Altruism and recognition in the antipredator defence of deer: 2. Why mule deer help nonoffspring fawns

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Both white-tailed deer, *Odocoileus virginianus,* and mule deer, *O. hemionus,* females defend fawns against coyotes, *Canis latrans*, but only mule deer defend nonoffspring conspecific and heterospecific fawns. During a predator attack, females may have to decide whether to defend a fawn while having imperfect information on its identity obtained from hearing a few distress calls. Although imperfect recognition can influence altruistic behaviour, few empirical studies have considered this point when testing functional explanations for altruism. We designed a series of playback experiments with fawn distress calls to test alternative hypotheses (by-product of parental care, kin selection, reciprocal altruism) for the mule deer's defence of nonoffspring, specifically allowing for the possibility that females mistake these fawns for their own. White-tailed deer females approached the speaker only when distress calls of white-tailed deer fawns were played and when their own fawn was hidden, suggesting that fawn defence was strictly a matter of parental care in this species. In contrast, mule deer females responded similarly and strongly, regardless of the caller's identity, the female's reproductive state (mother or nonmother) or the presence of their own offspring. The failure of mule deer females to adjust their responses to these conditions suggests that they do not defend nonoffspring because they mistake them for their own fawns. The lack of behavioural discrimination also suggests that kin selection, reciprocal altruism and defence of the offspring's area are unlikely to explain the mule deer's defence of nonoffspring. We identify causal and functional questions that still need to be addressed to understand why mule deer defend fawns so indiscriminately.

Like parents of many species, both mule deer, *Odocoileus hemionus,* and white-tailed deer, *O. virginianus,* mothers aggressively defend their young from predators (reviewed in: Montgomerie & Weatherhead 1988; Caro 2005). Mule deer females, however, take the defence of fawns further than white-tailed deer females (hereafter whitetails, whitetail female or fawn). Mule deer are more likely to defend fawns and will defend fawns that are not their own offspring, including whitetail fawns (Lingle et al. 2005). Mule deer females confront coyotes, *Canis latrans*, and defend fawns and even other adults throughout the year

(Lingle & Pellis 2002). In contrast, whitetail females generally defend only their own offspring and only during the first few months of a fawn's life. Subsequently, whitetail fawns as well as adults rely on flight to avoid predation with no direct assistance from other deer.

Active defence by mule deer females is clearly advantageous for individuals being helped, because it usually brings attacks to an end (Lingle & Pellis 2002; Lingle et al. 2005). Yet, there is no indication that it is advantageous for females to defend fawns that are not their own. On the contrary, there appear to be real costs. Battles between coyotes and mule deer are vigorous and prolonged, lasting several minutes and sometimes hours, so at a minimum, these consume time and energy (Hamlin & Schweitzer 1979; Truett 1979; Wenger 1981; Wilkinson & Douglass 2002; Lingle et al. 2005). Females that defend fawns are

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sometimes attacked themselves. Furthermore, mule deer commonly leave their offspring behind to defend another deer, potentially exposing their own fawn to greater risk.

The simplest explanation for why females help unrelated fawns is that such defence is a by-product of parental care (Brown 1983), in which females try to defend their own fawn or the area surrounding their fawn (Curio 1978) and incidentally help other fawns that are nearby. A second possibility is kin selection, in which case females obtain indirect as well as direct genetic benefits by preferentially assisting close relatives (Hamilton 1964a, b). A third possibility is reciprocal altruism, in which case females help the offspring of their closest companions, which would be expected to reciprocate such help in the future (Trivers 1971).

For any of these selective processes to lead to altruistic behaviour, individuals need a mechanism by which they can recognize suitable recipients of their help. However, recognition mechanisms are not perfect and may not function equally well in all contexts (Reeve 1989). Both empirical and theoretical work have shown that it is essential to consider recognition constraints to understand selective processes that lead animals to care for parasitic young (Lotem 1993; López-Sepulcre & Kokko 2002). Theoretical work similarly suggests that imperfect recognition influences altruistic behaviour in nonparasitic contexts (Reeve 1989; Agrawal 2001), but few empirical studies have considered the contribution of imperfect recognition when testing functional explanations for altruism.

During their first few months of life, fawns of both species remain sedentary and hidden, and their mothers visit them only periodically to nurse. Fawns that are discovered by coyotes utter loud distress calls (Richardson et al. 1983; Smith 1987). These calls seem to be the most conspicuous stimuli attracting females to fawns in danger and may provide the only basis for recognition. A quantitative analysis of fawn distress calls suggested that acoustic variation would probably be sufficient for females to discriminate between calls produced by fawns of the two species (Lingle et al. 2007). Even though acoustic differences are also present between individuals within each species, acoustic traits of calls made by different individuals nevertheless overlap considerably. Furthermore, females typically pause and sniff youngsters before accepting or rejecting their nursing attempts, underscoring the possibility that mothers may need additional information beyond that contained in offspring vocalizations to identify their own fawn. Given the large fitness costs that would be incurred if a female were to fail to defend her own offspring, we would not expect a female to ignore distress calls if there was a possibility that the fawn was her own.

