong (Fig. 3a,b).

White-tailed deer responses to manipulated mule deer calls were consistent with their response to the F0 of conspecific calls. White-tailed deer females that were present at the start of mule deer trials did not approach during seven trials in which the call stimulus was as high or higher than the mule deer reference call (mean >930 Hz), but they did approach in two of three cases when 0.6-F0 mule deer calls (mean = 580 Hz) were played (Fig. 4b).

Similar to mule deer, white-tailed deer responded strongly to calls from which FM had been removed (median, interquartile range: 9.0, 6–9, $N=4$). There was no statistical difference between their response to FM-removed calls and their response to reference calls (Mann–Whitney U test: $U=28.0$, $N_1=4$, $N_2=6$, $P=0.25$).

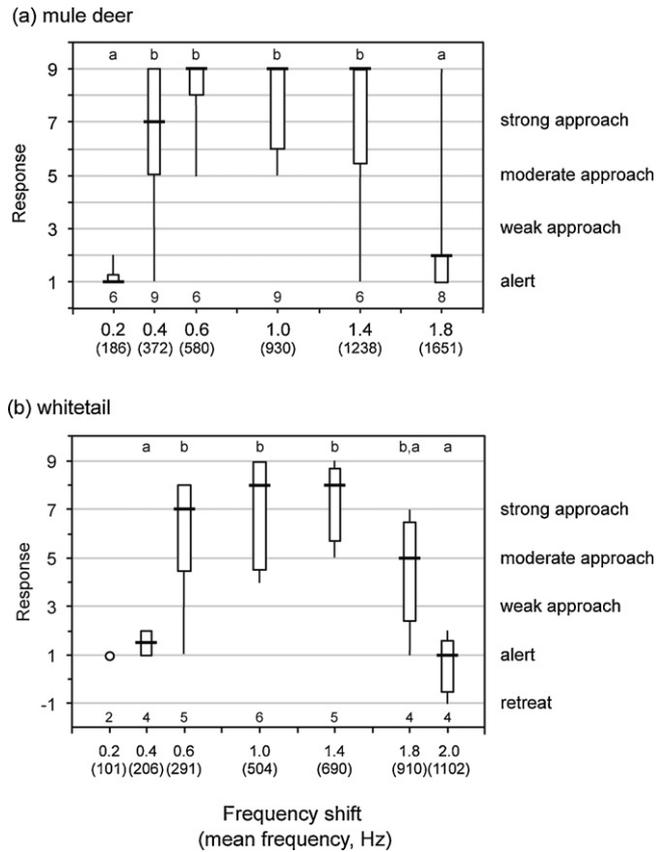


Fig. 3. Behavioural responses of (a) mule deer and (b) white-tailed deer to playback stimuli of conspecific calls that vary in F0. X-axis shows the magnitude of F0 manipulation (e.g., 0.6, 1.0, 1.4) with the mean F0 (Hz) for each manipulation in parentheses. Horizontal bars show median, boxes the 25th to 75th percentiles, and whiskers show the full range of data. Data points, and no box, are shown when only one or two trials were done for a particular category (0.2-F0 for white-tailed deer). Numbers at the base of each plot show the sample size for each manipulation. Groups that differ significantly are represented by a different letter at the top of graph.

4. Discussion

4.1. Overview of findings

We conducted an acoustic analysis followed by playback experiments to test the hypothesis that selective species such as white-tailed deer that fail to respond to heterospecific calls respond to acoustic traits distinctive of their species and less-discriminating species such as mule deer respond to acoustic traits shared across species. The acoustic results indicated that mean and maximum F0 enabled the greatest statistical discrimination of the six species while the basic pattern of FM was shared. Filter-related traits of energy quartiles and dominant harmonics contributed little to the discrimination, and nonlinear features were rare. Contrary to our initial hypothesis, playback experiments revealed that females of the two species respond similarly to manipulation of F0 and FM. Females of both species responded as strongly to calls from which FM was removed as to the original calls. The most surprising result was that white-tailed deer females, which do not approach when hearing mule deer calls (Lingle et al., 2007b), were as tolerant as mule deer to manipulations of F0. Females of both species responded at their maximum to calls with the mean F0 shifted by a factor of approximately 0.6 to 1.4 \times relative to the mean F0 of distress calls of conspecific neonates, and a female's response was extinguished once F0 was shifted beyond this range. A shift of 0.6 to 1.4 \times results in a larger absolute frequency range for animals such

