

Susan Lingle · Sergio M Pellis

Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer

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Abstract It is well known that prey of different size and morphology often use different antipredator strategies. The prevailing notion is that this occurs because size, morphology and weaponry determine the relative effectiveness of alternative strategies, and nowhere is this assumption more entrenched than in our view of the basic decision to stay, fight or flee. Here, we use observations of coyote (*Canis latrans*) packs hunting deer in winter to show that two ungulates of similar size and morphology, white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*), use different antipredator strategies when encountered or attacked. Mule deer typically responded by holding their ground and aggressively defending conspecifics, and were at high risk of being attacked and killed if they fled or were undefended. White-tails always fled when pursued or attacked by coyotes. Coyotes pursued fewer white-tails than mule deer they encountered regardless of prey response. Once pursued or attacked, white-tails faced a risk of attack and capture, respectively, that was intermediate between the high and low risk mule deer groups. The overall risk of capture per encounter for white-tails was similar to that facing mule deer that confronted coyotes, which was much lower than risk facing mule deer that fled and were undefended. Contextual variables such as the opportunity to improve one's position by joining another group, moving to rugged terrain, or the presence of companions that are willing to provide defense may explain why a mixed strategy is maintained in mule deer, despite the apparently detrimental effects of flight. These examples illustrate

the value of including prey behavior in models of hunting success in so far as prey defenses may not be coupled with differences in size and morphology.

Keywords Alternative tactics · Antipredator strategies · Cooperative defense · *Canis latrans* · Coyote predation

Introduction

It is well known that prey of different size and morphology often use different antipredator strategies (Jarman 1974; Peckarsky 1987, 1996; Longland and Price 1991; Caro and FitzGibbon 1992; Christensen and Persson 1993; Dewitt et al. 1999). The prevailing notion is that this occurs because size, morphology and weaponry determine the relative effectiveness of alternative strategies, and nowhere is this assumption more entrenched than in our view of the basic decision to stay, fight or flee. However, in few cases has the effectiveness of alternative strategies been measured, even though this information is needed to truly understand why prey animals employ certain behaviors. Moreover, the decision to use a certain strategy affects many aspects of a prey animal's lifestyle, including the habitats they select and the groups they form (Sih 1987; Lima and Dill 1990).

The effectiveness of antipredator defenses needs to be evaluated not only to understand prey behavior, but to understand foraging decisions made by predators. Models that have been developed to predict hunting success emphasize prey size and morphology (Thompson 1975; Schoener 1979; Molles and Pietruszka 1987; Stander and Albon 1993) and rarely incorporate prey behavior (but see Malcolm 1992). Nonetheless, studies across a variety of taxa have revealed that antipredator behavior greatly influences predatory success (Neill and Cullen 1974; Messier and Barrette 1985; Peckarsky 1987; FitzGibbon 1989, 1990; Ben-David et al. 1991; Cresswell 1994; Krause and Godin 1995). It is easier to include prey size in a model of hunting success than it is to observe and quantify prey behavior, but the former approach is poten-

S. Lingle (✉)
Large Animal Research Group, Department of Zoology,
University of Cambridge, Cambridge CB2 3EJ, UK

S.M. Pellis
Department of Psychology and Neuroscience,
University of Lethbridge, Lethbridge, AB T1K 3M4, Canada

Present address:

S. Lingle, Department of Psychology and Neuroscience,
University of Lethbridge, Lethbridge, AB T1K 3M4,
Canada, e-mail: susan.lingle@uleth.ca

tially misleading if prey defenses influence the outcome of predation attempts and are not fully correlated with size and morphology of prey.

