



Altruism and recognition in the antipredator defence of deer: 1. Species and individual variation in fawn distress calls

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Mule deer, *Odocoileus hemionus*, females actively defend fawns against predators, including nonoffspring conspecific fawns and heterospecific white-tailed deer, *O. virginianus*, fawns. We hypothesized that the defence of nonoffspring fawns was due to a recognition error. During a predator attack, females may have to decide whether to defend a fawn with imperfect information on its identity obtained from hearing only a few distress calls. We examined fawn distress calls to determine whether calls made by the two species and by different individuals within each species were acoustically distinctive. The mean and maximum fundamental frequencies of mule deer fawns were nearly double those of white-tailed deer fawns, with no overlap, enabling us to classify 100% of calls to the correct species using a single trait. A large proportion of calls was also assigned to the correct individual using a multivariate analysis (66% and 70% of mule deer and white-tailed deer fawns, respectively, chance = 6% and 10%); however, there was considerable statistical uncertainty in the probability of correct classification. We observed fawns approach conspecific females in an attempt to nurse; females probed most offspring fawns with their noses before accepting them, and always probed nonoffspring fawns before rejecting them, suggesting that close contact and olfactory information were needed to unequivocally distinguish nonoffspring from offspring fawns. Taken together, these results suggest that acoustic variation alone would probably be sufficient to permit rapid and reliable species discrimination, but it may not be sufficient for mothers to unequivocally distinguish their own fawn from conspecific fawns.

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Like parents of many species, mule deer, *Odocoileus hemionus*, and white-tailed deer, *O. virginianus*, females defend their young against predators (reviewed in: [Montgomerie & Weatherhead 1988](#); [Caro 2005](#)). Mule deer, however, defend fawns that are not their own offspring, including those of white-tailed deer (hereafter whitetails, whitetail female or fawn; [Lingle et al. 2005](#)). Whitetail females seem to restrict defence to their own offspring.

The protection provided by mule deer clearly benefits the individuals being helped. Fawns that are defended

against coyotes, *Canis latrans*, are unlikely to be killed ([Lingle et al. 2005](#)). However, the costs are more apparent than the benefits for females that defend nonoffspring. At the minimum, females devote considerable time and energy to defence ([Hamlin & Schweitzer 1979](#); [Truett 1979](#); [Wenger 1981](#); [Wilkinson & Douglass 2002](#)). Mule deer females sometimes leave their own fawns behind to defend another fawn, which could expose their own fawn to greater risk. Females themselves can be attacked after intervening ([Lingle & Pellis 2002](#); [Lingle et al. 2005](#)).

Fawns of both species are 'hidiers' ([Lent 1974](#)). They remain hidden in vegetation and bedded apart from their mothers during the first few months of their lives, except for short visits from their mother to nurse. Like the young of many taxa, fawns utter loud distress calls when discovered by predators ([Richardson et al. 1983](#); [Smith 1987](#)).

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These calls can summon females from hundreds of metres away. Mule deer females that respond typically defend an attacked fawn by intercepting it and then chasing and striking the predator with their forelimbs. Whitetail females are more likely to hover around the area in which an attack is taking place without intervening (Lingle et al. 2005).

One possible explanation for the responses of whitetail and mule deer females is that they are simply unable to distinguish calls produced by different fawns, including calls produced by fawns of the different species. Females may therefore be constrained to respond to all calls in the way that would prove adaptive when they hear their own fawn cry. Distress calls made by fawns of the two species may be similar because of their common ancestry. The structure of calls made by different individuals or by the two species may even have converged if selection favoured the recruitment of supernumerary defenders (Russ et al. 2004).

We also need to consider the perspective of animals receiving these signals. The urgency inherent in a predatory attack can influence the discrimination behaviour of potential helpers by affecting both the quality of information available to them and the fitness consequences of their decisions to accept or reject fawns as their own (Reeve 1989; Koops & Abrahams 1998). Under normal circumstances, a female returning to a bedded fawn has time to investigate the fawn thoroughly before deciding whether or not to nurse it. The cost of a temporary delay in the context of a nursing attempt is unlikely to be detrimental to a female's own offspring and probably has a greater overall benefit of sparing the female from nursing fawns other than her own. But if a fawn is being attacked by a predator and can only survive if defended immediately, a female may not have the time or close contact with the fawn needed to collect additional perceptual information. She may have to decide whether to help the fawn with imperfect information on its identity in the form of a few distress calls. Given fitness consequences if a female were to fail to defend her own fawn, we would not expect a female to ignore distress calls if there were a possibility that they were uttered by her own fawn.

Available reports suggest that females of most ungulate species obtain imperfect information on their offspring's identity from vocalizations alone. Neonates of some ungulate species utter contact or distress calls that have individually distinctive characteristics (Espmark 1975; Shillito Walser et al. 1981; Richardson et al. 1983; Terrazas et al. 2003). Mothers give stronger responses to calls of their own offspring than to those of alien offspring, but this preference is not absolute (Espmark 1971; Shillito Walser et al. 1981; Vanková et al. 1997; Terrazas et al. 2003). Female ungulates appear to require olfactory cues, gathered at very close range (<0.25 m), to unequivocally identify their offspring (Alexander 1978; Terrazas et al. 1999; Poindron et al. 2003), although they may be better able to use non-olfactory cues as the young animal ages (Ferreira et al. 2000).