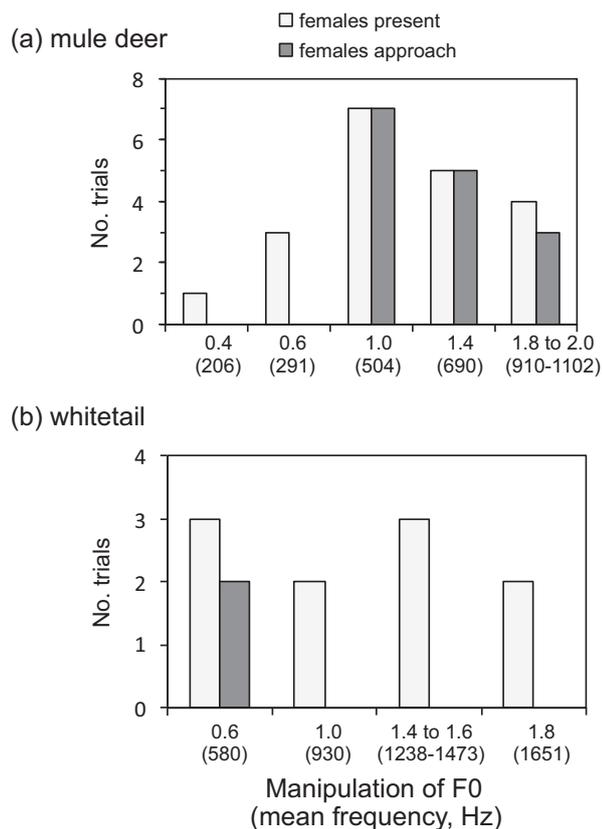


Fig. 4. Response of females to manipulations of heterospecific calls including: (a) response of mule deer females to manipulated white-tailed deer distress calls and (b) response of white-tailed deer females to manipulated mule deer distress calls. The primary subject during these trials was a conspecific female (data shown in Figs. 3 and 5). However, heterospecific females were sometimes present. “Females present” shows the number of trials in which at least one mule deer (a) or white-tailed deer mother (b) was present before a heterospecific call was played. “Females approach” shows the number of those trials in which at least one female approached the speaker when the heterospecific calls were played.

as mule deer that are tuned to a higher average F0, which could be the main reason (at a proximate level) for the asymmetrical response of females to heterospecific calls. This discovery suggests that mule deer females only appear less discriminating because they are tuned to the higher F0 of mule deer distress calls (964 Hz vs. 546 Hz), which results in a larger absolute response range that encompasses the F0 of white-tailed deer fawns.

Differences in F0 did not correspond to body size (Fig. 2a), nor to larynx size, as revealed by preliminary investigations of cadavers, and must instead be caused by differences in laryngeal control or vocal fold mechanical properties (e.g., Riede et al., 2010). Species differences in energy distribution can be partly explained by body size differences. The eland juveniles were the largest among the six tested species and, as expected, demonstrated lowest quartiles and dominant harmonics (Fig. 2b). Interestingly, low energy quartiles and dominant harmonics were also found for reindeer (Fig. 2b) and were not expected because reindeer neonates are much smaller than eland and close in size to white-tailed deer and mule deer juveniles. It is possible that distinctive features of the vocal tract of reindeer (Frey et al., 2007) affect resonance properties of juvenile vocalizations. These results are consistent with other studies reporting greater plasticity in F0 and its independence from body size (Riede and Titze, 2008; Reby et al., 2010) when compared to resonant frequencies, which are more constrained by the overall size and structure of the vocal tract (Frey et al., 2007; Taylor and Reby, 2010).