We designed a series of playback experiments using fawn distress calls to consider how imperfect recognition would influence the responses of subjects while testing four alternative hypotheses for the defence of nonoffspring fawns by mule deer: (1) the by-product of parental defence of an offspring coupled with a recognition error, (2) the by-product of parental defence of an offspring's area, (3) kin selection and (4) reciprocal altruism (Appendix).

First, to determine whether females discriminated among fawns based on acoustic information alone, we tested whether females responded more strongly to distress calls of their own species, and to calls of their own fawn than to calls of an unfamiliar conspecific fawn, when their own fawn was bedded apart from them and hidden from their view. Second, to assess whether any lack of discrimination found in the initial experiments was due to an inability to reliably recognize fawns by acoustic information alone, we tested the response of females to distress calls when their own fawn accompanied them and plainly was not the one uttering the calls. Last, we examined whether only mothers of fawns responded to distress calls, as predicted by the hypotheses of parental care or reciprocal altruism (Appendix), or whether nonmaternal females and males also responded. Playback experiments were conducted with whitetails as well as mule deer, because an understanding of the mechanistic and functional reasons for the absence of altruistic defence in whitetails might shed light on the reasons for its presence in mule deer.

METHODS

Study Site and Subjects

Research was conducted on a 225-km^2 cattle ranch in southern Alberta, Canada (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. The protocol (no. 0210) followed when capturing fawns and conducting playback experiments was approved by the University of Lethbridge Animal Care Committee in accordance with the Canadian Council on Animal Care Guidelines.

Preparation of Call Stimuli

We captured 73 mule deer and 49 whitetail fawns, ranging in age from newborn to 2 weeks, during summers of 2002–2004. Each fawn was restrained for about 8 min as we weighed it, identified its sex and attached an eartag to make future identification possible. Over half of these fawns uttered distress calls, which were recorded with an analogue tape recorder and shotgun microphone (Lingle et al. 2007). Calls made by a western meadowlark, *Sturnella neglecta,* a species common to the study site, were recorded for use as a neutral control sound to ensure that no component of the experimental set-up, other than the fawn distress calls themselves, might itself elicit defensive behaviour in subjects.

Analogue recordings were digitized with 16-bit accuracy at a sampling rate of 44.1 kHz after low-pass filtering at 20 kHz. We used PRAAT 4.0 (P. Boersma & D. Weenink, University of Amsterdam, The Netherlands) to prepare call stimuli from recordings of 33 whitetail and 36 mule deer fawns for which we had high-quality recordings of at least six calls per individual. We pasted eight calls, having an average duration of 0.5 s (range 0.3–1.6 s), into a 20-s clip, a call rate within the range of normal variation. We used a template so that calls of similar amplitude were

distributed in a similar order in call stimuli made from recordings of different fawns. Because meadowlark calls lasted 1.5 s, only three calls were included in the 20-s clip for the control sound. We standardized the maximum amplitude of all call stimuli in PRAAT. In the field, the 20-s clip was played three times in succession, for a total duration of 65 s including gaps between clips.

Playback Experiments

Playback experiments were conducted in July and August 2003 and 2004 and in October 2004. One person carried the speaker into place, taking great care not to alert deer to their presence. This person then moved to a location where they could remain hidden while operating an iPod, connected by a 60–90-m cable to a Crate TX15 speaker (in 2003) or to a Mipro MA101 speaker (in 2004). Trials were conducted when a suitable subject was within 200 m of the speaker (median = 100–150 m, range 60–200 m). We placed the speaker in an area where a deer was already present, or to which we expected deer to enter. Calls were played at an amplitude of 105 dB, measured 1 m from the speaker. The amplitude was increased when it was particularly windy but was held constant throughout a given trial.

Playback trials were distributed across a 125-km² area. We maintained a minimum distance of 1 km between locations where trials were conducted within a summer unless we were certain that the identity of a subject, as ascertained from eartags or physical markings, differed from subjects involved in previous experiments. This precaution was taken so that we could be confident that each female was tested only once and to minimize stress associated with the tests. We conducted the following experiments.

Species discrimination

To determine whether females discriminated between distress calls of the two species, we played calls made by an unfamiliar conspecific fawn (i.e. a fawn with a home range several kilometres from the location of the trial) and an unfamiliar heterospecific fawn when a female's own offspring was bedded apart from her and out of her direct view. These trials were conducted with females having fawns 3–10 weeks in age.