We hypothesized that mule deer females defend non-offspring because they are unable to reliably discriminate these animals from their own fawns during a predatory attack. The first step in testing this hypothesis was to investigate the signals uttered by animals seeking help. We recorded and analysed fawn distress calls to determine the

degree to which distress calls made by the two species and by different individuals within each species were acoustically distinctive. We also examined naturally occurring recognition behaviour to determine whether females appeared to rely on remote (visual or vocal) cues to identify fawns before accepting or rejecting their nursing attempts. Alternatively, females may need to establish close contact to collect olfactory information, which would probably not be available during a predator attack. In a companion paper (Lingle et al. 2007), we report a series of playback experiments used to determine how animals respond to acoustic variation identified here. Those experiments were designed to test alternative hypotheses for the apparently altruistic defence of nonoffspring fawns by mule deer, while examining how the information available on a fawn's identity affected a subject's response.

In contrast to most previous work on mother-offspring recognition in ungulates, this work was done with animals in a free-ranging population. Females living in a free-ranging population face challenges that potentially affect the cues needed to reliably identify their offspring, because females typically encounter a relatively large number of animals distributed over a large geographical range when searching for their offspring.

METHODS

Study Site and Subjects

Research was conducted on a 225-km² cattle ranch in southern Alberta (49°N, 112°W) dominated by rough fescue (*Festuca* spp.) grassland. Most habitat variation was topographical, with three slope systems traversing the study area. The majority of whitetail and mule deer females reared their fawns on or near these slopes (Lingle et al. 2005). Adult females of both species usually give birth to one or two fawns each June.

Recording of Vocalizations

We captured 73 mule deer and 49 whitetail fawns in the summers of 2002–2004 after spotting fawns that bedded down following a visit from their mothers. These fawns ranged in age (and weight) from less than 24 h (3–4 kg) to 2 weeks (9–10 kg). Each fawn was manually restrained while we identified its sex, measured its hind foot, weighed it and attached a coloured plastic All-Flex tag to one or both ears to enable future identification. During this time, one person stood 4 m from the fawn to record fawn vocalizations with an analogue tape recorder and shotgun microphone (Sony WM-DC6 with Sennheiser ME 66 in 2002; Marantz 222 with ME 80 in 2003, 2004), shielded by a professional windsock. Handling took about 8 min, after which the fawn was placed in an untrampled bed site and monitored from a distance to ensure that the fawn remained safely bedded or reunited with its mother. The protocol followed when handling and monitoring fawns was approved by the University of Lethbridge Animal Care Committee (protocol no. 0210) in accordance with the Canadian Council on Animal Care Guidelines.

Acoustic Analysis

Acoustic analysis was restricted to strong calls made with an open mouth. Recordings of 652 calls used in the analysis had a mean \pm SD maximum intensity of 83.0 ± 3.2 dB and background noise of 45.0 ± 6.6 dB. Because the recording level was adjusted in the field to obtain the best possible signal-to-noise ratio, these sound intensity measures do not represent the absolute intensity of calls produced by fawns.

Analogue recordings were digitized with 16-bit accuracy at a sampling rate of 44.1 kHz using the SpeechStation acoustics software (Version 1.1.2, Sensimetrics, Somerville, Massachusetts, U.S.A.) after low-pass filtering at 20 kHz. Each fawn's call rate (calls/min during the period of restraint) was determined at that time. Subsequent acoustic analyses were done in PRAAT 4.0 (P. Boersma & D. Weenink, University of Amsterdam, The Netherlands). The fundamental frequency (F0, perceived as the pitch) and sound intensity were sampled every 5 ms. These data were used to calculate several characteristics of the F0, including maximum F0, minimum F0, start F0, end F0 and average F0, and two characteristics of frequency modulation, including the F0 range (max–min F0) and the difference between the start and end F0 (start–end F0). We measured several aspects of temporal patterning, including the time of the maximum F0, the time of the minimum F0 and the time of the maximum sound intensity. We calculated the time elapsed from the start of the call to each of these events and expressed this as a proportion of the duration of F0. We also measured the correlation between F0 and sound intensity within each call.

In addition, we identified characteristics of the distribution of energy in each call. For this analysis, we obtained a fast Fourier transform (FFT) from an approximately 0.12-ms slice of each call using a Hanning window. From the resulting power spectrum, we measured the relative intensity of the three lowest harmonics (Intensity H1–Intensity H2; Intensity H1–Intensity H3; Intensity H2–Intensity H3, where H1 = F0). We also identified the frequency and intensity of the three strongest harmonics in the power spectrum, designating these the dominant harmonics (DH). The dominant harmonics were sorted by frequency, (i.e. lowest DH, middle DH, highest DH) and were used to calculate an average DH. Lastly, we reported the presence of subharmonics during a call using a discrete scale (0 = no subharmonics, 1 = faint and brief subharmonics, 2 = clear, strong subharmonics visible for part or all of the call).

