

Interspecific variation in antipredator behaviour leads to differential vulnerability of mule deer and white-tailed deer fawns early in life

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Summary

1. Ungulates are viewed as being highly susceptible to predation during the initial weeks or months of life. Yet aggressive defence by adult females is common in many ungulates and has the potential to reduce the vulnerability of the young significantly.

2. We observed naturally occurring predatory encounters between coyotes *Canis latrans* Say and deer fawns to test the hypothesis that a difference in aggressive defence leads to the differential vulnerability of mule deer *Odocoileus hemionus* Rafinesque and white-tailed deer *O. virginianus* Zimmermann fawns in summer, when fawns are 0–14 weeks in age. Whitetail fawns suffer higher levels of coyote predation than do mule deer fawns at that time. The two species of deer are similar in size, but are known to differ in their antipredator behaviour in winter when fawns are older.

3. Coyotes were less likely to attack mule deer than whitetail fawns they encountered, and were less likely to kill mule deer than whitetail fawns they attacked.

4. The presence of a mule deer, but not a whitetail, female with a fawn deterred coyotes from attacking the fawn. Once attacked, fawns of both species were less likely to be killed when females defended them, but mule deer females were far more likely to defend fawns.

5. Mule deer females defended fawns that were not their own offspring, including heterospecific fawns. Mule deer fawns were more likely to be defended if they had a larger number of females nearby when encountered. These observations raise the possibility that mule deer, and even whitetail, fawns may have improved survival in areas with higher densities of mule deer females.

6. These results show that higher levels of defence by mule deer females reduced the vulnerability of mule deer fawns, contributing to the lower predation rates reported for mule deer than for whitetail fawns of this age group.

Key-words: aggressive defence, cooperation, predation risk, temporal variation, vulnerability.

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Introduction

Animals employ a variety of tactics to avoid predation. Some tactics are thought to be particularly useful in protecting animals during certain times of an animal's life. For instance, aggressive defence by adults may be invaluable when offspring are too young to otherwise defend themselves, as has been well-documented in birds (Montgomerie & Weatherhead 1988). Despite

considerable variation in their antipredator behaviour, ungulates are viewed as being highly susceptible to predation during the initial weeks or months of life. Yet aggressive defence by adult females is common in ungulates (Lent 1974; Berger 1978; Smith 1987; Côté 1997) and has the potential to reduce the vulnerability of the young significantly (Kruuk 1972).

We examined the influence of aggressive defence and associated prey tactics on the vulnerability of deer fawns in a system involving coyotes *Canis latrans* Say, mule deer *Odocoileus hemionus* Rafinesque and white-tailed deer *O. virginianus* Zimmermann. The two deer species are closely related and similar in size (Mackie

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1964; Wishart 1986). They reproduce at the same time of year (Geist 1981) and have similar numbers of fawns (Beasom & Wiggers 1984). Mule deer have been associated with more open and rugged habitats, and whitetails with more closed and gentle habitats, even though the two species coexist in many areas (Swenson, Knapp & Wentland 1983; Wiggers & Beasom 1986; Mackie *et al.* 1998; Lingle 2002). Whitetails and mule deer have considerably more overlap when raising fawns in summer than they do in winter (Wood, Mackie & Hamlin 1989; Lingle 2000).

Despite their many similarities, whitetails and mule deer are known to employ different antipredator strategies in winter, by which time fawns are at least 5 months old and use antipredator tactics similar to those of adults. At that time of year, mule deer typically bunch together and confront coyotes, with adult females defending individuals that are attacked (Lingle 2001; Lingle & Pellis 2002). In contrast, whitetail fawns and adults flee to evade coyotes during winter and receive no direct assistance from other deer. Mule deer fawns suffered higher levels of predation than whitetail fawns during four winters of study (Lingle 2000; Lingle, unpubl. data). One might suspect that mule deer are simply more vulnerable to predators, at least to coyotes, throughout the year. However, in contrast to the situation for winter, coyotes capture more whitetail than mule deer fawns in summer, the season that corresponds to the first few months of a fawn's life (Whittaker & Lindzey 1999; Lingle 2000). The responses of the deer to coyotes have not been compared for this time of year.

The aggressiveness of mule deer females during winter made it seem plausible that they would also be more aggressive than whitetails during summer. Although maternal defence of young fawns has been reported for both species (whitetails, Garner & Morrison 1980; Smith 1987; mule deer, Hamlin & Schweitzer 1979; Truett 1979; Wenger 1981), differences in the frequency and intensity of aggressive defence could lead to the species difference in vulnerability during summer. We therefore observed naturally occurring predatory encounters between coyotes and fawns, 0–14 weeks in age, to test the hypothesis that a difference in aggressive defence contributed to the difference in predation rates on whitetail and mule deer fawns. Specifically, we tested: (1) whether coyotes were more likely to attack and kill whitetail than mule deer fawns they encountered; (2) whether mule deer females showed higher levels of aggressive defence than whitetail females in summer; and (3) whether aggressive defence was effective in protecting young fawns.

Materials and methods

STUDY SITE AND ANIMALS

The research was conducted on a cattle ranch in southern Alberta (49°N, 112°W, elevation 1080–1380 m). Observations from 1994 to 1996 were conducted in a 20 km²

area, extended to include a total of 50 km² from 1999 to 2004. Vegetation was dominated by native fescue and mixed grassland. Most habitat variation was topographical with three slope systems, formed by an escarpment and two river valleys, running through the study area.