The response of a subject to the two call stimuli was tested sequentially on one day to minimize variability in conditions (wind speed and direction, distance from speaker, group size) that could influence an animal's response. Once the first sequence of calls was completed, we attempted to wait until subjects resumed normal, nonalert behaviour before playing calls of the other species. This was not always possible because females sometimes started to leave the area after the first series of calls ended. If subjects were still alert but moving slowly from the area, we started the next series while they were still present. (This procedure applied only to mule deer, because whitetails that left departed quickly.) We varied the order in which conspecific and heterospecific calls were presented between trials on different subjects and tested for an effect of order on their responses. In this and the other experiments, we rotated among call stimuli made from different fawns to ensure that any similarity in the responses of subjects was not related to unique features of the vocalizations of any particular individual. Following initial observations that revealed females did not alert to the meadowlark stimuli, we always played this call before the fawn distress calls.

Individual discrimination

To determine whether females discriminated between distress calls made by their own fawn and those made by unfamiliar conspecific fawns, we played call stimuli prepared from these two categories of fawns to individual females when their own offspring was bedded apart from them. Other procedures were identical to those used in the species discrimination experiment.

Responses of females with reliable information that their own fawns were safe

We tested the responses of females to fawn distress calls when a female's offspring accompanied her and therefore was clearly not the source of the distress calls. Other procedures were identical to those used in the species discrimination experiment.

Reproductive state and the response of mule deer females

The effect of reproductive state on the response of mule deer females was examined by testing responses of nonmothers (also called nonmaternal females; i.e. females without a live fawn) and females with nearly weaned fawns. These trials were conducted in October, by which time fawns were about 4 months in age. We played calls made by unfamiliar mule deer fawns, presenting call stimuli prepared from different fawns to different subjects as in other experiments.

Responses of males

We recorded the responses of males present when conducting trials on other subjects. The responses of males in all-male groups were distinguished from those in mixed-sex groups.

Scoring Deer Responses

One or two observers sat at a location where they were unlikely to be detected by the subjects, 500–1500 m away, and used 15× binoculars or a high-resolution spotting scope (Swarovski ST-80 HD with 20× WA or 20–60× zoom lens) to observe the responses of subjects. A running description of the deer's response was recorded on audiotape and transcribed afterwards. When possible, trials were recorded on videotape. The intensity of a subject's response was scored on an ordinal scale based on the duration of alert behaviour, the tendency to approach the speaker, the closest distance to the speaker and, for deer moving within 5 m of the speaker, the tendency to maintain this proximity. The scale was as follows: 0 = briefly alert or leaves; 1 = continually alert during trial; 2 = approaches speaker from any distance, travels <5 m; 3 = travels >5 m

towards the speaker but remains >50 m from speaker; 4 = approaches within 50 m; 5 = approaches within 25 m; 6 = approaches within 10 m; 7 = approaches within 5 m; 8 = approaches within 5 m and maintains this proximity for >10 s. We used a topographical map to aid in distinguishing longer distance categories and an adult deer's body length (~1 m) when distinguishing shorter distance categories (5 versus 10 m). We recorded the latency that subjects began to approach the speaker following the time that they first showed alert behaviour, the number and age/sex class of deer within 200 m of the speaker at the start of a trial, and the number of deer that approached the speaker to any distance. Finally, we identified whether subjects approaching within 5 m of the speaker showed any form of aggressive behaviour, identified as leaning towards the speaker (typically with a rigid posture, piloerection and ears held to the side) or twisting and turning while facing the speaker.

Data Analysis

In the individual discrimination trials, we used data for a subject identified before a trial when comparing a female's responses to vocalizations of her own fawn and those of an unfamiliar conspecific fawn. In the species discrimination and other playback trials, we used data for the intensity of response only for the individual that approached the speaker most closely during the first series of calls when other individuals from the same category were present (e.g. females with bedded fawns, females with active fawns, males). The same individual was monitored when we played a second series of calls (in the species discrimination trials). This meant that data for only one subject from a given category were used in the analysis of the intensity of behavioural response, although we did at times collect data on individuals belonging to different categories (e.g. females with hidden fawns, females with active fawns) during the same trial.

To compare subjects from different categories, we used the response of mule deer subjects to the first call stimulus that they heard, regardless of the species of fawn making the call, but used the response of whitetail subjects to the first call stimulus that they heard only when it was made by a whitetail fawn. The difference between the method used for each species was based on the finding that mule deer but not whitetails responded equally to calls made by fawns of the two species (see results of species discrimination experiment). Nonparametric tests were used because data involved frequencies or were scored on an ordinal scale. Williams' correction was applied to G tests when comparing frequencies.

RESULTS

Responses of subjects varied from becoming alert for a few seconds and even leaving the area to rapidly approaching the speaker and confronting it aggressively (Supplementary Material, Videos S1–S3).

