

Deer Mothers Are Sensitive to Infant Distress Vocalizations of Diverse Mammalian Species

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ABSTRACT: Acoustic structure, behavioral context, and caregiver responses to infant distress vocalizations (cries) are similar across mammals, including humans. Are these similarities enough for animals to respond to distress vocalizations of taxonomically and ecologically distant species? We show that mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) mothers approach a speaker playing distress vocalizations of infant marmots (*Marmota flaviventris*), seals (*Neophoca cinerea* and *Arctocephalus tropicalis*), domestic cats (*Felis catus*), bats (*Lasiorycteris noctivagans*), humans (*Homo sapiens*), and other mammals if the fundamental frequency (F0) falls or is manipulated to fall within the frequency range in which deer respond to young of their own species. They did not approach to predator sounds or to control sounds having the same F0 but a different structure. Our results suggest that acoustic traits of infant distress vocalizations that are essential for a response by caregivers, and a caregiver's sensitivity to these acoustic traits, may be shared across diverse mammals.

Keywords: newborn cry, caregiver response, cross-species playbacks, distress vocalization, mother-infant communication, interspecific relationships.

Introduction

The distress vocalizations or cries of newborns are remarkably similar across mammals, including humans. Some distress vocalizations are made when infants are separated from their mothers (attraction or isolation calls), hungry, or physically uncomfortable (Zeifman 2001; Charrier et al. 2002; Insley et al. 2003; Newman 2004; Torriani et al. 2006; Zeskind 2013). Others, commonly called distress or capture calls, are louder and are uttered under a state of urgency, such as during a predator attack (Chaiken 1992; Benedict 2007; Lingle et al. 2007a). Mothers or other caregivers hearing these sounds quickly approach to ac-

company, retrieve, or feed the newborn (Zeifman 2001; Newman 2004, 2007; Lingle et al. 2012; Zeskind 2013) or to defend it against predators (Chaiken 1992; Benedict 2007; Lingle et al. 2007b). Crying is a primitive behavior in mammals and a behavior that is shared with other vertebrates (Newman 2004; Vergne et al. 2007, 2011; Lingle et al. 2012). Infant rats, cats, and humans cry even when the forebrain is absent or severed from the brainstem (Nielsen and Sedgwick 1949; Barnet et al. 1966; Kyuhou and Gemba 1998; Middlemis-Brown et al. 2005). On the basis of similarities in the acoustic structure of distress vocalizations of different species (Newman 2004, 2007; Lingle et al. 2012; Zeskind 2013; fig. 1), the contexts in which they occur (Zeifman 2001; Newman 2004, 2007; Lingle et al. 2012; Zeskind 2013), and the behavioral, neural, and neurochemical responses of animals hearing these sounds (Nelson and Panksepp 1998; Zeifman 2001; Newman 2004, 2007; Lingle et al. 2012; Panksepp and Biven 2012; Zeskind 2013), Newman (2004, 2007) proposed the existence of an integrated system that has been conserved throughout mammalian evolution and encompasses not only the production of cries but also the perception and processing of cries leading caregivers to respond.

Humans are sensitive to distress vocalizations emitted by domestic animals, including cats (McComb et al. 2009) and piglets (Tallet et al. 2010, 2013). Domestic dogs (*Canis familiaris*) may also be sensitive to the cries of adult humans (Custance and Mayer 2012). A sensitivity to emotional vocalizations of another species is sometimes viewed as being learned or having evolved through the association between humans and domestic animals, which spans the past few thousand to 40,000 years, depending on the species (Clutton-Brock 1999; Druzhkova et al. 2013). Another hypothesis that could explain a human's response to newborn cries of domestic animals, and vice versa, is a shared mammalian sensitivity that reaches back over a much longer period of evolution exceeding tens of millions of years (Belin et al. 2008; McComb et al. 2009; Tallet et al.

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2010; Andics et al. 2014). Biologists increasingly assert that specific acoustic elements are consistently associated with certain emotional states across species (Morton 1977; August and Anderson 1987; Owren and Rendall 2001; Briefer 2012; Zimmermann et al. 2013). However, few would suggest that the specific acoustic structure is shared sufficiently for vocalizations of living mammals to elicit responses in evolutionary and ecologically distant species.

A limitation to testing the hypothesis that newborn distress vocalizations of one species elicit a response in caregivers from another species has been the lack of knowledge of acoustic traits essential for an animal to respond to the distress vocalizations of conspecific infants. Certain acoustic traits of newborn distress vocalizations are similar across most mammals, including a rich harmonic structure, a simple pattern of frequency modulation, and simple temporal structure (Newman 2004; Lingle et al. 2012). Other traits differ, including the fundamental frequency (F0), energy distribution, call duration, and the presence of nonlinear features (Lingle et al. 2012). We expect certain traits, such as F0, call rate, and call duration, to show species-specific variation. Species can vary in their ability to produce sounds of a certain frequency and duration because of energetic constraints associated with body size and metabolism (Gillooly and Ophir 2010). Divergence in traits such as F0 may also arise to reduce recognition errors (Teichroeb et al. 2013) or to maximize transmission across particular habitat conditions (Hauser 1997). To test whether vocalizations contain shared elements that are capable of eliciting a response across species, one first needs to control for species-specific traits, an approach previously applied to adult distress calls of birds from different taxonomic orders (Aubin 1991).

A recent report shows that mule deer and white-tailed deer mothers respond to distress calls of conspecific infants as long as the F0 remains within a certain species-specific range, hereafter the “frequency response range” (Teichroeb et al. 2013). Females of both species respond strongly to conspecific distress calls as long as the mean F0 falls within approximately $\pm 50\%$ of the mean F0 of a conspecific infant’s distress call, which translates to approximately 400–1,400 Hz for mule deer and 300–800 Hz for white-tailed deer. Mule deer and white-tailed deer are sister species, and females of both species will respond to distress calls made by each other’s fawns as long as the F0 falls, or is manipulated to fall, within the frequency response range of their own species (Teichroeb et al. 2013).

If the acoustic structure of newborn distress vocalizations that is essential for a caregiver response is similar across distant mammalian species, with F0 being the main trait differentiating these sounds, we predict that caregivers will respond to distress vocalizations of different mammalian species as long as the F0 falls or is manipulated to

fall within a species-specific response range. We tested this prediction by playing distress vocalizations of taxonomically and ecologically diverse mammalian species, as well as control stimuli, to mule deer mothers and recording their response.