There are two obvious difficulties in evaluating the effectiveness of prey defenses. First, one must find similar prey that exhibit variation in antipredator defenses when facing a similar threat. Without variation in behavior, one cannot test the effectiveness of different behaviors. Second, one has to identify all the stages of a hunt to measure the effectiveness of antipredator tactics at each stage, because different tactics may be useful at different stages (Endler 1986). To illustrate the importance of this approach, one only has to picture one prey that relies on crypsis to avoid detection and another highly visible prey that relies on weapons to thwart capture once attacked. If one only sampled capture success once these animals were attacked, the armored animal would appear more successful, even though the success of the other animal in avoiding detection may outweigh its vulnerability once attacked. While the importance of considering all hunt stages may seem obvious, it has posed a problem in studies of hunting success in some predator-prey systems, particularly those involving large mammals. There are excellent descriptions of the stages that hunts pass through for large carnivores and their prey (Estes and Goddard 1967; Mech 1970; Kruuk 1972). But when measuring overall hunt success, biologists have typically defined hunts as active pursuits, specifically excluding travel done while searching or casually "testing" prey (Kruuk 1972; Stander and Albon 1993; Creel and Creel 1995). This is sometimes done because it can be difficult to know when a hunt has begun, particularly when observing animals such as wolves (*Canis lupus*) or wild dogs (*Lycaon pictus*) that habitually travel together.

A system that is conducive to examining the effectiveness of antipredator strategies involves coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Coyotes form packs that embark on excursions during which they hunt deer. These hunts are readily distinguishable from their other activities, including simple travel and hunts of smaller prey, and they have a relatively clear-cut start and end (Lingle 2000). The two species of deer are closely related and nearly identical in body size and overall morphology (Mackie 1964; Eslinger 1976; Wishart 1986). Juveniles and adult females of both species weigh approximately 40 and 70 kg as they enter winter in central Alberta (W. Wishart, unpublished data), and 32 and 60 kg in Montana (Mackie 1964). White-tails and mule deer have similar productivity (Beasom and Wiggers 1984; Mackie et al. 1998), breeding systems (Hirth 1977; Kucera 1978; Geist 1981) and feeding habits (Martinka 1968; Anthony and Smith 1977; Krausman 1978), but are associated with different habitats. White-tails tend to occupy gentle terrain with cover, whereas mule deer are found in more rugged and open areas (Swenson et al. 1983; Wiggers and Beasom 1986; Wood et al. 1989). Nevertheless, both species occupy a wide range of habi-

tats and coexist in many areas (Kramer 1973; Wiggers and Beasom 1986; Wood et al. 1989).

Coyotes are important predators of both species of deer (Cook et al. 1971; White et al. 1987; Unsworth 1999; Lingle 2000) but, curiously, there are seasonal differences in the vulnerability of white-tails and mule deer to coyote predation. Coyotes capture more white-tail than mule deer fawns in summer, during the first few months of life (Whittaker and Lindzey 1999; Lingle 2000), but more mule deer when fawns are older in winter (Lingle 2000). The differences in mortality within each season cannot be explained by their relative abundance or by differences in habitat use. Even though mule deer are more vulnerable than white-tails during winter, white-tails were more abundant and had greater overlap with coyotes during that period (Lingle 2000, 2002). The differences in risk facing white-tails and mule deer were more pronounced for animals occupying gentle terrain shared with the second species of deer (Lingle 2002). Another possible explanation for the difference in white-tail and mule deer vulnerability is that it is due to differences in their antipredator behavior.

Despite their many similarities, the two species of deer exhibit marked differences in their response to predators (Geist 1981). Captive mule deer are more likely to confront a tethered dog than are white-tails, which are more likely to move away immediately (Lingle 1989). In the wild, white-tails have been reported to flee when attacked by wolves and they do so by galloping (Mech 1970). In response to coyotes, mule deer frequently stay in place, at times attacking the predator (Bowyer 1987), and they also bunch together for protection (Lingle 2001). When they do flee, mule deer are more likely to stot than to gallop and, regardless of their gait, they are considerably slower than white-tails (Eslinger 1976; Lingle 1992). As yet, no one has compared the basic strategy – the decision to flee, stay or counter-attack – of white-tails and mule deer faced with the same predator during naturally occurring predation attempts. Here, we use observations of coyotes hunting sympatric white-tails and mule deer in winter to show that coyote encounters with the two species progress in different ways and that white-tails and mule deer employ different antipredator strategies. Mule deer showed variation in their tactics, some fleeing while others confronted coyotes. By evaluating the vulnerability of mule deer adopting these different tactics, and comparing these to the vulnerability of white-tails, which fled as their primary defensive strategy, we could assess the role of antipredator tactics in prey vulnerability and coyote hunting success.