Even though the two deer species were largely segregated in winter, there was considerable overlap between them in summer with the majority of whitetail and mule deer females rearing their fawns on or near the steeper slopes that mule deer occupy year-round (see Lingle 2000 for map). Females ≥ 2 years old usually had one or two fawns each summer with most fawns born between 5 and 25 June. There were about 1.1–1.5 times more mule deer than whitetail females and fawns in the original 20 km² study area during the summers of 1994 and 1995. Owing to high levels of winter predation from 1994 to 1999, which was biased against mule deer (Lingle 2000), there were about 1.4 times more whitetails in the same area by the summer of 2001 (Lingle, unpubl. data). Mule deer were more common in the portions of the study area added in 1999, so there were about 1.2 times more mule deer than whitetails in the overall 50-km² study area in the summers of 2000 and 2001. We identified coyote packs associated with 11 distinct dens in the 50-km² area, with three to eight adults (≥ 1 year) in a pack.

DEFINITION OF HUNTS AND HUNT STAGES

Coyotes went on regular excursions during which they hunted deer. The entire excursion was defined as a hunt, during which coyotes could encounter several groups of deer or none at all. Coyote packs assumed an in-line formation when moving from one area to another during a hunt, as they do in winter (Lingle 2000; Lingle & Pellis 2002). In summer, individual coyotes spread out within an area to search for fawns, which are hidiers (Lent 1974) that spend most of their time bedded apart from their mothers. Coyotes typically encountered several females but no fawns during hunts in June and July. Even though fawns were increasingly active as summer progressed, many of them continued to bed apart from females, at least some of the time, until late September. Coyote hunts of small prey, typically ground squirrels *Spermophilus richardsonii* Sabine, voles *Microtinae* L., grasshoppers *Acrididae* L. and Saskatoon berries *Amelanchier alnifolia* Nutt, were distinguishable from hunts of deer by the absence of a fixed leader or formation when travelling as a group and by different forms of search and attack behaviour (Wells & Bekoff 1982; Lingle 2000). Encounters between coyotes and fawns that occurred when the coyotes' primary activity was something other than searching for deer were designated opportunistic encounters.

A coyote–fawn encounter occurred when coyotes within 200 m of a fawn looked at the fawn. (Cases in which fawns avoided detection by coyotes will not be discussed here.) An approach occurred if coyotes

started to stalk, walk or run toward a fawn or a group containing a fawn, and escalated to a pursuit if the coyotes continued to approach after the deer reacted or the coyotes closed the distance to within 2 m. An attack began once coyotes focused their attention on a single fawn by a high-speed chase or by lunging at the fawn. Deer that were attacked escaped without serious injury or were killed, either outright or subsequently due to severe wounds sustained during the attack. To simplify presentation, most of the results were condensed into three stages: encounters (encounters, approaches, and pursuits), attacks and kills, only distinguishing the earlier stages when needed.

OBSERVATION OF HUNTS AND DATA COLLECTION

One or two observers (SL, WFW) sat at vantage points to view hunts in six areas covering 3–8 km² each. Vantage points were located 500–2000 m from the animals so that we did not interfere with the animals and so that we could monitor coyotes as they moved among different groups of deer. Observations were made with 15× binoculars and with high-resolution spotting scopes with fixed (15×, 20×, 30×) or zoom eyepieces (20–60×). From 1994 to 1996, observations were conducted from 05:30 h to approximately 16:00 h or from 10:00 h to dark (21:00–22:00). From 1999 to 2001, observations were conducted from 05:30 to 11:00 h, or from 17:00 h to dark, the times when most hunts were known to occur (Lingle 2000). An equal number of early and late sessions were conducted during each 2-week period. We rotated among viewing areas after two to three sessions or once a kill was made. Five additional attacks observed in the summers of 2003 and 2004 were included in the data set.

A running description of each interaction was recorded on audiotape. Deer were considered as having detected coyotes if they adopted an alert posture (erect neck, ears angled upward and facing the coyotes), exhibited an alarm signal (e.g. tail flag), or simply moved away from the coyotes. Coyotes found fawns that were active and accompanied by a female. These fawns had females in their groups (i.e. within 50 m), unless a fawn was briefly farther away as it moved to a bed site. Coyotes also found fawns that were active alone or bedded. Fawns that were active on their own had no conspecific female in their group. Bedded fawns included fawns that bolted in response to the coyotes' movement and fawns that were visible even though bedded. Females could be in groups with bedded fawns, but generally did not stay close to these fawns. A group was an aggregation in which each member had another deer within 50 m with the aggregation being over 50 m from the next closest deer.

We identified the number of coyotes in a hunting pack, the species of fawn encountered, the fawn's approximate age as indicated by the month of observation unless it was identified as less than 1 week old based on

mobility, and the number of females of each species known to be within 200 m of a fawn when it was first encountered. Two habitat variables were recorded because of their potential to confound results: the height of the fawn on a slope (in 7.5 m contour intervals identified from a topographical map) as an indication of the ruggedness of terrain, and the density of vegetation at the fawn's initial location (thin, xeric forbs or grass; or dense, mesic forbs or shrub found in depressions, gullies or on sheltered slopes). These variables were selected because rugged terrain is known to affect vulnerability of mule deer in winter (Lingle 2002), and young ungulates frequently use vegetation to avoid being detected or captured by predators (Lent 1974; FitzGibbon 1990).