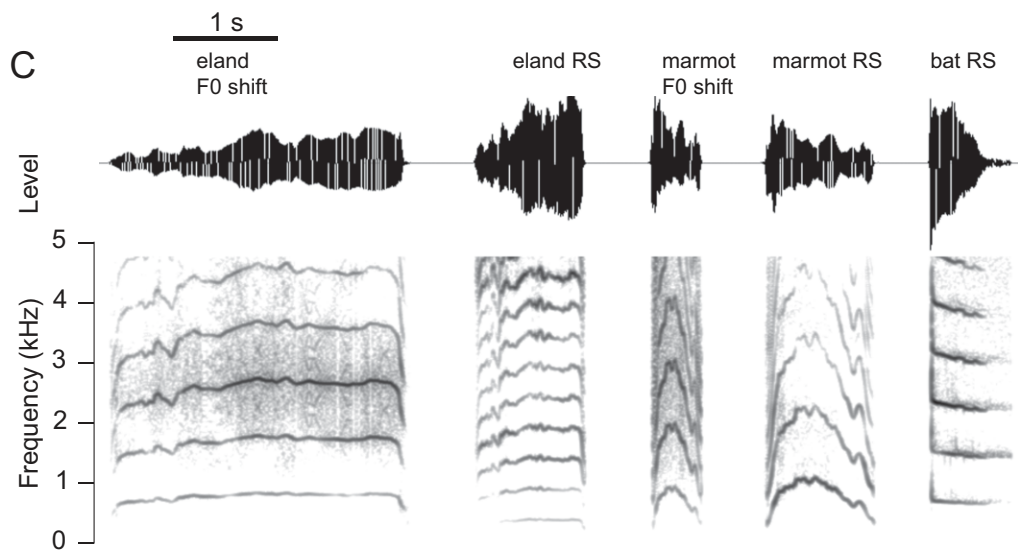
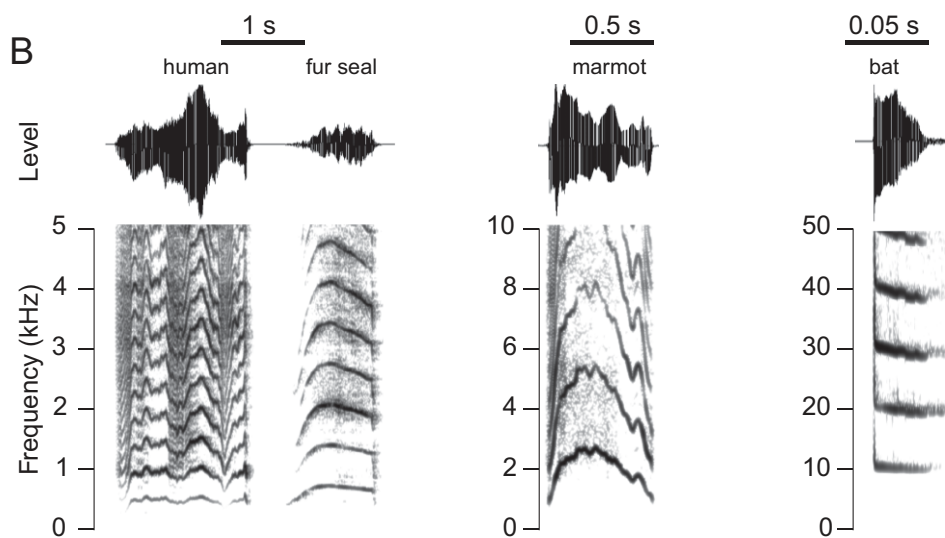
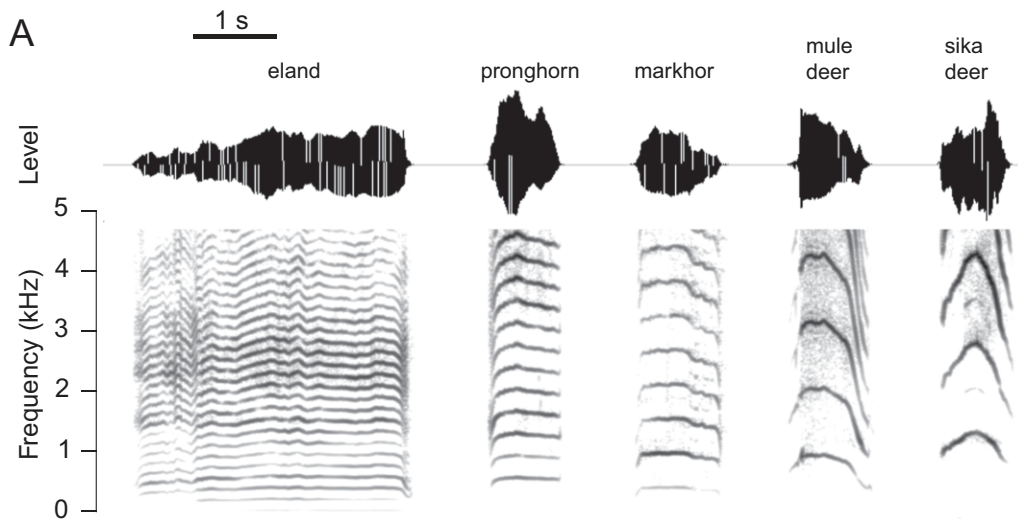
Playback stimuli were prepared from loud distress calls and lower-amplitude isolation calls recorded from species that included yellow-bellied marmot (order Rodentia), Australian sea lion and subantarctic fur seal (Carnivora), domestic cat and dog (Carnivora), silver-haired bat (Chiroptera), human (Primates), and several species of artiodactyl ungulate (eland *Taurotragus oryx*, red deer *Cervus elaphus*, fallow deer *Dama dama*, sika deer *Cervus nippon*, pronghorn *Antilocapridae americana*, and bighorn sheep *Ovis canadensis*). Rodents and primates belong to the superorder Euarchontoglires and artiodactyls, chiropterans, and carnivores to the superorder Laurasiatheria; it is estimated that these two groups last shared a common ancestor more than 90 million years ago (Springer et al. 2003).