Species Discrimination

Mule deer females approached the speaker in response to both mule deer and whitetail calls (G test: $G_1 = 0.31$, $P = 0.57$; Table 1), and the intensity of their responses to these call stimuli was similar (paired sign test: $N = 21$, $P > 0.77$; Fig. 1a). Mule deer typically came within 5 m of the speaker and maintained that proximity as long as the calls played, showing elements of aggressive behaviour in 11 of 14 trials in which they remained close to the speaker. The order in which calls were presented did not affect the response of mule deer females (Mann–Whitney U test using mule deer calls: $U = 45$, $N_1 = 13$, $N_2 = 8$, $P = 0.58$).

Whitetail females approached the speaker when it played whitetail calls but not when it played mule deer calls (G test: $G_1 = 29.16$, $P < 0.0001$; Table 1), responding

Table 1. Number of trials in which at least one subject from the identified category (e.g. mothers, nonmothers, adult males) approached the speaker, with the total number of trials in parentheses

Subject	Call stimulus	Approach (N)
Mule deer*		
Mothers, young fawns separated	Meadowlark call	0 (22)
	Whitetail call (first or second)	21 (22)
	Mule deer call (first or second)	19 (21)
Mothers, accompanied by young fawns	First call (whitetail or mule deer)	9 (9)
Mothers, accompanied by older fawns	First call (mule deer)	6 (6)
Nonmothers	First call (mule deer)	7 (8)
Adult or yearling males in-all male groups	First call (whitetail or mule deer)	0 (12)
Adult males in mixed-sex groups	First call (mule deer)	2 (6)
Yearling males in mixed-sex groups	First call (whitetail or mule deer)	6 (6)
Whitetails†		
Mothers, young fawns separated	Meadowlark call	0 (20)
	Whitetail call (first or second)	15 (19)
	Mule deer call (first or second)	0 (18)
Mothers, accompanied by young fawns	First call (whitetail)	2 (9)
Adult or yearling males in all-male groups	First call (whitetail)	0 (5)

*From 85% to 96% of mule deer females present approached the speaker in the different experiments.
†During trials in which females were separated from their young fawns, 58% of whitetail females present approached the speaker in response to the whitetail call. Even though at least one female present in those trials was known to be a mother, not all females present were mothers.
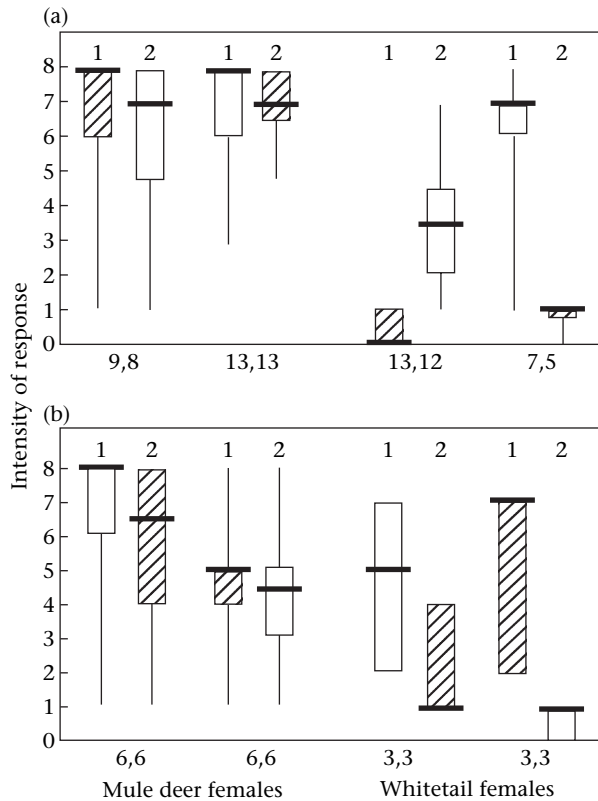
Figure 1. Behavioural discrimination of fawn vocalizations by mule deer and whitetail females when their own offspring (3–10 weeks old) were bedded apart from them. Female response to (a) calls made by an unfamiliar conspecific (□) versus an unfamiliar heterospecific (▨) fawn and (b) calls made by a female's own fawn (□) versus an unfamiliar conspecific fawn (▨). Horizontal bars show median, boxes show 25th–75th percentiles, and lines show full range of data. Numbers on X axis indicate sample size, and numbers above bars indicate order of presentation. Sample sizes are unequal when we were not able to conduct the second part of the trial. Ordinal scale is as follows: 0 = briefly alert or leaves; 1 = continually alert during trial; 2 = approaches speaker from any distance, travels less than 5 m; 3 = travels >5 m towards the speaker but remains >50 m from speaker; 4 = approaches within 50 m; 5 = approaches within 25 m; 6 = approaches within 10 m; 7 = approaches within 5 m; 8 = approaches within 5 m and maintains this proximity for >10 s.

more strongly to the whitetail call in all trials (paired sign test: $N = 18$, $P < 0.0001$; Fig. 1a). Whitetail females typically approached within 5 m of the speaker when the whitetail call was played first and within 50 m when it was second (Mann–Whitney U test: $U = 14$, $N_1 = 7$, $N_2 = 12$, $P = 0.02$). Whitetails that approached within 5 m tended to withdraw immediately and then remained outside that distance.