At the end of each hunt stage (i.e. when coyotes quit or the interaction escalated to a more advanced stage), we recorded the proximity between the fawn and closest conspecific female (also the heterospecific female in the case of whitetail fawns), fawn behaviour, and female behaviour. Female fawn proximity was scored as close (consistently within 5 m); outlying (5–25 m from female or intersperses periods of being close with being further away); or separated (consistently > 25 m apart). Fawn behaviour was distinguished into one of three categories: stay (stand in place or move around within one small area, e.g. if dodging lunges); move away as long as the coyote continues to approach; or no detection. Female behaviour was distinguished into one of four categories: aggressive; stay, not aggressive; move away; or no detection or not present. Females scored as being aggressive were within 5 m of a coyote and showed overt aggression (chasing, charging or striking a coyote) or at least one of the elements of a threat posture (neck leaning forward or ears held at right angles to the head with ear cups held forward or down). Deer were not considered aggressive if they stood near or followed a coyote without trying to displace it, for instance, only moving toward the coyote after the coyote moved away, and showed no elements of a threat posture. Lastly, we identified the number of females of each species defending fawns that were attacked.

DATA ANALYSIS

An encounter between a coyote and one or more fawns in a group was the sampling unit when analysing encounters, approaches or pursuits. Attacks involved individual fawns with one exception involving nearly simultaneous attack and capture of newborn whitetail twins. Observation of tagged fawns indicated that pseudoreplication, which could arise from repeated observation of the same animals, was unlikely to be a problem. We saw coyotes encounter 24 of 209 tagged fawns during four summers of observations, which was approximately 15–20% of all fawns present. Four tagged fawns were encountered twice, and none was attacked more than once. Because observations were distributed throughout the study area, they were

also distributed across the different coyote packs. Packs associated with the 11 known dens were observed to hunt deer, as indicated by their beginning or ending a hunt at a den or by observation of radio-collared coyotes. The identity of a deer or a coyote was one of many factors shaping a coyote–deer encounter and it was unlikely that other factors remained the same from one encounter to the next, even if some of the same animals were involved.

Data were collected and analysed in a manner to provide a relatively unbiased estimate of the rate at which encounters escalated to attacks and to kills. All observed encounters were recorded that occurred in the context of a deer hunt from 1994 to 1996 plus additional attacks stemming from opportunistic encounters. All encounters were recorded, regardless of the context, from 1999 to 2001. Consequently, the rate at which encounters escalated to attacks, and attacks to kills, was based on data from all years for deer hunts, but on data from 1999 to 2001 for opportunistic encounters. Additional attacks that were in progress when first observed or that were observed when we were not monitoring coyotes continuously were included in analyses of vulnerability as related to fawn age and behavioural responses. Most analyses involved standard univariate parametric or nonparametric tests. The Williams' correction was applied to G -values. In the one multivariate analysis, we used an ordinal logistic regression (JMP 5.0, SAS Institute, Inc.) to control for several variables while testing for an effect of species on the outcome of coyote interactions with fawns, which was treated as an ordinal variable (encounter = 1, approach = 2, pursuit = 3, attack = 4, kill = 5).

Results

THE VULNERABILITY OF FAWNS ONCE ENCOUNTERED

Coyotes devoted less attention to fawns encountered opportunistically than those encountered when coyotes appeared to search specifically for deer (Fig. 1, proportion of fawns attacked/encounter during deer hunts vs. opportunistic encounters: mule deer, $G_{\text{adj}} = 3.30$, d.f. = 1, $P = 0.07$; whitetail, $G_{\text{adj}} = 5.52$, d.f. = 1, $P = 0.02$). For instance, on three occasions packs of four to five coyotes that were resting looked at but did not approach solitary fawns that stood up less than 10 m away. Another coyote was hunting ground squirrels when a 3-week-old mule deer fawn stood up 1 m away, unprotected by any female, and the coyote made no attempt to capture it. Subsequent analyses will therefore be restricted to encounters occurring during deer hunts to minimize differences in the coyotes' motivation.

When hunting deer, coyotes were more likely to attack and kill whitetail than mule deer fawns (Fig. 1, attacked/encounter, $G_{\text{adj}} = 6.04$, d.f. = 1, $P = 0.01$; killed/attack, $G_{\text{adj}} = 9.48$, d.f. = 1, $P = 0.002$). The species difference in vulnerability cannot be explained by the

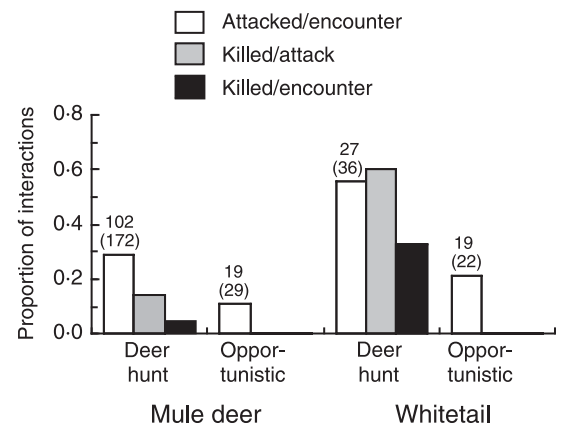


Fig. 1. The proportion of fawns attacked and killed depending on the species of fawn and the coyotes' behaviour. Coyotes encountered fawns when they appeared to search specifically for deer (deer hunt) and during opportunistic encounters that occurred when coyotes engaged in activities such as travelling, hunting small prey or resting. The number of independent encounters, with the total number of fawns in parentheses below, is shown above the open bars. The proportion of fawns attacked/encounter or killed/encounter was based on the number of independent encounters. None of the opportunistic encounters resulted in a kill.