The F0 of some species, including pinnipeds, humans, and certain ungulates, naturally fell within the frequency response range of mule deer. When the F0 fell outside this frequency range, we did playbacks with the original calls and with the same calls after F0 was manipulated to fall within the species frequency response range. To determine whether female response was determined solely by the F0, we tested their response to control sounds having the same F0 but a different temporal and spectrographic structure. To test the alternative hypothesis that females approached the speaker to mob a predator (Curio 1978) that might be present rather than to aid a fawn that appeared to be in distress, we tested the response of mule deer to sounds associated with predators, including a coyote bark and an alarm snort; the latter is produced when deer are disturbed or detect predators. Following positive responses by mule deer females, we conducted several playbacks with white-tailed deer to ensure generality of the results. The fact that a white-tailed deer mother will approach a speaker only when there is a possibility that her own offspring is in danger means that a positive response is more suggestive of a maternal motivation (Lingle et al. 2007b). The disadvantage of working with white-tailed deer is that they are less tractable than mule deer, making playbacks with free-ranging white-tailed deer particularly difficult.

Methods

Playback Stimuli

Distress vocalizations of newborns from different species were obtained from other researchers (marmot, fur seal, sea lion, bat), from websites (human, domestic cat and



dog [www.freesound.org and www.audiosparx.com]), and by recording or coordinating the recording of juveniles in free-ranging (mule deer, white-tailed deer, pronghorn, bighorn sheep) or captive (eland, red deer, fallow deer, sika deer) populations of ungulates (see Teichroeb et al. 2013 for details of recording). Pinnipeds and bats were recorded when the mother and offspring were separated, with the sounds identified as attraction or isolation calls. Ungulates and marmots were recorded when the animal was held, with the sounds identified as distress or capture calls. Cats and dogs were recorded when isolated from their mother or human owner or in a context that was not specified. Nonhuman animals were less than 1 month in age, with the exceptions of one cat (<2 months), two dogs (<2 months), and one other dog of unknown age (assumed <3 months). Parents recorded human infants, including a 1-week-old infant during a diaper change and a 2-day-old infant and a 6-week-old infant in unspecified contexts. Recordings for four to eight distinct calls for each of two to five individuals were available for all species except pinnipeds, for which only one call was available for each individual (one fur seal and two sea lions). For sounds associated with a predator, we recorded alarm snorts made by mule deer females and coyote barks at the field site where playback experiments were conducted.

The F0 was not manipulated when it fell within the response range of mule deer, even when it fell near the low end of this range (calls of human, fur seal, sea lion, bighorn sheep). When the F0 fell outside the frequency response range of mule deer, we did playbacks with these calls before and after the F0 was manipulated to fall within the species frequency response range, using two different techniques—(1) multiplication of F0, hereafter “F0-shift,” and (2) overriding the sampling frequency, hereafter “RS”—to ensure that subjects were responding to variation in F0 and not to another acoustic trait that might be affected by the manipulation. Calls of domestic cats and dogs fell within but toward the upper boundary of the mule deer’s frequency response range (mean F0: cat, 1,023–1,226 Hz; dog, 1,122–1,367 Hz). We played F0-shifted as well as unmanipulated calls. (For examples of playback stimuli, see fig. 1; fig. A1; audio files A1–A12; apps. A and B, fig. A1, and audio files A1–A12 available online.)

Control stimuli that were used to ensure that the deer were not simply responding to something related to the experimental setup included the advertisement song of a

meadowlark (*Sturnella neglecta*) male and filtered white noise (band-pass-filtered 400–1,500 Hz to approximate the mule deer response range). We prepared two control stimuli that had a mean F0 similar to that of mule deer calls, to test whether deer responded to any sound having the same F0. We selected one stimulus that had a more complicated spectrographic and temporal structure than newborn distress calls: this was the same meadowlark song, with the mean F0 shifted to the mean value for mule deer distress calls.

We synthesized another control sound, referred to as a “sine wave stimulus,” having the same F0 but no additional harmonics, no frequency modulation, and a longer call duration (5 s), after determining that synthesized distress calls were as effective as natural distress calls in eliciting a response (see “Results”). For synthesized distress calls, we modeled the mean F0, call duration, and formant structure on values for a natural distress call of a particular mule deer fawn, using calls of two fawns having a mean F0 higher and two fawns having an F0 lower than the species average. The frequency modulation was modeled on average values for the species. Amplitude modulation was minimized over the center 80% duration of the call, with a smooth slope-in or slope-out for 10% of the call duration at the beginning and end of a call, respectively. The sine wave stimulus had the same mean F0 and pattern of amplitude modulation as the synthesized distress call for a particular fawn but no harmonic structure, no frequency modulation, and a longer duration: 5 s of sound alternating with 5 s of silence. We modified the harmonic and temporal structure because studies suggest that these traits may be important in eliciting responses by conspecific caregivers to infant distress vocalizations (e.g., Ehret 1992; Charrier et al. 2002; Liu et al. 2003).

Playback stimuli were prepared in Praat (Boersma and Weenink 2011), consistent with the approach described previously for preparation of playback stimuli from conspecific calls (Lingle et al. 2007b; Teichroeb et al. 2013). We manipulated the F0 of eland, marmot, cat, dog, and meadowlark vocalizations by using the “multiply pitch frequencies” function of Praat’s Manipulation Editor to preserve the relationship between the relative range of F0 and the mean F0. This method of manipulating pitch keeps the duration of the call constant (app. B; table B1; tables B1–B4 available online) and is designed to treat F0 and formant features independently, so that energy distribution of the original call can be maintained. A small shift in

Figure 1: Oscillograms and spectrograms (top and bottom, respectively, of each panel) for infant distress and isolation calls representative of several mammalian species. Vocalizations of ungulates (A), other mammalian species (B), and calls that were manipulated to shift the fundamental frequency (F0) into the mule deer frequency response range by either multiplying F0 (F0-shift) or overriding the original sampling frequency (RS; C).

energy distribution is inevitable when lower frequencies are either removed or introduced as the F0 is increased or reduced, respectively. We previously used this method (Teichroeb et al. 2013) to manipulate the F0 of mule deer and white-tailed deer distress vocalizations, with which responses to the call stimuli used in this study were compared. We also manipulated the F0 of eland, marmot, and bat calls by using the “override sampling frequency” function of Praat. The manipulation of F0 by this method results in an inverse effect on F0 and call duration (fig. A1; table B1). The high frequency of bat calls was beyond the capabilities of our playback equipment, so we did not play the original bat calls to the deer.