Statistical Analysis

For the analysis of the distinctiveness of calls made by the two species, we calculated a mean value for each acoustic feature for each individual using 400 calls made by 33 mule deer and 252 calls made by 22 whitetails. A general linear model, GLM (JMP 5.0, SAS Institute, Cary, North Carolina, U.S.A.), was used to compare acoustic features of the two species while controlling for confounding effects of sex or weight. A discriminant function analysis was used as

a classification procedure to evaluate whether calls could be assigned to the correct species at a rate better than expected by chance. In a first test, we used mean values for individual fawns to ensure the independence of data points. In a second test, we used the data from each of the 652 individual calls. In both cases, the results were cross-validated using a jackknife procedure, in which all calls except the one to be classified were used to generate a classifying function that was then used to assign the excluded call to one or the other species. The procedure was repeated serially until all calls were classified.

For the analysis of the distinctiveness of calls made by individuals, we used data for individuals for which we had recorded 15–20 high-quality calls, which included 16 mule deer (average = 19.5 calls/fawn) and 10 whitetail fawns (18.6 calls/fawn). We used data for only one fawn when we had data for maternal twins. We undertook an initial screening of acoustic features using a metric that quantifies the degree of interindividual relative to intra-individual variation (Robisson et al. 1993; Bee & Gerhardt 2001; Charrier et al. 2002). This metric is labelled the 'potential for identity coding' (PIC), and is the ratio of the between-individual coefficient of variation to the within-individual coefficient of variation (i.e. CV_b/CV_w). The CV_b for each trait was calculated from mean values for acoustic traits for each individual; the CV_w was calculated as the mean CV for acoustic traits for all individuals, using the formula for small samples in both cases (Sokal & Rohlf 1995). When values below zero were present for a trait (i.e. differences in intensities, start–end frequency), we added a constant so that all values were greater than zero before calculating CVs. A PIC value greater than 1.0 is generally considered to indicate that between-individual variation exceeds within-individual variation and, therefore, that the trait in question has the potential to be useful for individual recognition.

In the discriminant function analyses that followed, we included acoustic features with PIC values of at least 0.80, then used a stepwise procedure to eliminate features that contributed little unique variance, as indicated by non-significant *F* ratios. We initiated this analysis with PIC values below one, because while the PIC metric is wholly intuitive, its utility has not been critically evaluated. One ordinal trait, the presence of subharmonics, was included in the function. As with the species analysis, discriminant functions used to assign calls to individuals were cross-validated using a jackknife procedure. Observed versus expected classification success was compared using *G* tests with Williams' correction.

A priori probabilities for groups were set at equal when running the discriminant function analysis and when comparing expected versus observed classification success. This procedure is in accordance with Tatsuoka (1988), who indicated that the occurrence of groups in the natural population, not the test sample itself, should be used to establish a priori probabilities. Even though mule deer and whitetail fawns were equally common, mule deer are easier to capture, so we were able to record more mule deer individuals and calls. The expected classification success would have been higher than that observed (75% versus 50%) if it had been weighted towards the larger sample

obtained for mule deer. Nevertheless, given the unambiguous success of classification (100% using a single trait), this approach would not have changed the statistical or biological significance of the analysis. Any differences in analyses of individual variation would have been trivial if a priori probabilities or expected classification success had been adjusted to the sample size, because there were only slight differences between the number of calls used to compare acoustic features of individuals (mule deer: 12 fawns with 20 calls, one with 19 calls, one with 18 calls, one with 17 calls; whitetails: seven fawns with 20 calls, one with 16 calls, two with 15 calls).

When assigning a case to a group, discriminant function analyses calculate the probability that a specific case belongs to each of the available groups, then assigns the case to the group to which it has the highest probability (Tatsuoka 1988). This means that a particular call can have a relatively low probability of membership (e.g. 0.25) in the group to which it was assigned. In this study, we report the probability of group membership (posterior probability) as an indication of the statistical certainty with which an individual case was classified. If distinctions between groups are large and cases consistently fall near the centroid for the correct group, high probabilities of group membership would be expected.

Observation of Female–Fawn Meetings

We observed female–fawn meetings to determine whether females typically probed fawns with their noses, presumably to gather olfactory information, when fawns attempted to nurse. We observed fawns that rose from bed sites, at which time they typically searched for their mothers and often encountered other females. Females also actively search for their fawns. When a fawn approached a female with a suckling posture, we identified whether the female visibly extended her nose to the fawn's body and whether she then accepted the fawn to nurse or rejected it. A female was identified as rejecting a fawn if she pulled her udder away from the fawn, which was often followed by kicking the fawn. Fawns that were not permitted to suckle and then departed to search for another female were assumed to be alien (nonoffspring) to that female. Fawns allowed to suckle, which then remained with the female, were assumed to be offspring. We did not include a few observations in which a fawn simply accompanied a female but did not suckle (females alert to humans or coyotes sometimes refused to nurse their own offspring but it stayed with them) or observations of additional suckling attempts occurring after a mother and fawn had been together. Like many ungulates (Terrazas et al. 1999; Ferreira et al. 2000), female deer rapidly form exclusive nursing relationships with their own offspring. Females occasionally tolerate brief suckling bouts by non-offspring in captivity, but we found no evidence of this while observing marked individuals in this free-ranging population (S. Lingle, personal observation). Nevertheless, fawns frequently attempt to suckle from females other than their mothers and sometimes appear to succeed for a second or two before being rejected.