Similar numbers of females were present during trials with each species (median, interquartile range, range: mule deer: 2.0, 1–3.25, 1–5; whitetails: 2.0, 1–2.75, 1–5; Mann–Whitney U test: $U = 62$, $N_1 = 22$, $N_2 = 7$, $P = 0.43$). The number of females approaching the speaker was not positively correlated with the number of females present for either species (Spearman rank correlation: mule deer: $r_s = -0.027$, $N = 22$, $Z = -0.125$, $P = 0.90$; whitetails: $r_s = -0.311$, $N = 7$, $Z = -0.761$, $P = 0.45$). There was no

difference between the latency to approach for whitetails and mule deer that came within 5 m of the speaker (median, range, both species: <1 s, <1–5 s; Mann–Whitney U test: $U = 39$, $N_{WT} = 6$, $N_{MD} = 16$, $P = 0.42$, using data from both species discrimination and individual discrimination trials).

Individual Discrimination

Both mule deer and whitetail females responded similarly to distress calls made by their own fawns and to calls made by unfamiliar fawns of their own species (Fig. 1b). As with the species discrimination trials, neither the order of presentation nor the identity of the fawn influenced the response of mule deer females (paired sign test: order of presentation: $N = 12$, $P = 0.38$; fawn identity: $P = 0.99$). Even though there was variation among the responses of mule deer females tested in different trials (and females present during the same trial), each focal subject responded similarly to the two call stimuli. The intensity of response of mule deer females was not correlated with the number of females present or with their initial distance from the speaker (Spearman rank correlation: number of females present: $r_s = -0.021$, $N = 12$, $Z = -0.069$, $P = 0.95$; start distance: $r_s = -0.156$, $Z = 0.517$, $P = 0.61$).

The order of presentation, but not the identity of the fawn making the call, affected the response of whitetail females (paired sign test: order of presentation: $N = 6$, $P = 0.03$; fawn identity: $P = 0.99$). The response of whitetails decreased considerably after the first round of calls, and no whitetail female approached within 10 m of the speaker during the second portion of the trial.

Responses of Females with Reliable Information That Their Own Fawns Were Safe

Mule deer females approached the speaker when distress calls were played, even when their fawns stood next to them (Table 1). Indeed, their responses were strong and did not differ from those of females whose fawns were separated and hidden (Mann–Whitney U test: $U = 82$, $N_1 = 9$, $N_2 = 22$, $P = 0.37$; Fig. 2). Females that were accompanied by fawns did not simply follow other females to the speaker that had hidden fawns. They moved closer to the speaker in six of nine cases in which both types of females were present.

In contrast to mule deer, whitetail females were unlikely to approach the speaker when their own fawns accompanied them (Table 1). Their responses differed significantly from those of females whose fawns were separated ($U = 4$, $N_1 = 7$, $N_2 = 9$, $P = 0.003$; Fig. 2). The two whitetail females that approached the speaker when their fawns were present only took a few steps towards the speaker while remaining over 75 m from the speaker and within 5 m of their fawns.

Reproductive State and the Responses of Mule Deer Females

Reproductive state was not significantly related to the response of mule deer females. Nonmaternal mule deer females and females accompanied by older fawns, close to
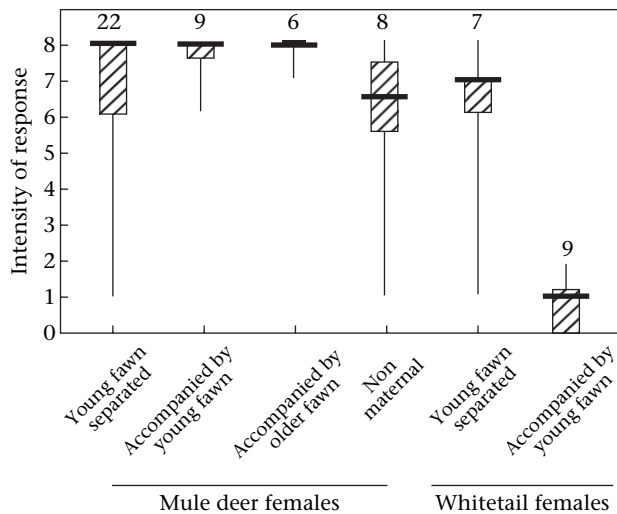
Figure 2. Responses of different classes of females to fawn distress calls. For mule deer, this includes females when their young offspring (3–10 weeks old) were bedded apart from them (young fawn separated), females accompanied by young offspring, females with older nearly weaned fawns, and nonmaternal females. For whitetails, this includes females when their young offspring were bedded apart from them and females accompanied by young offspring. Horizontal bars show median, boxes show 25th–75th percentiles, and lines show full range of data. Numbers above bars indicate sample size. See Fig. 1 for description of ordinal scale.

the age of being fully weaned, still approached the speaker when hearing fawn distress calls (Table 1). The responses of these classes of females did not differ significantly from each other or from those of females with young hidden fawns, although females with older fawns showed a nonsignificant tendency to respond more strongly than did nonmaternal females (Kruskal–Wallis test: $H_2 = 4.67$, $P = 0.10$; Fig. 2).