Table 1. Logistic ordinal regression used to test whether species was related to the outcome of coyote interactions with fawns when controlling for other variables. Type of variable given in parentheses, including nominal (nom) and continuous (cont)

Variable	d.f.	Wald χ^2	P
No coyotes (cont)	1	2.25	0.13
Height of deer on slope (cont)	1	0.60	0.44
Density of vegetation (nom)	1	1.92	0.17
Year (nom)	4	7.29	0.12
Fawn age (nom)	3	1.51	0.68
Species (nom)	1	9.50	0.002

Model $\chi^2 = 32.25$, $n = 114$, $r^2 = 0.09$, $P = 0.0007$. Species and habitat interactions (species \times height; species \times vegetation density) were not significant. Data from 1996 were excluded due to a small sample for that year.

size of coyote packs, which did not differ for encounters with the two species (mule deer, median, interquartile ranges = 3.0, 2.0–5.0; whitetail, 4.0, 3.0–4.0; Mann–Whitney $z = -0.853$, $n_{\text{md}} = 102$, $n_{\text{wt}} = 27$, $P = 0.39$), nor by the breakdown in age of encountered fawns, which was similar for the two species ($G_{\text{adj}} = 3.68$, d.f. = 3, $P = 0.30$). The difference between the vulnerability of whitetail and mule deer fawns persists after controlling for the number of coyotes, height of the deer on slope, density of vegetation, year of observation and fawn age (Table 1). Even though age-related variation in vulnerability within the first 4 months of life would likely be detected with a larger sample, these results show that the species difference in vulnerability detected here

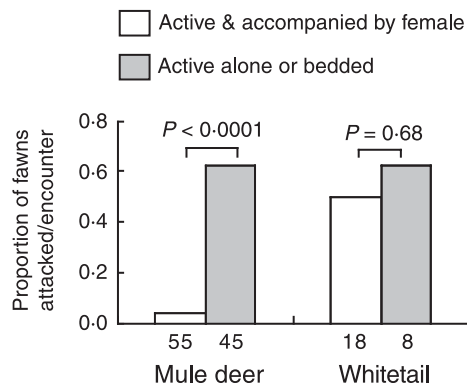


Fig. 2. Proportion of fawns attacked depending on whether they were active and accompanied by a female or active alone or bedded. The number of encounters is shown on the *x*-axis.

cannot be attributed to differences in their age. (The proportion of mule deer captured/encounter appeared stable during summer: June, 0.06, July, 0.04, August, 0.00, September, 0.06; the proportion of whitetails captured/encounter seemed to peak in July and August: June, 0.27, July, 0.45, August, 0.50, September, 0.13.)

HOW DO COYOTES FIND FAWNS TO ATTACK?

The majority of fawns encountered by coyotes were active and accompanied by females (55% of mule deer, 69% of whitetails). Coyotes also found unaccompanied fawns. This included fawns that were active without a female in their group (20% of mule deer), fawns that bolted from bed sites as coyotes moved through an area (17% of mule deer, 19% of whitetails) and fawns that were visible even though bedded (5% of mule deer, 4% of whitetails). The remaining fawns were unaccompanied, but we do not know to which subcategory they belonged.

Coyotes were far less likely to attack mule deer fawns that were accompanied by females than they were to attack unaccompanied mule deer fawns (Fig. 2; $G_{\text{adj}} = 44.48$, d.f. = 1, $P < 0.0001$). The presence of a whitetail female near a fawn did not similarly deter coyotes (Fig. 2; Fisher exact test, $P = 0.68$). Coyotes were less likely to attack mule deer fawns accompanied by mule deer females than whitetail fawns accompanied by whitetail females ($G_{\text{adj}} = 18.49$, d.f. = 1, $P < 0.0001$).

THE RESPONSE OF FEMALES AND FAWNS TO COYOTES

Mule deer females that detected coyotes nearly always stood their ground when fawns were encountered and only fled to accompany fleeing fawns (Fig. 3a). As long as a mule deer female was present, mule deer fawns usually remained in place, typically moving close to a female or vice versa. If a female was not present or failed to detect coyotes, mule deer fawns fled (Fig. 3a). The association between the response of females and fawns during encounters was significant (76% of 78 fawns that detected coyotes stayed in place when a

Table 2. Proportion (Prop.) of fawns that stayed in place when attacked depending on their age (as indicated by the month in which the attack occurred)

	Mule deer		Whitetail	
	<i>n</i>	Prop. stay	<i>n</i>	Prop. stay
≤ 7 days	0	–	4	1.00
June, 7 days	1	1.00	1	0.00
July	17	0.71	7	0.14
August	7	0.57	4	0.00
September	7	0.57	2	0.00

Fawns that stayed in place because they did not detect coyotes were excluded from this table.

female was present vs. 0% of 17 when a female was not present; $G_{\text{adj}} = 38.2$, d.f. = 1, $P < 0.0001$).

Mule deer females were increasingly aggressive as coyotes continued to approach. Aggression was more common in encounters in which coyotes approached more closely (19 of 31 encounters ending at the approach or pursuit stage vs. two of 35 ending at the encounter; $G_{\text{adj}} = 26.40$, d.f. = 1, $P < 0.0001$), and aggression was the most common response once a fawn was attacked (Fig. 3c). In the three cases in which females were alert but were not aggressive, they bunched together with other members of their group, a tactic commonly used by fawns and adults in winter (Lingle 2001). If defended by a female, mule deer fawns that were attacked usually remained in the same location – standing in place or dodging lunges, often trying to stay near a female (Fig. 3c). If mule deer fawns were not defended, they usually fled. The association between female defence and the fawns' response when attacked was significant (Fig. 3c, 87% of 23 fawns that detected coyotes held their ground when defended vs. 12.5% of eight fawns that were not defended; Fisher exact test, $P < 0.0001$). Age was not significantly related to the behavioural response of mule deer fawns (Table 2; Mann–Whitney test, $z = -0.936$, $P = 0.35$).