The mule deer playback stimuli had eight calls distributed over a 20-s clip, resulting in a duty cycle of 3.84–7.26 s (mean, 5.2 s) per 20 s due to variation among individuals (table B1). We used a mule deer stimulus as a template when preparing stimuli for distress calls made by other species and other sounds. We adjusted the number of calls used for different species to try to keep the duty cycle within 4–7 s per 20 s clip while also limiting calls to a maximum of eight per 20 seconds. The same principles were followed when creating the meadowlark, white-noise, coyote-bark, and alarm-snort stimuli. Because of the short call duration, the duty cycle was shorter than 4 s for bat call stimuli (2.68 s), deer alarm snorts (3.50 s), and coyote barks (1.40 s; table B1). The duty cycle was longer than 7 s for the fur seal (8.34 s; table B1). Synthesized distress calls were identical in duration and duty cycle to natural distress calls. The sine wave stimulus was longer in duration because we deliberately manipulated traits other than F0 (harmonic structure, frequency modulation pattern, and call duration). To avoid having too much silence between sounds, we alternated 5 s of sound with 5 s of silence, resulting in a 10-s duty cycle. The average intensity of playback stimuli was standardized within Praat. Sound files were saved and played as uncompressed .wav files.

Playback Experiments

We conducted playback experiments with mule deer and white-tailed deer females that had 2–14-week-old fawns in a free-ranging population from August to September 2011 and from June to August 2012 and 2013, on a 225-km² cattle ranch in southern Alberta, Canada (49°N, 112°W) dominated by rough fescue (*Festuca* spp.) grassland. We avoided testing the same subject more than once by distributing trials widely and by monitoring ear tags or physical markings on animals that enabled us to distinguish individuals. We conducted four to six trials for each of the original and manipulated call types with mule deer females (eland, marmot, bat, pinniped, cat, and hu-

man), with five trials combined for the two dog stimuli (unmanipulated and F0-shifted). These trials were supplemented with trials in which calls of other ungulates were played, including a variety of cervids, bovids, and pronghorn (see table B3). Some mule deer females that were tested had fawns that were bedded and separated from them (“in hiding”), and others had fawns accompanying them; previous work has revealed that the presence of a fawn does not affect the response of mule deer (Lingle et al. 2007b).

After positive responses of mule deer females, we conducted two playbacks with white-tailed deer mothers for most playback stimuli (eland original, eland F0-shift, eland RS, fur seal, human, marmot original, marmot F0-shift, and pronghorn). White-tailed deer mothers were tested only when their fawns were bedded apart from them because they will not approach when close to their fawns (Lingle et al. 2007b).

The person who operated the speaker crawled into place, using terrain or vegetation to avoid being detected by the deer (video A1; videos A1–A11 available online). The person attempted to place the speaker upwind of the subject at a distance between 100 and 200 m (100–200 m in 86% of trials; median, 125–150 m; full range, 75–300 m). Once the speaker was in place, the person hid 25–50 m from the speaker and operated an iPod connected by cables to the speaker (Mipro MA 101; 45 W, 16 Hz–15 kHz frequency range). We played these stimuli at a peak amplitude of 105 dB(C) SPL (sound pressure level), measured 1 m from the speaker, an amplitude that is typical of fawn distress calls. Speaker and iPod settings were maintained across trials. With the exception of the meadowlark and white-noise stimuli, to which we could not necessarily expect an animal to display alert behavior, responses of females to distress vocalizations were used only if the female oriented her head and ears toward the speaker after the playback began. If a female did not alert, we moved the speaker to a different or closer location. We stopped trials after playing the stimulus for 60 s or, if a subject was still approaching the speaker, after the female stopped her approach for 10 s.

Behavioral Observations

One or two observers sat at a location where they were unlikely to be detected by the subjects, 500–1,000 m away, using binoculars and high-resolution spotting scopes for observation. 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. The intensity of a subject’s response was scored on an ordinal scale based on the duration of alert behavior (brief or intermittent vs. continuous), the general

response (alert, approach, or retreat), the distance to which the female approached the speaker, and, for deer moving within 10 m of the speaker, the tendency to maintain this proximity (Lingle et al. 2007b; Teichroeb et al. 2013).

The scale was as follows: -1 = retreat; 0 = no behavioral response, including no alert behavior (relevant only to certain control stimuli); 1 = weak alert: turns head and ears toward speaker briefly or intermittently; 2 = sustained alert: remains alert and oriented to speaker throughout trial; 3 = approaches speaker but travels no more than 5 m; 4 = travels less than 25 m toward the speaker and remains more than 50 m from speaker; 5 = travels more than 25 m toward speaker but remains more than 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 at least 10 s. Categories 3 and 4 were considered weak approaches, with animals appearing to adjust their position only to have a clearer view of the speaker area. Categories 5 and 6 were considered moderate approaches, with mule deer typically moving 50–75 m (median category) closer to the speaker in trials scored as a “5” (videos A7, A11). Categories 7–9 were considered strong responses (videos A1–A6, A10). For deer arriving within 10 m of the speaker, we identified whether subjects displayed any form of defensive behavior, identified as leaning toward the speaker or twisting or turning while facing it—typically with ears held to the side and fur flared—or hopping around the speaker.

We also recorded the total number of females coming within 10 m of the speaker during each trial, whether any of these displayed defensive behavior, and whether the person hiding near the speaker heard any grunts (contact calls) when a female had come within 25 m of the speaker. We did not record female vocalizations during initial trials, so this variable was scored as “unknown” for those trials. After the trial, we used a GPS unit to measure the distance between a subject’s original location and the speaker, unless topographical features enabled us to accurately estimate this distance using a map. The subject’s closest distance to the speaker was determined with the GPS unit or the body length of an adult deer (~1 m) if the female was within approximately 10 m of the speaker.