We identified the body site that females sniffed and, for fawns that were allowed to suckle, whether the female sniffed the fawn before, simultaneous with, or following acceptance of the fawn. Females were scored as smelling a fawn that they accepted only if they smelled it before or simultaneous with the moment of acceptance or rejection. We recorded the fawn's known age if it had an eartag, and otherwise estimated its age, from less than 1 to 12 weeks based on the median birth date for each summer and variation in fawn size. We tested whether the presence of an eartag on a fawn was related to female recognition behaviour to ensure that this visual cue did not confound our results.

RESULTS

Fawns of both species made tonal calls with a rich harmonic structure (Fig. 1; see [Supplementary Material, ESM 1](#)). The F0 tended to be low at the onset of the call, to rise to a maximum during the first half of the call, and then to drop as low or lower than the onset frequency by the end of the call (Table 1). Breaks in the F0 of calls were rare, as were noisy (atonal) calls. Subharmonics were visible in 24% of calls, although they were often faint and brief.

Relation between Acoustic Structure and a Fawn's Species, Sex and Weight

The F0 of mule deer calls was nearly twice as high as the F0 of whitetail calls (Table 1). This difference was evident in all aspects of the F0, but was more pronounced at the high than at the low end of the fawns' frequency range. There was no overlap between the species in mean or maximum F0, even when examining individual calls made by fawns (Fig. 2). The frequency modulation of calls was also greater for mule deer than for whitetail calls, as evidenced by the larger frequency range of mule deer calls and the larger

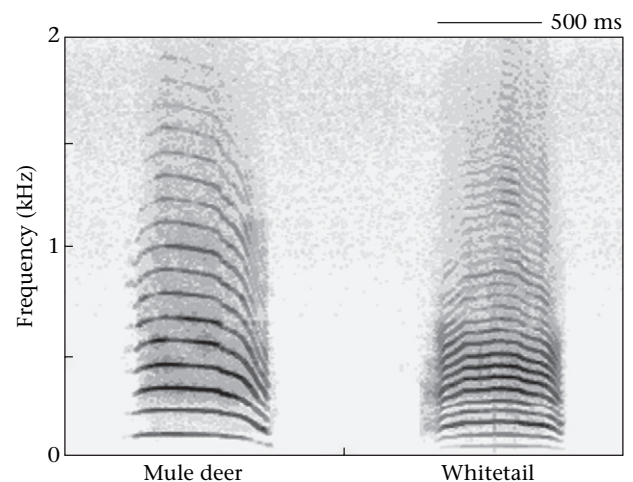


Figure 1. Sonagram of distress calls made by a mule deer fawn (7.3-kg male, mean F0 = 1016 Hz for call) and a whitetail fawn (5.8-kg male, mean F0 = 509 Hz for call). See [Supplementary Material ESM 1](#) for sound (.wav) files for these calls.

Table 1. Acoustic structure of fawn cries calculated from average values for individuals ($N = 33$ mule deer, 22 whitetails)