Responses of Males

Neither mule deer nor whitetail males approached the speaker when in separate groups from females. However, males sometimes followed females to the speaker when they were in the same group (Table 1).

DISCUSSION

The acoustic stimulus of fawn distress calls was sufficient to elicit responses by whitetail and mule deer females similar to those observed when coyotes attack fawns (Lingle et al. 2005). Differences in the experimental cues and conditions eliciting responses in each species can be used to evaluate hypotheses for the defence of nonoffspring in mule deer and the absence of this behaviour in whitetails.

Traditional Explanations for Altruism: By-product of Parental Care, Kin Selection and Reciprocal Altruism

The selective response of whitetail females was consistent with the hypothesis that defence of fawns in this species is strictly a form of parental care. Whitetail females

approached the speaker only when there was a possibility that a female's own fawn was in danger, that is, when whitetail calls were played while the female's own fawn was separated from her. The rare occurrence when more than one whitetail female chases coyotes (Garner & Morrison 1980; Lingle et al. 2005) can therefore probably be considered the by-product of their defence of their own offspring. Rather than mutual defence, whitetail females more commonly enter an area in response to distress calls and then stand alert to the location of an attack without assisting the victim (Lingle et al. 2005).

The preferential response of whitetail females to calls of their own species, but not to calls of their own fawns (compared to those of unfamiliar conspecific fawns), suggests that whitetails could reliably discriminate between the species but not among conspecifics from the acoustic stimulus. Discrimination of calls at the species but not the individual level is consistent with inter- and intraspecific variation identified in an acoustic analysis of fawn distress calls (Lingle et al. 2007).

In contrast to whitetails, the willingness of mule deer females to approach the speaker even when their own fawns were with them strongly suggests that the defence of nonoffspring is not simply a by-product of their efforts to defend their own fawns coupled with a recognition error. Furthermore, if defence were simply a form of maternal care, nonmaternal females should not have responded similarly to maternal females, as they did.

One variant of the parental care hypothesis is that animals are attempting to keep predators out of an area (Curio 1978), which in this case would be the area surrounding a fawn. This 'move-on' hypothesis predicts that prey will respond preemptively to signs that a dangerous predator is in the area (Curio 1978; Caro 2005). The observed response of mule deer to heterospecific calls would be expected, because distress calls made by different species serve equally well to indicate that a predator is in the vicinity (Russ et al. 2004). On the other hand, mule deer females do not usually respond preemptively when coyote packs encounter visible fawns. They tend to withhold their aggression for times when an individual has been attacked, even in cases in which the coyote's behaviour is highly threatening (Lingle & Pellis 2002; Lingle et al. 2005).

The move-on hypothesis also predicts that prey will respond more strongly when obligated to remain in one location or when close to home, which typically takes the form of a nest or a burrow (Curio 1978; Swaisgood et al. 1999). Females with bedded fawns, which should be more obligated to remain in the area, did not respond more strongly than females with active fawns that were in a position to leave. In fact, in six cases, females already in the process of taking their fawns out of the area following the first round of calls turned back 100–300 m to the speaker when the second series of calls began. The move-on hypothesis seems insufficient to explain the mule deer's active assistance of other individuals, although aggression by mule deer may serve a move-on function in other contexts, such as when a female's offspring are bedded. Alternative but related hypotheses suggesting that prey approach predators to increase their own safety or to communicate to the predator (Dugatkin 1997;

Ostreiher 2003) seem unlikely for the same reason: the actions of females appeared to be devoted to aiding an individual in distress, rather than focused on a predator.

The playback experiments provided no behavioural evidence that mule deer preferentially defend close relatives, as predicted by the theory of kin selection (Appendix). The failure of mule deer females to respond preferentially to calls of their own fawn over those of an unfamiliar conspecific fawn could be due to a recognition problem, given that whitetail females also did not respond preferentially to the voice of their own fawn. However, if mule deer females adjusted their defence to their degree of genetic relatedness to the apparent victim, they should have responded more weakly when their own fawn stood next to them, but they did not. The finding that nonmaternal females responded more strongly than males was the only support for the kin selection hypothesis. However, several yearling and adult males who still lived in their natal area and were present during trials failed to respond altogether, which is inconsistent with the kin selection hypothesis.