Data Analysis

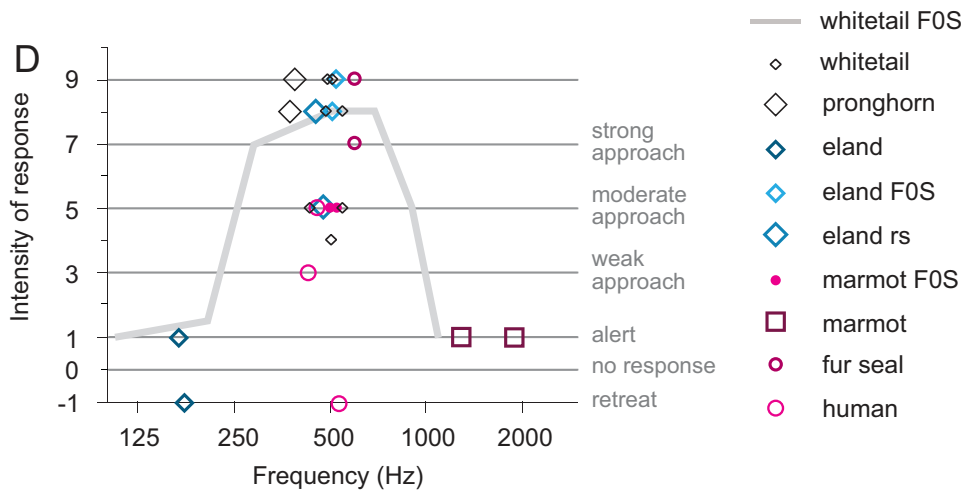
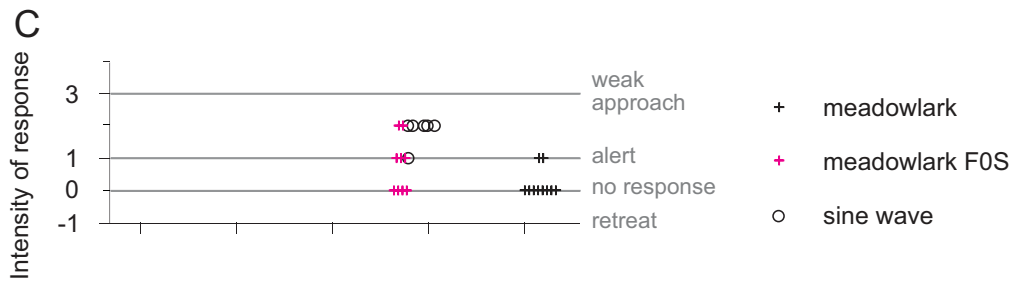
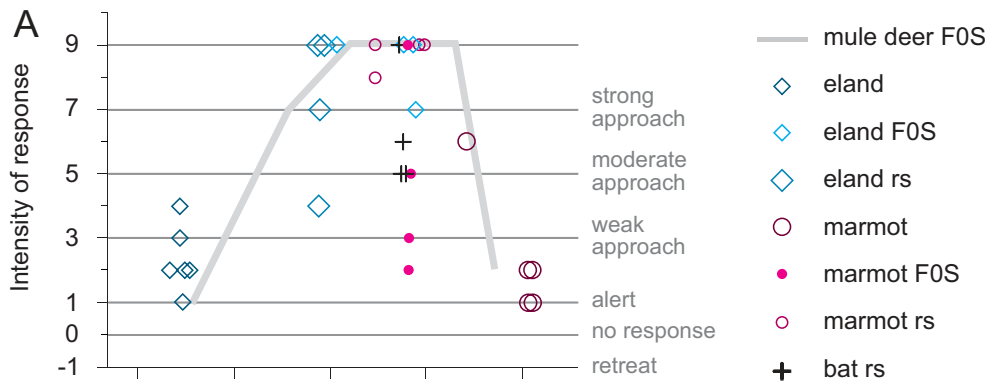
We examined the relationship between F0 and female response by plotting mean F0 (*X*-axis) and female response (*Y*-axis) for all trials for the different call stimuli, and we overlaid these data on a line showing the median response of females to conspecific calls with the F0 manipulated by multiplying the pitch frequency in Praat (data for conspecific calls from Teichroeb et al. 2013). We used a logistic

regression to determine whether the mean F0 of calls emitted by species other than mule deer had a significant relationship with the probability that a female would display a moderate-to-strong approach (defined as a response ≥ 5 on the ordinal scale) that was similar to the relationship between the mean F0 of mule deer calls and female response to mule deer calls. To test for the predicted curvilinear relationship (i.e., intermediate values of F0 are necessary to elicit a response), we treated mean F0 as a quadratic term “mean F0 \times mean F0,” also including F0 as a main effect. We similarly tested the relationship between other acoustic variables and female response, including the quadratic term and the main effects for each trait, with the similar expectation of stronger responses at intermediate values (table B2). A female’s distance from the speaker at the start of the trial and the number of females in the subject’s group were tested as a potential covariates, even though these variables were not related to female response in previous playback experiments (Lingle et al. 2007b; Teichroeb et al. 2013). We used a Kruskal-Wallis test to test whether synthesized distress calls and the sine wave stimulus elicited the same response as natural distress calls.

Results

The mean F0 of newborn distress vocalizations had a significant curvilinear relationship with the probability of mule deer females displaying a moderate-to-strong approach to the playback speaker, regardless of whether the sounds were produced by mule deer newborns (logistic regression, mean F0²: $\beta \pm \text{SEM} = 9.88 \pm 3.06$; Wald $\chi^2 = 10.4$, $P = .001$) or by other species ($\beta \pm \text{SEM} = 8.88 \pm 2.88$; Wald $\chi^2 = 9.52$, $P = .002$; figs. 2A, 2B, 3; app. B; table B2). When the mean F0 fell below (eland) or above (marmot) the mule deer frequency response range, females alerted but failed to move more than a few steps toward the speaker at their most intense response (fig. 2A; table 1; video A2). Once the mean F0 of eland or marmot calls was shifted into the mule deer frequency response range, mule deer mothers usually moved directly toward the speaker (fig. 2A; table 1; video A3). They also moved directly toward the speaker when the mean F0 naturally fell within their response range (e.g., pinnipeds, humans [video A4], other ungulate species; fig. 2B; table 1).

Similarly to their response to mule deer calls, females typically (i.e., median response) came within 10 m of the speaker in response to fur seal, marmot RS, and cat F0-shift vocalizations (video A5) and ungulate calls falling within their frequency response range, including both forms of manipulated eland calls (2A, 2B; table 1). They sometimes displayed defensive behavior or uttered grunts



in response to these stimuli, as they sometimes do when mule deer calls are played (table B3). Females typically came within 25 m in response to cat (unmanipulated) and sea lion vocalizations and within 50 m in response to the human and manipulated bat (video A6) vocalizations. They displayed weaker responses to the marmot F0-shift (ranging from a weak to strong approach) and dog vocalizations (alert behavior to a moderate approach for the F0-shift and unmanipulated combined; video A7; table 1). A female's distance from the speaker at the start of a trial, the number of females in the group, and acoustic variables other than mean and maximum F0 were not significantly related to the response of females (table B2). Call duration had a nonsignificant tendency to be related to female response, with stronger responses at intermediate values (mean call duration²: $\beta \pm \text{SEM} = 1.30 \pm 0.89$; Wald $\chi^2 = 2.14$, $P = .14$; app. B; table B2).