Whitetail females and fawns sometimes stayed in place when coyotes encountered or attacked a fawn, but their most common response was to flee (Fig. 3b,d). In contrast to mule deer, whitetail fawns that remained in place after being attacked dropped to the ground to assume a prone response. Only one fawn older than 1 week in age did this (Table 2) and that followed a prolonged chase in which coyotes consistently gained ground. The response of a whitetail fawn was significantly related to its age, with less of a tendency to be related to defence by a female (fawn age and fawn behaviour, Mann–Whitney test, $U = 4$, $P = 0.003$; female defence and fawn behaviour, Fisher exact test, $P = 0.10$). Even though older whitetail fawns attempted to find new hiding spots after running a distance, they continued to bolt when coyotes came near. Whitetail females were less likely than mule deer females to defend fawns that

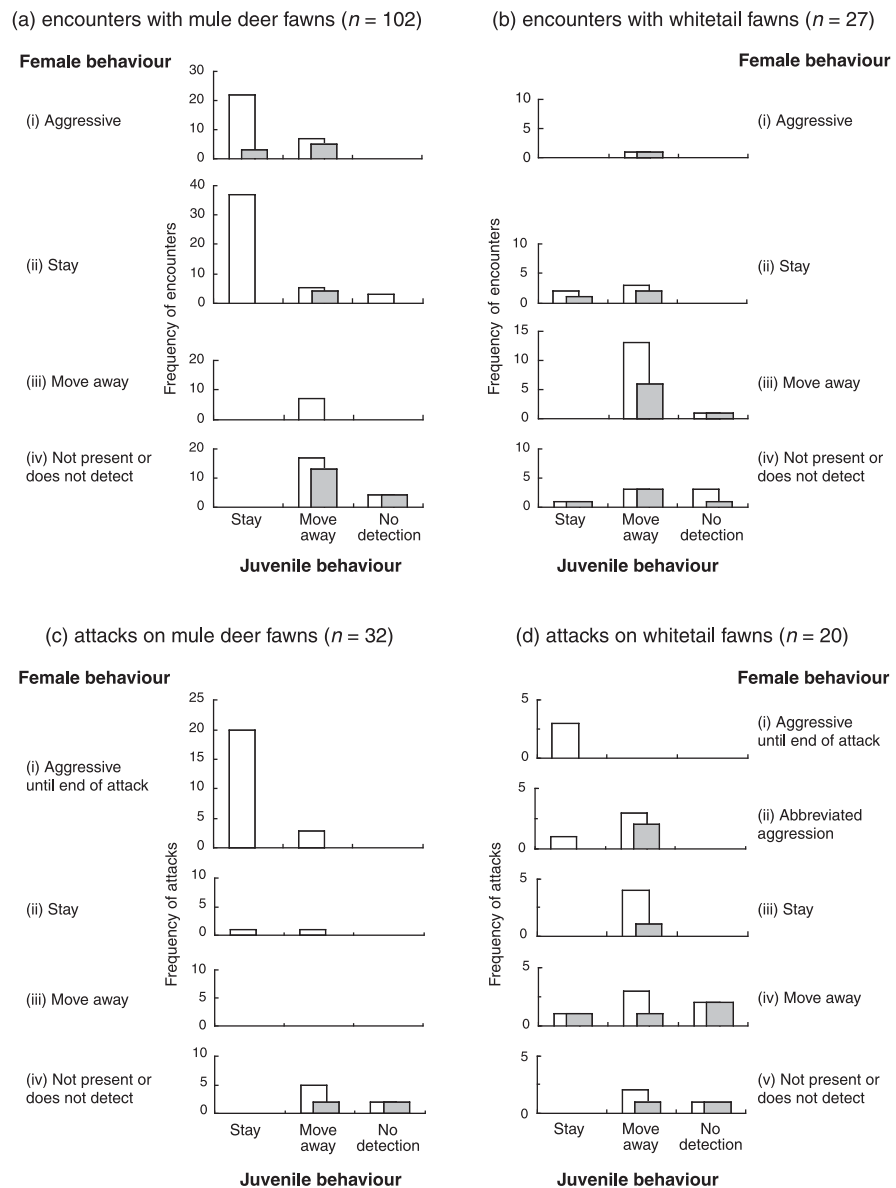


Fig. 3. Responses of deer during: (a) encounters with mule deer fawns; (b) encounters with whitetail fawns; (c) attacks on mule deer fawns; and (d) attacks on whitetail fawns. Fawn (juvenile) behaviour shown on x-axis and female behaviour on y-axis. Open bars show the response of the deer at the end of the encounter (a,b) or attack (c,d). Shaded bars show the number of those encounters or attacks escalating to an attack or kill, respectively.

were attacked (Fig. 3d, whitetail females defended fawns in seven of 17 attacks; mule deer females defended fawns in 23 of 26 attacks in which the female was present and alert; $G_{\text{adj}} = 10.58$, d.f. = 1, $P = 0.001$). The defence of whitetail females was often fleeting (Fig. 3d).