The ability to identify and preferentially help close relatives facilitates but is not essential for altruistic behaviour to arise through kin selection (Hamilton 1964b; Brown 1983). Indiscriminate help can still be kin selected if relatedness levels are sufficiently high and the cost-to-benefit ratio sufficiently low to satisfy Hamilton's rule (Agrawal 2001). Even though we cannot rule out this possibility, it is prudent to consider other possibilities.

In contrast to kin selection, the ability to discriminate among individuals seeking help is essential for reciprocal altruism (direct reciprocity), because otherwise the system is susceptible to cheaters (Trivers 1971). The failure of mule deer to discriminate calls made by different mule deer fawns, let alone the acoustically distinctive calls of the two species, rules out reciprocal altruism as an explanation for the mule deer's defence of nonoffspring. The related hypothesis of indirect reciprocity (Nowak & Sigmund 2005) would predict that females defend fawns to build their reputations, which could lead witnesses to help them in the future. This explanation seems unlikely, given that females did not respond more strongly when more deer were present.

The playback results suggest that the traditional explanations tested for altruistic behaviour, as a by-product of parental care, kin selection and reciprocal altruism, are unlikely to provide a primary explanation for the defence of nonoffspring fawns by mule deer females. Mule deer females responded indiscriminately to distress calls, but not because they lacked information on the safety of their own offspring.

Why Do Mule Deer Females Defend Fawns Indiscriminately?

It has been suggested that motivational constraints associated with parental care may result in automatic and unselected caregiving when animals are exposed to a stimulus, such as begging chicks in a nest, that they normally do not encounter (Jamieson & Craig 1987). The motivation to respond to distress calls is not tied inextricably to offspring defence in ungulates, however, given the ability of whitetail mothers as well as red deer, *Cervus elaphus* (Vanková et al. 1997), and reindeer, *Rangifer tarandus* (Espmark 1971), mothers to refrain from responding to distress calls when their own offspring are present. Aggressive defence is also unlikely to be selectively neutral in ungulates, given the vigour with which animals defend their young and the apparent risks that they appear to accept by doing so (Kruuk 1972; Berger 1978; Côté et al. 1997; Wilkinson & Douglass 2002). At the same time, the mule deer's motivation to respond to distress calls does not seem entirely adaptive; otherwise, subjects should have adjusted their behaviour to indications of need (Heinsohn & Legge 1999). Mule deer females should have responded at a reduced level, as did whitetail females, once they investigated the speaker during the first round of calls and found no predator or fawn. Instead, mule deer gave a sustained response as long as distress calls were played.

It is important to note that different females responded at different intensities, and this was not a function of their distance from the speaker. Variation in aggressive response may be related to variation in physical condition (Smith 1987), age (Côté 2000) or enduring individual differences (Johnson & Sih 2005).

One explanation consistent with our results is that a female's ability to defend her own offspring hinges on an overriding motivation to respond aggressively as soon as she hears distress calls. Fawns utter distress calls only when capture is imminent, and the consequences can be fatal if females delay a few seconds before helping. One might argue that the more selective response of whitetail females to fawn distress calls indicates that deer should be able to restrict their defence to their own fawns with relative success. Indeed, whitetail females began to approach the speaker as quickly as did mule deer. However, as discussed above, the tendency of whitetails to approach an area in response to distress calls does not reliably predict their willingness to defend a fawn. In contrast, mule deer females remained close to the speaker as long as distress calls played and often confronted it aggressively, suggesting that the acoustic stimulus alone was sufficient to elicit aggressive defence.

This idea is consistent with the aggressive-spillover hypothesis (Arnqvist & Henriksoon 1997; Johnson & Sih 2005), used to explain individual differences in aggression that persist across behavioural contexts, even though an individual's behaviour may be adaptive in one case but not in the other. Applied to the deer system, this hypothesis suggests that a female's motivation to respond with immediate aggression at the sound of any distress call (rather than waiting to assess whether her own fawn is at risk) ensures that she defends her own offspring, even though she may incur costs from defending nonoffspring. Selection would favour the behaviour if the overall benefits, across contexts and over time, outweigh the overall costs of responding in this way (Sih et al. 2004). A reliable and effective form of aggressive defence may be especially important to mule deer because of this species' reliance on aggression as an antipredator strategy year-round, in contrast to whitetails and many other species that restrict aggressive defence to very young animals. Conversely, the reliance of

whitetails on flight for most of the year and most of their lives may constrain their ability to mount an effective form of aggressive defence in summer (Lingle et al. 2005).