Mule deer responded strongly and similarly to synthesized and natural mule deer distress calls (fig. 4). They alerted but did not approach to the sine wave stimulus, which had an F0 matched to mule deer distress calls but was longer in duration and had no harmonics (figs. 2C, 4; table 1; Kruskal-Wallis $\chi^2 = 14.07$, $df = 2$, $P < .0001$; video A8). Females did not approach in response to the song of a male meadowlark, the same meadowlark song with the F0 shifted into the mule deer's frequency response range, or band-pass-filtered white noise (fig. 3C; table 1). Mule deer alerted but did not approach in response to sounds associated with a predator, including coyote barks and deer alarm snorts ($n = 7$ for each, table 1; video A9).

Like mule deer, white-tailed deer mothers approached the speaker when infant distress vocalizations fell within their frequency response range naturally (fur seal, video A10; human, video A11) or after manipulation of F0 (fig. 2D; table B4). They did not approach to distress vocalizations with a mean F0 above (marmot) or below (eland) their frequency response range.

Discussion

We show that deer mothers respond strongly to newborn distress vocalizations of seals, marmots, cats, bats, humans, and other mammals if the F0 either falls naturally or is manipulated to fall within the deer's frequency response range. They did not display a similar response to control sounds having the same F0 but a different structure. Despite species-specific variation in F0, these findings suggest that acoustic traits of infant distress vocalizations that are essential for a response by caregivers, and a caregiver's sensitivity to these traits, are shared across diverse mammals.

Female deer moved to the speaker when distress vocalizations of diverse species were played as though they were going to assist a fawn in distress, an interpretation supported by the finding that mule deer females sometimes emitted contact calls when near the speaker, as they do when responding to their own offspring. The distress vocalizations of these animals might alternatively have been a cue that a predator was present, with females moving to the speaker to mob a predator (Curio 1978). If that had been the case, females should also have approached the speaker when sounds associated with predators were played. On the contrary, mule deer females simply alerted and did not approach when coyote barks or alarm snorts of deer were played. The response of white-tailed deer was particularly revealing of a maternal motivation. White-tailed deer mothers are known to be selective, approaching only in response to conspecific distress vocalizations when they do not see their own offspring and therefore are unable to confirm that their own offspring are safe (Lingle et al. 2007b).

Future studies are needed to assess whether a species' capacity for vocal recognition of conspecific infants influences its response to newborn distress vocalizations made by other species. Humans provide just one example of a species in which caregivers display strong emotional and

Figure 2: Response of mule deer and white-tailed deer females plotted against the mean fundamental frequency (F0) for each playback stimulus. *A*, Response of mule deer mothers to cries of infant eland (original and manipulated), marmots (original and manipulated), and bats (manipulated). F0S = calls having F0 manipulated by multiplying the F0 by a certain factor (F0-shift); rs = calls having F0 manipulated by overriding the sampling frequency. The gray line (mule deer F0S) shows and connects median values for the response of mule deer to manipulated mule deer calls (F0 shifts include 0.2, 0.4, 0.6, 1.0, 1.4, and 1.8 \times F0; data from Teichroeb et al. 2013). *B*, Response of mule deer mothers to unmanipulated infant cries of mule deer, ungulates other than eland, human, subantarctic fur seal, and Australian sea lions and to unmanipulated and manipulated (F0-shift) infant cries of cats and dogs. *C*, Response of mule deer mothers to three control sounds, including sine wave and unmanipulated and F0-shifted meadowlark song. *D*, Response of white-tailed deer mothers to infant cries of different species: unmanipulated calls of subantarctic fur seal, pronghorn, human, eland, and marmot and manipulated cries of eland and marmots. The gray line (whitetail F0S) shows and connects median values for the response of white-tailed deer to manipulated white-tailed deer calls (F0 shifts include 0.2, 0.4, 0.6, 1.0, 1.4, 1.8, and 2.0 \times F0; data from Teichroeb et al. 2013). For all panels, when X and Y values of two or more data points were substantially or fully overlapping, data points were jittered along the X-axis so they would be visible. See table 1 notes for definition of ordinal response categories, with more details in "Behavioral Observations." The underlying data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.pj891> (Lingle and Riede 2014).

physiological response to cries of nonoffspring (Stallings et al. 2001; Zeifman 2001) even though they can recognize the cries of their own progeny (Wiesenfeld et al. 1981; Stallings et al. 2001; Gustafsson et al. 2013). The ability to identify one's own offspring therefore does not preclude a mother from responding to cries emitted by other infants and will not necessarily preclude her from responding to the cries of infants from other species.

Species-Specific Acoustic Traits and Shared Traits

Previously, we showed that the mean F0 of a manipulated conspecific distress vocalization must fall between approximately 400 and 1,400 Hz to elicit a strong response by mule deer females or between 300 and 800 Hz for white-tailed deer (Teichroeb et al. 2013). The current results demonstrate that variation in F0 similarly influences the responses of these deer to newborn distress vocalizations of taxonomically distant mammals, including species from different orders. Conversely, this finding suggests that divergence in F0 is necessary for animals to be selective in their response, bringing insight into why F0 is among the traits that consistently differs the most across isolation and distress calls made by different individuals (Charrier et al. 2002; Blumstein et al. 2008; Lingle et al. 2012) or species (Lingle et al. 2007b; Teichroeb et al. 2013). This finding is directly applicable to vertebrate vocalizations made in other contexts, such as begging (Levréro et al. 2009), alarm (Fallow et al. 2013), and courtship (Bass and McKibben 2003; Reby et al. 2010) calls, for which F0 is also one of most differentiated and influential traits. These results are consistent with reports for alarm calls of birds, which suggest that similarity in F0 between species is critical for a response to calls of heterospecifics in the absence of prior experience and opportunities for learning (Fallow et al. 2013).