| Acoustic trait | Mule deer | Whitetail | Species | Sex | Weight |
|-----------------------------------|------------------------------------|------------------------------------|---------------------|------------------|------------------|
| | Mean \pm SD (range) | Mean \pm SD (range) | $F_{1,51}$ * P | $F_{1,51}$ * P | $F_{1,51}$ * P |
| Fundamental frequency (F0) | | | | | |
| Maximum (Hz)† | 1030 \pm 102.0 (844–1304) | 583 \pm 49.8 (485–685) | 550.80 <0.0001 | 75.0 0.009 | 0.41 0.53 |
| Minimum (Hz)† | 613 \pm 92.5 (431–818) | 411 \pm 43.9 (309–473) | 117.53 <0.0001 | 5.56 0.02 | 0.32 0.58 |
| Mean (Hz)† | 927 \pm 99.2 (771–1203) | 541 \pm 47.8 (442–624) | 443.43 <0.0001 | 7.69 0.008 | 0.83 0.37 |
| Range (Hz)† | 417 \pm 85.5 (183–613) | 172 \pm 35.2 (103–236) | 196.42 <0.0001 | 0.21 0.65 | 0.09 0.76 |
| Start–end (Hz)† | 201 \pm 125.2 (2.0–461) | 51 \pm 11.6 (–86–155) | 27.07 <0.0001 | 0.02 0.89 | 0.18 0.67 |
| Temporal patterning | | | | | |
| Duration F0 (s)† | 0.577 \pm 0.117 (0.300–0.796) | 0.540 \pm 0.153 (0.256–0.894) | 1.44 0.23 | 1.19 0.28 | 0.96 0.33 |
| Time max F0/duration F0† | 0.39 \pm 0.11 (0.20–0.60) | 0.39 \pm 0.14 (0.07–0.70) | 0.007 0.94 | 2.08 0.16 | 1.06 0.31 |
| Time max intensity/duration F0† | 0.47 \pm 0.11 (0.25–0.74) | 0.51 \pm 0.16 (0.33–0.95) | 1.09 0.30 | 0.35 0.56 | 0.36 0.55 |
| Time min F0/duration F0‡ | 0.99 (0.97–1.0) (0.02–1.0) | 0.98 (0.44–1.0) (0.03–1.0) | $Z = -0.97$ 0.33 | — | — |
| Correlation: F0 and intensity | 0.65 \pm 0.14 (0.31–0.92) | 0.60 \pm 0.23 (–0.01–0.91) | 0.92 0.34 | 0.01 0.92 | 0.74 0.39 |
| Energy distribution | | | | | |
| Lowest DH (Hz)† | 1499 \pm 798 (891–2992) | 1668 \pm 667 (1049–4070) | 1.60 0.21 | 2.17 0.15 | 0.74 0.39 |
| Middle DH (Hz)† | 2968 \pm 527 (2236–4454) | 2727 \pm 830 (1548–5088) | 2.95 0.09 | 0.78 0.38 | 0.22 0.64 |
| Highest DH (Hz)† | 4500 \pm 798 (3095–7108) | 3844 \pm 806 (2537–5601) | 9.76 0.003 | 0.01 0.91 | 0.59 0.45 |
| Average DH (Hz)† | 2990 \pm 527 (2226–4191) | 2748 \pm 726 (1756–4920) | 2.92 0.09 | 0.65 0.42 | 0.57 0.45 |
| Intensity H1–intensity H2 (dB) | 1.4 \pm 8.3 (–13.8–17.2) | –13.0 \pm 5.3 (–20.9–2.7) | 51.45 <0.0001 | 0.27 0.60 | 0.87 0.36 |
| Intensity H1–intensity H3 (dB) | –1.1 \pm 6.0 (–9.9–15.6) | –15.4 \pm 6.8 (–24.6 to –2.3) | 71.65 <0.0001 | 3.61 0.06 | 0.83 0.37 |
| Intensity H2–intensity H3 (dB) | –2.5 \pm 5.8 (–11.7–9.7) | –2.5 \pm 8.8 (–16.4–11.5) | 0.0007 0.98 | 1.28 0.26 | 0.02 0.89 |

* F ratios obtained from effect tests derived from a general linear model used to test for effects of species, sex and weight on each acoustic trait ($F_{3,51}$ for whole model for each acoustic trait).

†These traits were log-transformed to standardize variances between the species. A constant was added before transforming data when a variable had values below 1.0.

‡Median, interquartile ranges and full range of data for individual fawns were used as sample statistics for the time of the minimum F0/duration F0 because distributions were bimodal. The Mann–Whitney U test, and the resulting Z value, was used to test for an effect of species on this trait. Effects of sex and weight were not tested.

frequency drop from the start to the end of their calls (Table 1). Differences in energy distribution were also evident. The F0 was typically much weaker than the second and third harmonics in calls of whitetail deer but not mule deer (Table 1). Despite the species difference in F0, their dominant harmonics were remarkably similar (range 1499–4500 Hz for mule deer; 1668–3844 Hz for whitetails; Table 1). Only the highest dominant harmonic showed a clear species difference. Nevertheless, the magnitude of this difference was considerably smaller than the nearly two-fold difference in their F0.

Species differences in F0 were not due to weight. There was no correlation between F0 and weight for either species, even though fawn weights varied considerably for each species (range 3.9–9.2 kg for mule deer; 4.1–9.4 kg

for whitetails; Pearson correlation: mule deer: $r_{31} = -0.082$, $Z = -0.449$, $P = 0.65$; whitetails: $r_{20} = -0.255$, $Z = -1.13$, $P = 0.26$), and no effect of weight on F0 when considering data for both species together (Table 1).

Sex differences in F0 were apparent when considering data for both species together, although the effect of sex was much weaker than the effect of species on the same traits (Table 1). Males of both species tended to make calls having a lower mean, minimum and maximum F0 (e.g. mean \pm SD: F0: male whitetails: 529 \pm 39.9 Hz, $N = 11$; female whitetails: 552 \pm 53.8 Hz, $N = 11$; male mule deer: 888 \pm 76.2 Hz, $N = 18$; female mule deer: 974 \pm 105.6 Hz, $N = 15$). Sex differences were not large or reliable enough to remain significant for the whitetail analysis alone, but were still apparent for maximum and mean F0 for mule