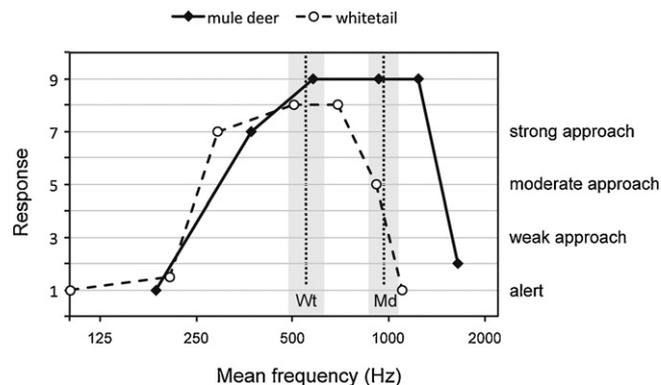


Fig. 5. The response range of mule deer females and white-tailed deer females relative to variation in mean F0, as depicted by the median behavioural response during playback trials. Gray shading represents the range of mean F0 values for distress calls of individuals of each species measured in this study (Wt = white-tailed deer; Md = mule deer). The dotted vertical line shows the mean of the mean F0 (Fig. 1).

4.2. Female discrimination and juvenile distress call F0

The two species tolerate similar levels of variation in F0 when expressed on a logarithmic scale (Fig. 5), which is the appropriate scale from a perceptual perspective since hearing curves and the perception of F0 follow a logarithmic scale in mammals (e.g., Heffner and Heffner, 1998; Fay and Popper, 2000). However, this similar relative response range translates to a larger absolute response range for mule deer when expressed on a linear scale, because the mean F0 of mule deer distress calls is higher (Fig. 3). The consequence is that the mean F0 of calls emitted by white-tailed deer fawns (546 Hz) falls within the F0 range to which mule deer respond strongly (Fig. 4). In contrast, the mean F0 of mule deer calls (964 Hz) lies above the F0 to which white-tailed deer females respond strongly (Fig. 5).

White-tailed deer females displayed a moderately strong response to 1.8-F0 calls, which coincides with the lower F0 emitted by certain mule deer fawns, suggesting it is possible that white-tailed deer females might respond to mule deer calls if sufficiently low in F0. Although white-tailed deer approached the speaker in response to mule deer calls lowered by 0.6 (Fig. 4), we have not observed them approach in response to unmanipulated mule deer calls during this or a previous study (Lingle et al., 2007b). Given that the removal of FM did not reduce the response of females, it should be possible to obtain a more precise representation of the response range of each species by playing calls that differ in F0 but lack FM.

These findings lead to more general predictions about signal evolution and female discrimination of heterospecific calls. F0 was well differentiated among five of the six species examined in this study, while other features overlapped or were similar: FM, the time of peak amplitude, harmonic structure, filter-related traits such as dominant frequencies and energy distribution, and the near absence of nonlinear features. These acoustic results suggest two testable hypotheses: first, that divergent evolution in F0 was central to the evolution of distress calls in many ungulate species and, second, that F0 is critical to the response of animals from a variety of species to conspecific and heterospecific vocalizations.

We propose that females will have a larger absolute response range, and therefore appear to be less discriminating, when they belong to a species having juveniles that produce higher F0 calls. A consequence of being tuned to a high F0 is that the response range will tend to overlap calls of low F0 species more than the reverse, potentially leading animals from high F0 species to respond to many more stimuli than is adaptive. This assumes that females tolerate a similar extent of relative F0 variation, as found for these two species. The hypothesis that animals will appear to be less

discriminating when they belong to a high F0 species may apply broadly to animal vocalizations, given that F0 is the most differentiated trait in many behavioural contexts (Levréro et al., 2009; Reby et al., 2010; Fallow et al., 2011) and is critical to the response of animals in contexts other than mother–infant communication (Reby et al., 2010). This line of reasoning also raises the possibility that there may be more competition among sympatric species for acoustic space in the range of lower frequencies, with divergence in alternative traits such as temporal features for low F0 species.