A salient feature of mule deer aggression was their tendency to band together to defend fawns. More than one mule deer female defended an attacked fawn in 20 of 26 cases in which females defended mule deer fawns (Fig. 4a). (Three cases involved females that did not detect coyotes until fawns were mortally wounded so scored as 'no detection' for the basic response; Fig. 3c.) Mule deer females even defended whitetail fawns that were attacked (Fig. 4b). Similar cooperative defence was not observed in whitetails. There was only one case in which more than one whitetail female was aggressive

to coyotes while an individual whitetail fawn was being attacked. In all other cases, at most one female defended the fawn and it always appeared to be the fawn's mother. Whitetail females were not observed to defend heterospecific fawns.

THE EFFECTIVENESS OF PREY TACTICS

Overall, mule deer fawns were at high risk of being attacked and killed if they fled rather than held their ground (Fig. 3a, 39% of 36 encounters led to attacks when fawns fled vs. 5% of 59 when they stayed in place; $G_{\text{adj}} = 36.80$, d.f. = 1, $P < 0.0001$; 22% of nine attacks resulted in a kill when fawns fled, but none of 21 in which they held their ground; Fisher exact test, $P = 0.08$). However, the proximity of a female to a

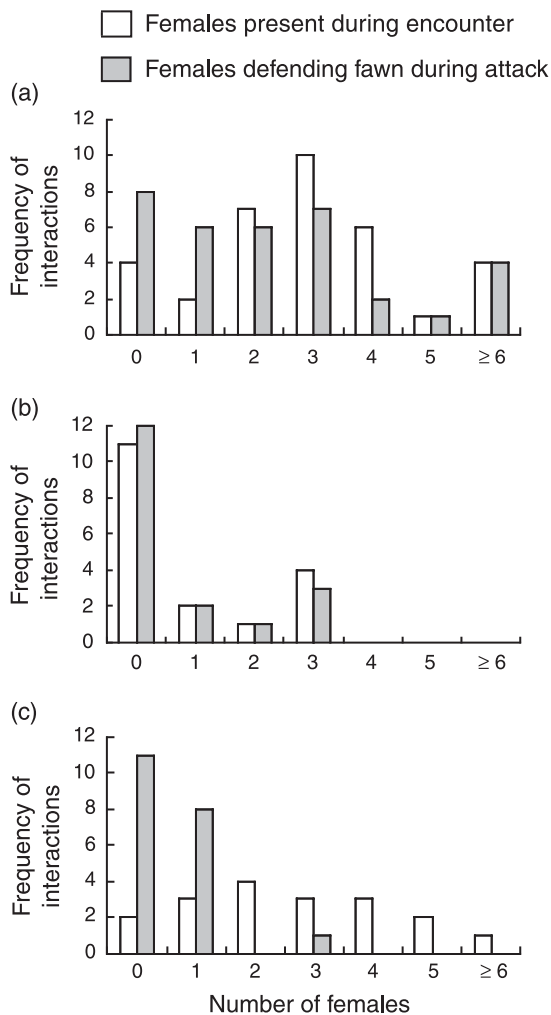


Fig. 4. For interactions involving fawns that were attacked, the number of females within 200 m of a fawn when the fawn was first encountered by coyotes and the number of females aggressive to coyotes once the fawn was attacked. (a) Mule deer females during attacks on mule deer fawns; (b) mule deer females during attacks on whitetail fawns; and (c) whitetail females during attacks on whitetail fawns.

fawn, which was influenced by the behaviour of both the fawn and the female, seemed to matter more than the animal's behaviour *per se*. As long as a mule deer fawn was within 5 m of a female, it was unlikely to be attacked or captured (Fig. 5a,b). The majority of mule deer fawns were close to females when attacks ended (Fig. 5b), revealing a tendency for mule deer females and fawns to move close to each other during these interactions. Whitetail fawns tended to be attacked less often when they were close to females (Fig. 5a). But once attacked, their proximity to a female was not associated with a lower risk of capture (Fig. 5b). Owing to flight by the females or fawns, the majority of whitetail fawns occupied outlying or isolated positions when attacks ended.

Female defence was highly effective in protecting mule deer fawns from being captured (Fig. 5c). Not surprisingly, the proximity of a conspecific female to a mule deer fawn was strongly associated with defence by females