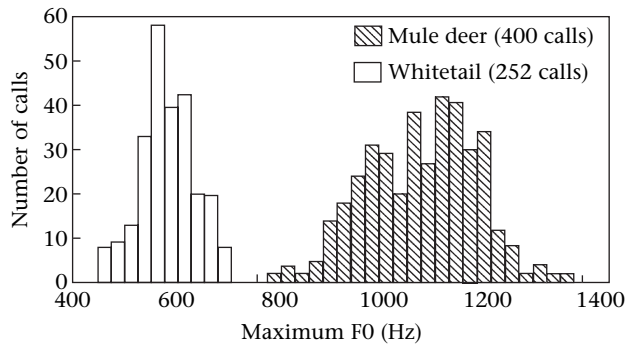


Figure 2. Distribution of values for maximum F0 for 400 calls made by 33 mule deer (range 783–1319 Hz) and 252 calls made by 22 whitetails (range 456–692 Hz). Values for mean F0 also had no overlap (whitetail deer: range 415–643 Hz; mule deer: range 667–1221 Hz).

deer calls (GLM: effect of sex on mean F0 controlling for weight: whitetails: $F_{1,19} = 2.36$, $P = 0.14$; mule deer: $F_{1,30} = 16.69$, $P = 0.01$).

The temporal patterning of frequency or amplitude was not related to the species, sex or weight of a fawn (Table 1). Call rate was not related to a fawn's species or sex (Mann–Whitney U test: species: $Z = -1.027$, $N_{\text{md}} = 53$, $N_{\text{wt}} = 26$, $P = 0.30$; sex: $Z = -0.31$, $N_{\text{female}} = 32$, $N_{\text{male}} = 47$, $P = 0.76$), but it did increase with the weight of the fawn (Spearman rank correlation: $r_s = 0.333$, $Z = 2.94$, $N = 79$, $P = 0.003$). (In this study, most variation in weight can be assumed to reflect variation in age. We could not control for age to test whether weight itself was directly related to call rate.)

Although many traits varied between the species, a discriminant function analysis using only the maximum F0 classified 100% of cases to the correct species (jackknife procedure). This was true for the test using mean values for the 55 fawns and also for the test using the 652 individual calls. The probability of group membership was uniformly high (<0.99 in only four of 652 cases).

Individual Variation in Acoustic Structure

Characteristics of the F0 appeared to have the greatest potential for distinguishing individuals of both species, as indicated by high PIC values (see [Supplementary Material, ESM 2: Tables S1 and S2](#)) and by large coefficients in the discriminant functions (see [Supplementary Material, ESM 2: Tables S3 and S4](#)). As in many studies of interindividual acoustic variation (e.g. [Robisson et al. 1993](#); [Phillips & Stirling 2000](#); [Lengagne 2001](#)), univariate ANOVAs were significant for nearly all variables (ESM 2: Tables S1 and S2), offering little basis to assess their relative importance in assessing individuality. Using the discriminant functions and the jackknife procedure, 70% of 186 calls from 10 whitetail fawns (using 8 variables) and 66% of 312 calls from 16 mule deer fawns (11 variables) were classified correctly and at a rate much higher than chance (ESM 2: Tables S3 and S4; G test: whitetails: chance = 10%; $G_1 = 152.5$, $P < 0.0001$; mule deer: chance = 6%; $G_1 = 265.4$, $P < 0.0001$).

There was no indication of a difference between the distinctiveness of vocalizations made by individuals of the

two species. A similar number of calls was classified correctly for individuals of each species when using the same number of fawns and an identical set of four variables for each species. Fifty-seven per cent of whitetail and 59% of mule deer calls were classified to the correct individual using maximum, minimum, mean F0 and the average dominant harmonic (less conservative 'all cases included' procedure, 10 fawns/species).

It is useful to be aware of the extent of the differences in acoustic structure between individuals, given that these statistical procedures identify structural differences that may or may not be perceptually salient to an animal. Average values for 10 whitetail fawns spanned 216 Hz for maximum F0 and 142 Hz for the mean F0. Average values for 16 mule deer fawns spanned 238 Hz for maximum F0 and 278 Hz for mean F0. For these traits, it was not possible to identify a value unique to any individual other than at the absolute lowest or highest end of the data range for each species. There was also considerable overlap in the multivariate analysis. Classification success varied substantially across individuals (range 35–95% for individuals in both species). For calls that were classified to the correct individual, the average probability of group membership was 0.80 for both species, ranging from a low of 0.29 to a high of 1.0 for individual calls. Less than 22% of calls that were assigned correctly had a high probability of group membership (>0.95). These points indicate that there is more overlap in acoustic features among individuals than might be implied by the overall success of classification.

Observation of Female–Fawn Meetings

Females investigated most fawns closely before they accepted or rejected their attempts to nurse by contacting the fawns' noses or rumps with their own noses. Mule deer females were more likely to investigate fawns that they accepted, which were presumably their own offspring, when fawns were less than 4 weeks of age than when they were 4–12 weeks of age (G test: 100% of 10 versus 57% of 37; $G_1 = 9.11$, $P = 0.002$; Fig. 3a). For fawns older than 4 weeks, mule deer females were more likely to investigate fawns that they ultimately rejected, presumably alien fawns, than fawns that they accepted ($G_1 = 9.11$, $P = 0.003$). The presence of an eartag on a fawn was not related to the likelihood that a female would investigate a fawn before accepting it (mule deer females investigated 54% of 13 tagged fawns older than 4 weeks and 58% of 24 nontagged fawns; $G_1 = 0.07$, $P = 0.80$). Similar patterns were evident in the data for whitetails (Fig. 3b), but the sample size was insufficient for statistical analysis.