The response of mule deer females to white-tailed deer distress calls is not the only unusual aspect of mule deer behaviour. Even when a mule deer female has reliable information that her own offspring are safe, such as when her fawns stand next to her, she will nevertheless approach a speaker in response to distress calls (Lingle et al., 2007b) and will defend non-offspring against coyotes (Lingle et al., 2005). These forms of cooperative behaviour have not been observed in white-tailed deer. It is important to stress that the results of this study explain the asymmetry in white-tailed deer and mule deer responses to distress calls, but do not explain the tendency of mule deer females to help unrelated fawns when their own offspring are safe.

4.3. Why do females respond to such a broad range of F0?

Females of both species responded strongly to a range of F0 that extends much higher and lower than the mean F0 emitted by neonates of their respective species (Fig. 5). Data for ungulates suggest that an individual's F0 declines during the rapid period of growth that occurs during the first few months of life (Richardson et al., 1983; Torriani et al., 2006; Efremova et al., 2011; Briefer and McElligott, 2011). The response range of females might therefore be broad so as to encompass sounds produced by older juveniles as well as newborns. The mean F0 of mule deer neonates appears to lie toward the higher end of the female's response range, as would be expected if the female's response range encompassed frequencies emitted by older fawns. To test this hypothesis, changes in F0 during the fawn's initial months of life need investigation. More exact information is also required on the upper and lower limits of the female response range for each species.

An alternative hypothesis that might explain the response of females to such a broad range of F0 and especially their strong response to calls lacking FM and to calls made by different individuals despite considerable acoustical differentiation in these calls (Lingle et al., 2007a,b) is that a female's level of discrimination might depend on the urgency involved in a particular behavioural context (Clark et al., 2006; Lingle et al., 2007b). Female deer typically hear distress calls that are produced by fawns from a distance of 100–500 m. The signal can be degraded considerably when traveling through vegetation, topographical variation or wind, which implies an advantage for females that are not overly selective. When a predator attacks a fawn, females do not have the luxury of time to delay to collect additional acoustic or other information before deciding whether or not to help.

It would be useful to determine whether females of these species are more selective about acoustic cues when responding to low amplitude contact calls that are emitted at closer proximity such as when fawns try to find their mothers to suckle. Similarly, it would be informative to test whether species that display individual recognition of contact calls such as most otariid (Innsley et al., 2003) and some ungulate species (Espmark, 1971; Briefer and McElligott, 2011) respond preferentially to the calls of their offspring when these calls are played at a high amplitude that reflects greater urgency. The urgency of the situation and costs of making a recognition error might override the benefits of being selective

even in species such as these, which have been shown to be selective in a less urgent context (Lingle et al., 2007b).

5. Conclusion

Our results show that F0 is the most differentiated trait in the distress calls of the six species of ungulates and is critical to the responses of female deer to distress calls. The female's response to variation in F0 appears to explain the response by white-tailed deer and mule deer to heterospecific as well as to conspecific distress calls. The finding that females from the two species respond to a similar relative range of F0 leads to more general hypotheses about female discrimination and juvenile F0. We propose that animals from species that emit vocalizations with high F0 may appear to be less discriminating in their responses to heterospecific vocalizations than animals from species emitting lower F0, because the absolute response range of a high-F0 species will be larger and more likely to overlap with calls emitted by the low-F0 species than the reverse. F0 has frequently been found to be the most differentiated trait in other behavioural contexts, so this prediction may be more far reaching than the context of mother–infant communication.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2012.09.011>.

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