Our goal in this study was to control for sources of species-specific variation that might conceal commonalities in distress vocalizations produced by the different species included in this study. We expect that call duration is another important source of species-specific variation that must be controlled for to test for commonalities in newborn distress vocalizations across an even wider spectrum of species. Considerable variation in call duration occurs in nature, as expected from basic energetic constraints (Gillooly and Ophir 2010). There was a nonsignificant tendency for call duration to be related to female response in our study; through acoustic manipulations, this trait has been shown to be perceptually salient to female mice (*Mus musculus*) hearing infant distress vocalizations (Ehret 1992).

Our results suggest that an acoustic trait or combination of traits other than F0 is held in common across the distress

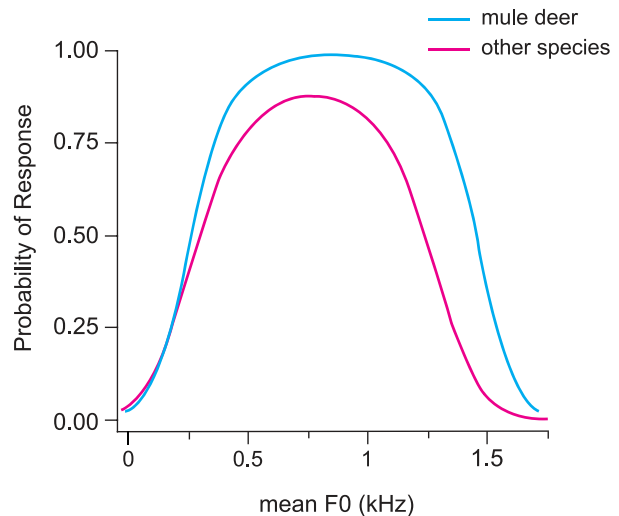


Figure 3: Logistic plot showing the relationship between mean fundamental frequency (F0) and the probability a mule deer female displays a moderate-to-strong response (intensity of response ≥ 5 in fig. 2, which represents a minimum approach of 25 m toward the speaker) to newborn distress vocalizations made by species other than mule deer (pink line; raw data for responses of mule deer to vocalizations of eland, other ungulates, marmot, pinniped, bat, cat, dog, and human shown in 2A, 2B) and to mule deer vocalizations (blue line), including those having the F0 manipulated. Data for response to mule deer vocalizations are from Teichroeb et al. (2013). The parameter “mean F0 \times mean F0” was significantly related to the female’s response to vocalizations of other species ($\beta \pm \text{SEM} = 8.88 \pm 2.88$; Wald $\chi^2 = 9.52$; $P = .002$) and to vocalizations of mule deer ($\beta \pm \text{SEM} = 9.88 \pm 3.06$; Wald $\chi^2 = 10.4$; $P = .001$). Data underlying this figure and the statistical analysis of the relationship between acoustic traits and female response (table B2, available online) are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.pj891> (Lingle and Riede 2014).

vocalizations of different species and is essential to elicit a response by caregivers. Otherwise, females should have approached in response to other sounds having the same mean F0 but a different structure, including the F0-manipulated meadowlark song and the sine wave stimulus. Alternative acoustic traits shared across infant distress calls that may be essential for a caregiver response include characteristics of the harmonic structure (Lingle et al. 2012). Indeed, previous studies found that the F0 without harmonics elicited little or no response by fur seal mothers to attraction calls of their offspring (Charrier et al. 2002) or by starlings to adult distress calls of conspecifics (Aubin and Bremond 1992). The relative simplicity of the temporal structure and frequency modulation that are characteristic of infant distress vocalizations may also be critical to a response by caregivers (Lingle et al. 2012). A caregiver’s motivation to assist an infant might be disrupted by the introduction of more complex temporal elements,

Table 1: Response (median and full range) of mule deer mothers to infant distress vocalizations

Call stimuli	<i>n</i>	Mean F0 (Hz)	Median response (full range)
Infant distress vocalizations:			
Mule deer, natural			
distress call	6	933	9 (5–9)
Eland	6	172	2 (1–4)
Eland F0S	4	916	9 (7–9)
Eland RS	4	465	9 (4–9)
Marmot	4	2,121	1.5 (1–2)
Marmot F0S	4	810	4 (2–9)
Marmot RS	4	792	9 (8–9)
Bat RS	4	849	5.5 (5–9)
Subantarctic fur seal	2	589	8.5 (8–9)
Australian sea lion	3	519	7 (5–7)
Domestic cat	4	1,124	7 (2–9)
Domestic cat F0S	4	838	8 (4–9)
Domestic dog	2	1,244	3 (3–3)
Domestic dog F0S	3	808	2 (2–5)
Human	4	489	6.5 (5–7)
Mule deer, synthesized			
distress call	8	935	9 (6–9)
Control stimuli:			
Sine wave	6	935	2 (1–2)
Meadowlark	10	2,209	0 (0–1)
Meadowlark F0S	9	884	1 (0–2)
White noise, filtered	7	NA	1 (0–2)
Predator stimuli:			
Coyote bark	7	NA	2 (1–2)
Alarm snort	7	NA	2 (1–2)

Note: A female's response was evaluated on an 11-point scale, as follows: -1 = retreat; 0 = no behavioral response, including no alert behavior; 1 = brief or intermittent alert behavior; 2 = sustained alert; 3 = approaches speaker but travels ≤ 5 m; 4 = travels < 25 m toward the speaker and remains > 50 m from speaker; 5 = travels > 25 m toward speaker but remains > 50 m from speaker; 6 = travels > 25 m toward speaker and comes within 50 m of speaker; 7 = approaches within 25 m; 8 = approaches within 10 m; 9 = approaches within 10 m and maintains this proximity for ≥ 10 s. See "Behavioral Observations" for more details. *n* = number of trials; F0S = F0 (fundamental frequency) is manipulated by multiplying the F0 by a certain factor (F0-shift); RS = F0 is manipulated by overriding the sampling frequency; NA = not applicable.

such as multipart calls, or complex spectral elements, such as frequency oscillations or nonlinear phenomena.

The Relationship of Infant Distress Vocalizations to Other Social Vocalizations

The infant's need for assistance has led to a tightly adapted system involving the structure of infant vocalizations and hearing anatomy (Ehret and Haack 1981; Ehret 1992; Aitkin et al. 1996; Bohn et al. 2006), physiology (Nelson and Panksepp 1998; Newman 2007), and behavior of caregivers (Lingle et al. 2012; Parsons et al. 2012; Zeskind 2013).