DISCUSSION

Distress calls made by mule deer and whitetail fawns were acoustically distinctive, with substantial differences in the fundamental frequency and frequency modulation. The average maximum fundamental frequency of the calls of mule deer fawns was nearly double that of whitetails, with

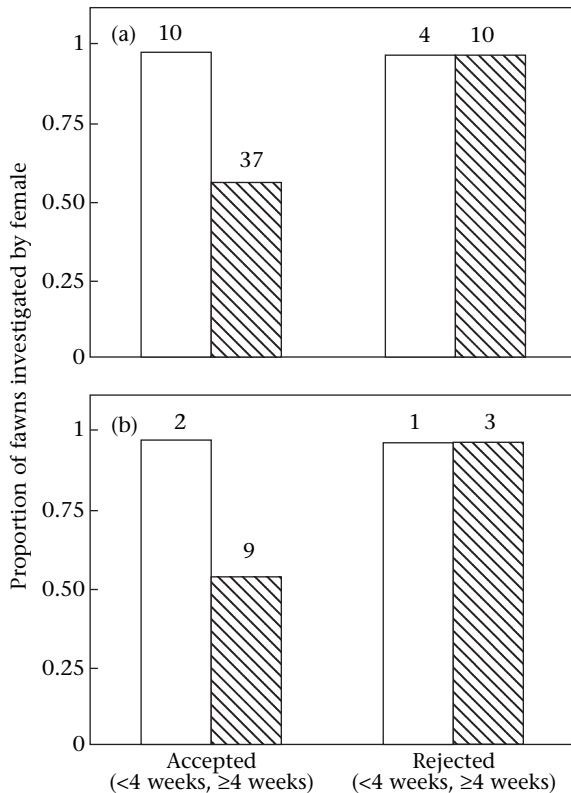


Figure 3. Proportion of (a) mule deer and (b) whitetail females extending their nose to a fawn's body during a suckling attempt, depending on the age of the fawn and whether it was accepted or rejected. Fawns that were accepted were assumed to be offspring. Fawns that were rejected and then left to search for another female were assumed to be nonoffspring. The sample size is shown above each column.

no overlap. Given the magnitude of the difference, it seems unlikely that females would fail to perceive differences between calls made by neonatal fawns of the two species.

Species differences in acoustic structure were not due to size differences between fawns. The range of weights for fawns of the two species was similar, and there was no relationship between weight and any acoustic feature other than call rate. We assume that a relationship between the F0 of calls and weight would be found if much older and, therefore, larger fawns were studied, because F0 typically declines as young animals mature. Richardson et al. (1983) found that 6-month-old whitetail fawns produced calls with a mean F0 of 120 Hz, compared to a mean of 492 Hz as neonates. In addition to the species difference in F0, we identified a sex difference in this acoustic feature; male fawns had a slightly lower F0 than female fawns. Here again, the difference was not due to a size (weight) difference between male and female fawns.

When compared with the nearly two-fold species difference in F0 (a 'source' effect related to the rate of vocal fold vibration), the similarity in frequency of the dominant harmonics made by the two species (Table 1) suggests that these emphasized frequencies are related to resonances that result from filtering effects of the vocal tract (Fant 1960). Given the similarity in size of young

fawns of the two species, it is plausible that their vocal tract cavities are also similar in size and length, which would give them common filtering properties and impart a similar resonance pattern in spite of the difference in F0.

Calls were classified to the correct individual at rates much greater than chance for both species, suggesting that potentially useful information related to a fawn's individual identity is available in these calls. Our classification rates of 66% for 16 mule deer and 70% for 10 whitetail fawns compare favourably with studies of other mammalian species reported to have highly individualized vocalizations that are discriminated by conspecifics (fur seal, *Arctocephalus australis* pups: Phillips & Stirling 2000; Charrier et al. 2002; African elephants, *Loxodonta africana*: McComb et al. 2002) including neonatal ungulates (domestic Mexican Creole goats, *Capra hircus*: Terrazas et al. 2003). Classification rates for the deer fawns were notably higher than those achieved for species reported to have moderately individualistic vocalizations that nevertheless do not appear to be discriminated by conspecifics (monk seals, *Monachus schauinslandi*: Job et al. 1995; grey seals, *Halichoerus grypus*: McCulloch et al. 1999).

The distinctiveness of calls made by the two species of deer and by individuals within each species, as well as the similarity in results for whitetails living sympatrically (this study) or allopatrically (Richardson et al. 1983) to mule deer, suggests that no special convergence in acoustic structure has occurred within or between these species to conceal cues to a fawn's identity. Given the similar size of fawns of the two species but considerable differences in acoustic structure between them, it seems more likely that the calls made by mule deer and whitetail fawns have diverged.