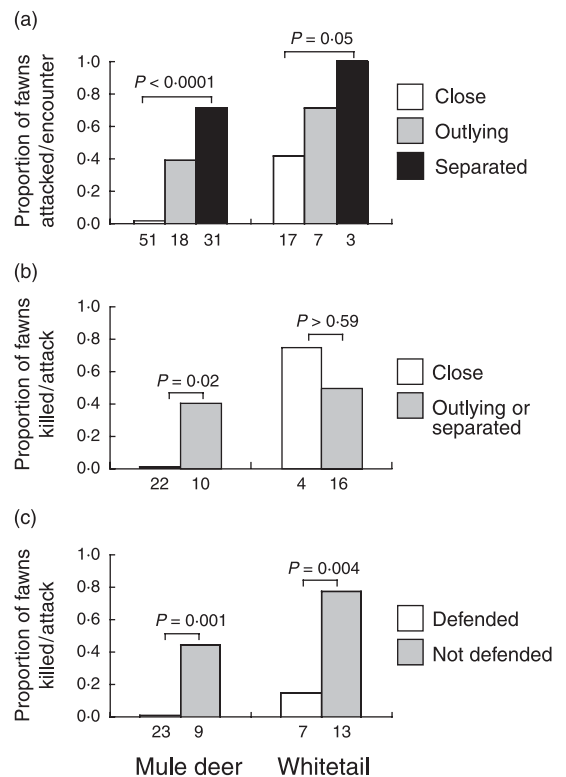


Fig. 5. The relationship between female fawn proximity, female defence and the risk of being attacked or captured. The number of interactions is shown on the x-axis. (a) The proportion of encounters resulting in an attack depending on the proximity of the closest conspecific female to a fawn (mule deer, $G_{\text{adj}} = 49.41$, d.f. = 2, $P < 0.0001$, close \neq outlying \neq separated; whitetail, $G_{\text{adj}} = 3.82$, d.f. = 1, $P = 0.05$, close \neq outlying & separated, which were pooled). (b) The proportion of attacks resulting in a kill depending on the proximity of the closest conspecific female to a fawn (mule deer, $G_{\text{adj}} = 9.22$, d.f. = 1, $P = 0.02$; whitetail, Fisher exact test, $P > 0.59$). (c) The proportion of attacks resulting in a kill depending on female defence (mule deer, $G_{\text{adj}} = 10.06$, d.f. = 1, $P = 0.001$; whitetail, Fisher exact test, $P = 0.004$). Fawns were only considered 'defended' when females were aggressive until the attack ended. Mule deer defended whitetail fawns in four of seven attacks.

(21 of 23 fawns that were defended were close to a female, one of 10 that were not defended; $G_{\text{adj}} = 22.53$, d.f. = 1, $P < 0.0001$). Aggressive defence by females was also effective in protecting whitetail fawns from being killed (Fig. 5c), with mule deer females defending whitetail fawns in four of seven cases in which whitetail fawns were defended until the attack ended.

All mule deer fawns that were defended survived attacks (Fig. 5c), regardless of whether they were defended by one or more females. It was therefore not possible to test whether multiple females were more effective than single females in defending fawns. The willingness of mule deer females to help fawns other than their own offspring nevertheless appeared to benefit fawns, because it increased the chance that a fawn would be defended. Mule deer fawns were more likely to be defended if they had a larger number of females within 200 m when initially encountered (defended fawns, median, interquartile ranges = 3.0, 2.0–4.0; undefended

fawns, 2.0, 0.0–3.0; Mann–Whitney test, $z = -2.07$, $n_{\text{defence}} = 21$, $n_{\text{no defence}} = 10$, $P = 0.04$). The number of females present was positively correlated with the number defending a fawn ($r_s = 0.459$, $z = 2.52$, $P = 0.01$). Perhaps more telling of the benefits of cooperation were at least six cases in which females defended fawns when the fawns' own mothers were not available to defend them, because the mothers were not alert or present. [It is important to add that even though the number of females near a fawn when encountered was not significantly related to the likelihood that a fawn was attacked (Mann–Whitney test, $z = -1.64$, $n_{\text{encounter}} = 71$, $n_{\text{attack}} = 30$, $P = 0.10$), the tendency was for fewer attacks to occur in areas with more females.]

Discussion

The aggressiveness of mule deer females had deterrent and defensive effects that reduced the likelihood of mule deer fawns being attacked and killed by coyotes. The presence of a mule deer, but not a whitetail, female near a fawn deterred coyotes from attacking the fawn. Once attacked, fawns of both species were less likely to be killed when females defended them, but mule deer females were far more likely to defend fawns. The species difference in vulnerability did not stem from a difference in encounter rate. As mule deer were encountered more often than whitetails (see below), we should have expected a similar or higher proportion to have been attacked and killed (Holling 1959). One exception to this would be if mule deer numbers were sufficient to saturate the predator and dilute the risk facing individuals (Kruuk 1972; Clark & Robertson 1979). This was not the case, given the absolute number of whitetails killed was larger than the number of mule deer killed. These results support the hypothesis that higher levels of aggressive defence by mule deer females reduced the vulnerability of their fawns, when compared with whitetails.

The difference in the vulnerability of whitetail and mule deer fawns seems to contribute in large part to differences in their mortality (Whittaker & Lindzey 1999; Lingle 2000). Whitetail fawns were about 7.5 times more likely to be captured once encountered in this study. We observed 3.1 times more coyote encounters with mule deer fawns in early summer (June and July), reducing the whitetail's overall risk of capture to approximately 2.4 times the risk facing mule deer if fawns of the two species were equally abundant. Mortality of marked fawns attributed to coyote predation during early summer was 2.5 times higher for whitetail than for mule deer fawns living in the original 20 km² study area (2.3 in 1994, 2.0 in 1995, 3.2 in 2000, and 2.5 in 2001; Lingle 2000; Lingle, unpubl. data). (We restricted this analysis to early summer because extremely high predation on whitetail fawns prevented subsequent comparison in 2000 and 2001.) Mule deer were more common (1.1–1.5 times more) during the first 2 years, and whitetails were more common in the latter 2 years

(1.1–1.4 times more) in this area. The consistent bias in mortality against whitetail fawns would not be expected from the variation in relative abundance or from the higher encounter rates with mule deer. It can only be explained by a species difference in vulnerability.

Mule deer fawns benefited from the willingness of mule deer females to defend fawns that were not their own offspring. The main benefit, from the fawn's point of view, seemed to rest in the increased likelihood that the fawn would be defended, in which case it was unlikely to be killed. Fawns were more likely to be defended when more females were nearby, and they were defended at times when their own mothers were not available to defend them. Mule deer females moved long distances, frequently leaving their own fawns behind, to defend fawns that were attacked. In contrast, there was only one instance in which more than one whitetail female simultaneously chased coyotes and these three females had fawns bedded in the area they defended. Other reports similarly suggest that mule deer are both more aggressive and cooperative in their aggression (whitetails: Garner & Morrison 1980; Smith 1987; mule deer: Hamlin & Schweitzer 1979; Truett 1979; Wenger 1981). These results suggest that mule deer fawns could have better survival in habitats with higher densities of mule deer females, because fawns would be more likely to be defended in such areas. The defence of whitetail fawns by mule deer females raises the possibility that whitetail females could improve the survival of their fawns by rearing them alongside mule deer. Beneficial associations with a species that is more aggressive to predators have been reported in birds (Dyrce, Witkowski & Okulewicz 1981; Burger 1984).