From an adaptive perspective, a hard-wired response to newborn distress vocalizations can be considered a classic example of a speed-accuracy trade-off (Trimmer et al. 2008; Chittka et al. 2009), in which it pays to respond, in case the newborn in distress is one's own offspring, rather than delay action until confirming the animal's identity, for such a delay could increase the risk of the infant being harmed or killed (Lingle et al. 2007b). From a mechanistic perspective, our results suggest a tight and nonarbitrary relationship—and one that extends across species—between the motivation of the infant, the structure of the sound, and the motivational effect it induces on receivers (Morton 1977; Owren and Rendall 2001; Rendall et al. 2009). Further work that investigates the behavioral, neural, and neurochemical responses of diverse species to newborn cries is needed to determine the generality of these results and to probe whether similarities in call structure and caregiver responses are the result of convergence (Morton 1977) or shared ancestry (Nelson and Panksepp 1998; Newman 2004, 2007; Bass et al. 2008; Belin et al. 2008; Andics et al. 2014).

Despite the powerful effect of infant cries on caregivers, we do not use these results to suggest that acoustic and cognitive mechanisms involved in the production and processing of infant cries are discrete from those involved in

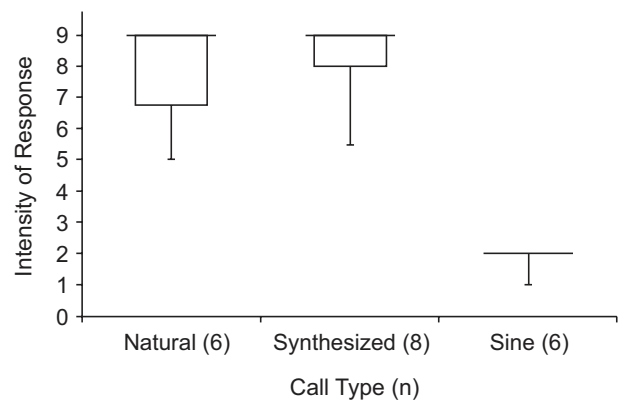


Figure 4: Response of mule deer females to natural distress calls of mule deer, synthesized distress calls, and sine wave stimulus. Boxes represent interquartile range and whiskers the full range. From left to right, median values are 9, 9, and 2 (identical to seventy-fifth percentile, with the twenty-fifth percentile also the same for the sine wave stimulus). Mule deer females responded more weakly to the sine wave stimulus than to the synthesized and natural distress calls (Kruskal-Wallis test: $\chi^2 = 14.07$, $df = 2$, $P < .0001$; response to the sine wave stimulus differs from response to natural and synthesized distress calls). Whereas females typically came within 10 m of the speaker when natural and synthesized distress calls were played (score of 8–9), they simply alerted to the sine wave stimulus (score of 1–2). Data underlying this figure are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.pj891> (Lingle and Riede 2014).

other categories of social vocalizations. On the contrary, consistent with Morton (1977) and other researchers (Owren and Rendall 2001), we expect to find similar units of sound in different behavioral contexts as long as the unit of sound serves a common function in the different contexts, such as attracting conspecifics or repelling adversaries. The role of oxytocin in promoting maternal care, sexual interactions, and more-general social interactions reveals similarities in the brain chemistries that mediate these seemingly different categories of behavior (Carter et al. 2008; Carter 2014). These points are especially relevant to our topic. Oxytocin is released in response to infant crying (McNeilly et al. 1983); oxytocin and a gene associated with a more efficient form of oxytocin receptor are associated with both increased responsiveness to infant cries (Riem et al. 2011a, 2011b) and more effective processing of auditory information in other social contexts (Tops et al. 2011).

Conclusion

Recent studies have probed the evolutionary basis of emotional communication by identifying acoustic cues associated with arousal and valence (Briefer 2012; Tallet et al. 2013; Zimmermann et al. 2013), responses of humans to vocalizations of other primates and domestic animals (Belin et al. 2008; McComb et al. 2009; Tallet et al. 2010; Andics et al. 2014; Faragó et al. 2014), and responses of domestic animals to human vocalizations (Custance and Mayer 2012; Andics et al. 2014). We advance this body of work by conducting “cross-species playbacks” with undomesticated animals, using vocal stimuli from species that are taxonomically and ecologically distant from the subject species. Our results suggest that animals can be sensitive and show behavioral responses to newborn distress vocalizations of diverse species without proposing a special human capacity for empathy, a recent history of association, or a close taxonomic relationship. This line of research may bring insight into mechanisms underlying interspecific relationships, for it suggests that nonhuman animals are sensitive to cues associated with infants even when those cues are present in different species.

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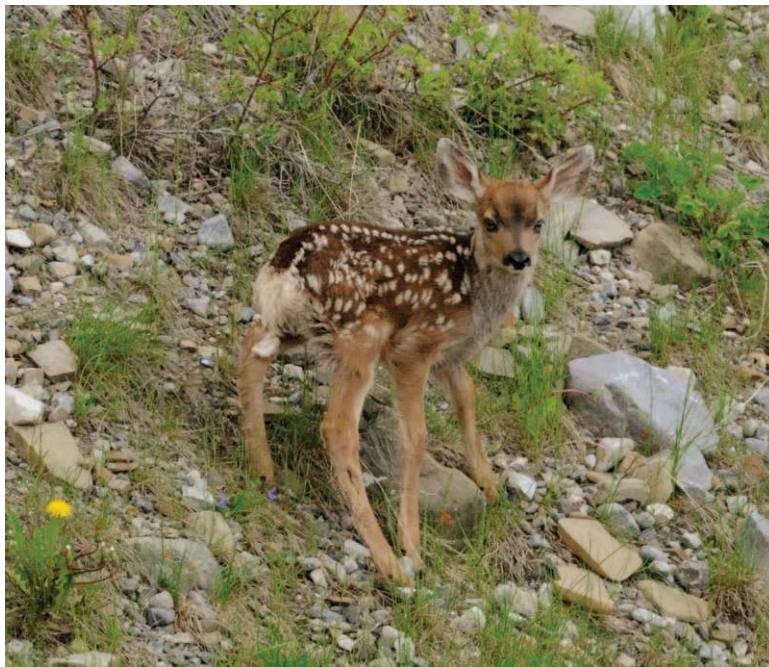
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Left, mule deer fawn (*Odocoileus hemionus*). Photo credit: Peter Neuhaus. Right, a white-tailed deer female (*Odocoileus virginianus*) grooms her hybrid fawns immediately after their birth. Photo credit: Susan Lingle.