Acoustic researchers typically use the level of classification success obtained by discriminant function analysis to gauge the potential for vocal recognition in animals. From that perspective alone, we would expect female deer to show a high level of recognition. However, a closer look at this statistical technique may be needed, because the success of classification does not necessarily convey the reliability of classification. In this study, individual calls were assigned to the correct species with nearly 100% probability of group membership in every case, revealing potential for reliable as well as successful classification of individual calls to the species producing the call. Despite a high classification success, the small proportion of calls classified to the correct individual with a high probability of group membership (<22% of calls with probability >0.95) suggests a large proportion of calls could not be assigned to the correct individual with certainty. Statisticians have suggested that it is useful to adjust the probability of group membership with a value representing the costs of misclassification, because these costs may differ depending on the purpose of the classification (Tatsuoka 1988).

This statistical point underscores the biological idea that, when an animal has imperfect information on the identity of another individual, its acceptance threshold is likely to shift depending on the costs of acceptance or rejection errors in different behavioural contexts (Reeve 1989). Even if acoustic variation is sufficient to attract

a female's attention in the direction of her offspring more often than in the direction of an alien offspring (Espmark 1971; Vanková et al. 1997; Terrazas et al. 2003), this variation may not be sufficient for a female to make a decision to reject a young animal when the fitness consequences are more dire as would be the case in either the context of a nursing attempt or a predatory attack. Despite its obvious importance, few empirical studies have considered the way in which the behavioural context influences discrimination behaviour (but see Clark et al. 2006).

The finding that females typically probed conspecific fawns with their noses before accepting them to nurse, and always did this before rejecting them, suggests they were not able to distinguish nonoffspring from offspring fawns conclusively without olfactory cues. In a study of captive ewes that had been rendered anosmic (unable to smell), females developed a limited preference for their own lamb by the time the young animal was 1 month old, even though they still performed far more poorly than did intact females (Ferreira et al. 2000). Our results indicate that unaltered female deer living in natural conditions may also have been better able to use remote cues to recognize their offspring as the young animal aged. Nevertheless, olfactory cues obtained through close contact appeared to be essential, because females continued to use their noses to investigate all fawns that they rejected, regardless of the fawn's age.

In contrast to the intraspecific situation, fawns rarely attempted to suckle from heterospecific females, and females were never observed to approach heterospecific fawns when searching for their own fawns, suggesting that visual or auditory cues were sufficient for females to distinguish the two species. In three cases in which whitetail fawns were observed to approach mule deer females in an attempt to suckle (i.e. showed a suckling posture), over many years of observation, the female avoided the fawns without allowing them to get close (S. Lingle, personal observation).

On a different tack, it is reasonable to question whether females would ever have the opportunity to learn the sound of their offspring's distress calls, given that these vocalizations would be uttered only occasionally. Fawns routinely make softer contact calls when searching for their mothers or approaching their mothers to nurse. The mouth is usually closed, although animals will open their mouths and utter louder calls as the period of separation persists (Richardson et al. 1983), leading some researchers to label these distress calls (Espmark 1975). We are not aware of a thorough comparison of the structure of these call types for either mule deer or whitetail or for other ungulates. Nevertheless, the similarity in tonality and call structure, evident from the spectral structure of these vocalizations (Richardson et al. 1983), makes it plausible that a female's ability (or inability) to recognize her fawn's contact calls would transfer to its distress calls.

Female deer should be more likely to recognize acoustic features that persist over time (Lengagne 2001). We cannot say whether traits found to be distinctive in a young fawn's life would remain distinctive when it was older, because we were able to sample an individual's vocalizations on only one day. The practice of sampling an individual's

vocalizations on one day, or at most over a short time window of 5 days, was similarly followed in other studies of neonatal ungulates used for comparison here (Espmark 1975; Richardson et al. 1983; Vanková & Málek 1997; Terrazas et al. 2003).

As fawns age, the fundamental frequency of calls of mule deer fawns would probably fall within the range of frequencies obtained for younger whitetail fawns. Such an age-related change has the potential to explain the asymmetry of mule deer females responding to whitetail fawns without whitetail females responding to mule deer fawns. However, the possibility that mule deer females mistake the voice of a young whitetail fawn for the voice of an older version of their own offspring was not borne out by playback experiments. Mule deer females responded to these calls even when their own offspring stood next to them (Lingle et al. 2007).

In summary, the magnitude and reliability of acoustic differences between the calls of neonatal mule deer and whitetail fawns suggest that the observed defence of whitetail fawns by mule deer females is unlikely to be due to a failure to perceive differences in their vocalizations. The situation is less clear within each species. Even though there was no evidence of special convergence in signals used to elicit help, there was greater overlap in acoustic features among individuals, and females appeared to require close contact to collect olfactory information to unequivocally distinguish nonoffspring from offspring fawns through the first 12 weeks of the fawn's life. Through a series of playback experiments (Lingle et al. 2007), we did find that females of one species, whitetails, discriminated between calls made by the two species but not between calls made by different individuals of their own species, a finding consistent with the level of acoustic differentiation reported here. Mule deer females, however, did not adjust their response to either the acoustic stimuli or the behavioural context, suggesting that different explanations are needed to account for fawn defence in these two species.

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Supplementary Material

Supplementary material for this article can be found, in the online version, at doi:10.1016/j.anbehav.2006.11.003.

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