Another hypothesis that cannot be excluded with our results concerns a form of mutualism called group augmentation, which suggests that animals obtain direct fitness benefits by helping others as long as their reproductive success is positively correlated with group size or density (Kokko et al. 2001; Clutton-Brock 2002). This hypothesis is appealing because the group dynamics of mule deer, but not whitetails, are consistent with those expected from group augmentation. For instance, mule deer are at extremely high risk of predation when in groups below a minimum size (Bowyer 1987; Lingle 2001). Mule deer do not simply obtain passive benefits by dilution, but have to respond in a cohesive manner, bunching closely together and standing their ground, to deter and abort attacks. In contrast, whitetails obtain no obvious antipredator benefits from increased group size, and their groups quickly disintegrate when encountered by predators (Lingle 2001; Lingle & Pellis 2002). Mule deer therefore have more to gain in terms of antipredator benefits by maintaining the number of potential associates through active defence. Indeed, mule deer form larger, more stable groups than do whitetails from autumn to winter (Lingle 2003), mirroring the difference in antipredator benefits associated with their grouping patterns.

Mule deer females would not be expected to discriminate behaviourally among distress calls of conspecific mule deer fawns if either motivational constraints or group augmentation explain the altruistic defence of conspecific individuals. The evolution of an indiscriminate response to conspecifics in the allopatric context could mean that whitetails would be able to parasitize the system, even though defence of whitetail fawns would not be expected to lead to fitness benefits for mule deer females.

To summarize, the indiscriminate response of mule deer females observed during playback experiments did not support predictions associated with traditional explanations for altruistic antipredator defence including the byproduct of parental care, kin selection or reciprocal altruism or the possibility that females defend nonoffspring because they mistake them for their own fawns. The species difference in discrimination suggests that, in the context of antipredator defence, the costs of discrimination outweigh the benefits for mule deer but not for whitetails. Several questions still need to be addressed to understand factors underlying this difference. From a causal perspective, the mule deer's rigid response to fawn distress calls raises the possibility that a motivational constraint, rather than a recognition error, leads females to defend fawns other than their own offspring. From a functional perspective, such a shift in mechanism may have arisen because of a greater need for a dependable and effective form of defence, given that aggression is the primary antipredator strategy for mule deer throughout the year. Substantial differences between the group dynamics of these species in winter, if not in summer, raise the additional possibility that mule deer obtain greater direct fitness benefits by defending nonoffspring individuals because of antipredator benefits associated with increased group size.

Supplementary Material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.anbehav.2006.11.004.

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Appendix

Table A1. Predictions (P) for responses of mule deer subjects to playback experiments associated with alternative, nonmutually exclusive, hypotheses for defence of nonoffspring by mule deer females, and support for each prediction

Hypotheses and predictions	Support
Hypothesis 1. By-product of parental care: defence of own offspring with a recognition error	
P1. If this hypothesis explains the defence of conspecific fawns, mothers should approach the speaker in response to distress calls made by their own fawn and other conspecific fawns at times when their own fawn is bedded apart from them, but not when their own fawn accompanies them.	No
P2. If this hypothesis explains the defence of heterospecific fawns, mothers should approach the speaker in response to distress calls made by heterospecific as well as conspecific fawns at times when their own fawn is bedded apart from them, but not when their own fawn accompanies them.	No
P3. Nonmaternal females and males should not approach the speaker because they do not have fawns of their own to defend.	No
Hypothesis 2. By-product of parental care: defence of offspring's area ('move-on')*	
P1. Females with bedded fawns should approach the speaker in response to heterospecific and conspecific calls, because both serve equally well to indicate the presence of a predator.	Yes
P2. Females with bedded fawns, which are obligated to remain in the area, should respond more strongly than females with active fawns, which are in a position to leave the area.	No
P3. Females already in the process of taking their fawns out of an area would not be expected to return to the speaker.	No
P4. Nonmaternal females and males should not approach the speaker because they do not have fawns of their own to defend.	No
Hypothesis 3. Kin selection	
P1. Mothers should respond preferentially to the vocalizations of their own fawn compared with the vocalizations of unfamiliar and less related fawns living several km away (but see P3).	No
P2. Mothers should not respond to calls of heterospecific fawns (but see P3).	No
P3. Mothers should respond at a reduced level when accompanied by their own fawn (even if unable to discriminate distress calls as per two previous predictions), compared with times when their fawn is separated from them.	No
P4. Nonmaternal females should respond, on average, more strongly than males because of greater female philopatry (Mathews & Porter 1993) and, therefore, higher average female–fawn than male–fawn relatedness.	Yes
Hypothesis 4. Reciprocal altruism	
P1. Maternal females should respond preferentially to vocalizations made by familiar conspecific fawns, in this case to the voice of their own fawn than to the voice of an unfamiliar fawn. If this result was positive, we would have tested their ability to distinguish finer levels of familiarity.	No
P2. Mule deer mothers should not approach the speaker in response to whitetail calls, because whitetail females would not be expected to provide reciprocal defence or another complementary service.	No
P3. Nonmaternal females and males should not respond to fawn distress calls because they do not have fawns of their own and, therefore, would not engage in reciprocal caregiving arrangements.	No

*Predictions for the effect of the prey's aggression on the predator are central to the move-on hypothesis but were not tested in this study.