The tendency of mule deer females and fawns to stay close together and to co-ordinate their behaviour probably makes the fawns easier to defend. Even though 5 m was used to distinguish fawns that were 'close' to females from those farther away, in reality most mule deer fawns and females stood side by side. A similar level of co-ordination was not evident in whitetails. A whitetail fawn's tendency to flee increased with its age, and was not related to the behaviour of a female. On two occasions mule deer females vigorously tried to rescue whitetail fawns that continued to flee, repeatedly separating themselves from the defending females. Three mule deer females gave up after defending one of these fawns for 9 min, after which the coyotes caught the fawn. In the other attack, coyotes killed the fawn when it was about 10 m in front of the defending mule deer. Observations such as these suggest the young animal's behaviour has an essential role in facilitating its own defence (Kruuk 1972) and that mule deer fawns behave in ways that make them more defensible than whitetail fawns.

The most successful and common strategy for a mule deer fawn encountered or attacked by coyotes was to stay near a mule deer female. However, females were not always alert to coyotes or present, in which case, fawns fled. Even though mule deer fawns were at higher

risk of being attacked and captured when fleeing, they sometimes avoided these consequences by ducking behind vegetation to escape from the coyotes' view. This is not to imply that mule deer fawns always behaved in a manner yielding the best outcome, but that there were times when flight was an appropriate tactic.

Whitetails appear to have a lifelong bias to flee and this may constrain their ability to commit to the aggressive defence of fawns in summer. By the time whitetail fawns are 5 months old, they can outdistance coyotes in most situations (Lingle & Pellis 2002). Whitetails are renowned for their flightiness compared with mule deer (Geist 1981) and this behavioural difference in temperament persists even when the two species are bottle-raised together in captivity (Lingle 1989). This strong tendency to flee may even expose whitetail females to more risk if they are unable to follow through in their attempts to defend fawns. When whitetail females ran toward a coyote to defend a fawn, they typically dashed away if the coyote lunged at them. Whitetail females staying near fawns ended up being attacked in three cases, with less severe pursuits on other occasions. Even though mule deer females spent considerably more time close to coyotes, there was only one instance in which a mule deer female was attacked after defending a fawn in summer.

Differences in locomotory patterns may also affect the ability of whitetails and mule deer to defend fawns. The two species use different gaits, with mule deer stotting and whitetails galloping, both when they flee from predators and also when they chase coyotes (Lingle 1993; Lingle & Pellis 2002). When attacking a coyote, a mule deer hops primarily on its hind limbs while yanking the fore limbs down to hit the predator. In contrast, each of the limbs has an essential role in propelling the galloping whitetail so none of the limbs can be devoted to hitting the predator. Deer that stot are also highly manoeuvrable and able to make sharp turns both to track coyotes they chase as well as to avoid lunges (Lingle 1993; Lingle & Pellis 2002). In these ways the stot, more than the gallop, lends itself to aggressive tactics and evasive manoeuvres employed at close distance to a predator.

Social and aggressive antipredator tactics similar to those seen in mule deer tend to be found in animals living in open habitats (Jarman 1974; Lima 1993). Mule deer generally inhabit more open habitats than whitetails, which may in part explain why they rely more on aggression and less on hiding and flight than do whitetails. At first glance, one might not be surprised that mule deer fawns had higher survival rates than whitetail fawns at this field site, which is more open than most landscapes occupied by these species. However, the situation changes by winter. Mule deer fawns continue to rely on defence by adults, but suffer higher predation rates than whitetail fawns throughout winter (Lingle 2000; Lingle, unpubl. data), even though the landscape is even more open at that time of year due to the desiccated vegetation.

It is not uncommon for one species to be more vulnerable than another (Kotler & Brown 1988; Werner & McPeck 1994) or for two species to be more vulnerable in different habitats (Mercurio, Palmer & Lowell 1985; Christensen & Persson 1993). What is intriguing about this situation is that fawns of one species, whitetails, are more vulnerable to coyotes at the start of life, whereas fawns of the other species, mule deer, are more vulnerable to the same predator when older (Lingle 2000; Lingle & Pellis 2002). The temporal shift in relative vulnerability of whitetail and mule deer fawns may simply be a striking artefact of antipredator behaviour suited to different habitats. Mule deer may have been better positioned to develop an effective aggressive strategy in summer, because they use the same habitats and similar aggressive behaviour during the rest of the year.

On the other hand, temporal variation in predation risk can stem from variation in the predator species (Ballard, Whitman & Reed 1991; Adams, Singer & Dale 1995), alternative prey (Lingle 2000) and prey vulnerability itself (Molinari-Jobin *et al.* 2004). In tandem with habitat conditions, temporal variation in predation risk could act as a selective pressure that shapes the specific form of antipredator behaviour if certain strategies are most effective in protecting animals at certain times of their lives. The prevalence of aggressive defence in the context of protecting young animals (ungulates, Smith 1987; birds, Montgomerie & Weatherhead 1988; insects, Coccoft 2002) suggests this strategy has repeatedly arisen in response to the increased vulnerability of young animals. The idea that temporal variation in predation risk could have led some prey species to be particularly skilled in protecting their young at the start of life, and other prey species to cope with predators better at subsequent life stages, deserves attention.

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