Materials and methods

Study site and subjects

The research was conducted at a 20 km² study site on a 225 km² cattle ranch in southern Alberta (49°N, 112°W). Census data showed that about 135 mule deer and 250 white-tails lived in the study area in the winters from 1994 to 1996. Mule deer tended to

occupy the higher and steeper slopes (rising >60 m from the base, >10° in slope), whereas white-tails tended to occupy gently rolling (<5°) or flat terrain. Both species used the lower, gentler slopes (<60 m high, <10°; see map of distributions in Lingle 2000). The study area was open prairie, with native grassland covering 83% of the area. Non-native grasses had been seeded in the remainder during the 1980s. Seven coyote packs that had dens in or near the study area used rendezvous sites within the study area during winter. More recent observations of radio-collared individuals indicate that additional coyotes may have frequently entered the area and participated in deer hunts.

Definition and observation of hunts

Coyote packs 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. In 15 hunts observed from start to end, the average pack contained 4.4 coyotes and traveled 2.5 km (Lingle 2000). Group members traveled in-line at a fast walk, following a leader who usually remained the same throughout the hunt. Coyotes appeared to search for deer by looking around as they traveled, pausing to scan from high points, and looking directly at visible deer. Hunts of small prey, typically voles or ground squirrels, were distinguishable from hunts of deer by smaller pack sizes, the absence of a fixed leader or formation, and by different forms of searching and attack behavior (Bekoff 1978; Wells and Bekoff 1982; Lingle 2000). Coyotes frequently encountered deer while traveling, hunting small prey, or resting, but in winter such encounters rarely led to predation attempts on deer (Lingle 1998). Data presented here are therefore restricted to encounters observed during continuous pack hunts of deer.

Hunts were observed by sitting at a vantage-point located relatively far from the coyotes (500–1,000 m), which enabled monitoring of coyotes as they moved amongst different groups of deer, often for the entire hunt. Observations were made with 7×42 binoculars and a 20–45 ED spotting scope. The observer (S.L.) rotated among four main vantage-points, usually spending a day at each. All vantage-points provided views of exclusive white-tail habitats, three provided views of shared habitats, and two provided views of exclusive mule deer habitats. After spotting a pack starting to hunt, groups of deer that were present and the coyotes route were plotted on a topographical map. While this method of viewing and mapping hunts was established by the winter of 1995–1996, data on coyote-deer encounters were recorded on audio-tape while observing smaller portions of hunts the two previous winters. Observations were generally made from shortly after dawn to dusk, although we found that most hunts occurred around mid-day in winter (Lingle 2000).

Hunts were classified as *single species* if coyotes restricted their travel to a habitat used exclusively by one deer species, or as *both species*, if they traveled through a shared habitat or began in a habitat used by one deer species and then moved to a habitat used by the other. Coyotes showed little interest in white-tails encountered during hunts in which they also traveled in a habitat typically used by mule deer (Lingle 2002). In contrast, the presence of white-tails during these hunts did not affect their attention to mule deer. Data for white-tails were therefore restricted to hunts in which coyotes traveled in an exclusive white-tail habitat, whereas data for mule deer included hunts in which coyotes entered habitats used by both deer species and hunts in which they restricted their travel to an exclusive mule deer habitat.

Data collection

Coyote-deer interactions were distinguished into several stages. An *encounter* occurred whenever coyotes within 200 m of a group of deer either looked at the group or appeared to have an unobstructed view. An *approach* occurred when coyotes first started to stalk, walk or run toward a group or individual deer. A *pursuit* en-

sued if coyotes continued to approach after the deer reacted to them or after they closed the distance to within 2 m. Pursuits could be made of entire groups or they could consist of a short lope after an individual, possibly to “test” it (e.g., Mech 1970; Kruuk 1972; Creel and Creel 1995). Attacks were intense attempts to capture individual deer, either by chasing or lunging, that appeared in immediate danger of being captured. Pursuit of a single deer was distinguished from an attack by slower gaits on the part of both coyotes and deer and the readiness of coyotes to shift their attention to another individual. Deer that were attacked could escape without serious injury or be *killed*. The latter category was used to describe deer that were killed immediately and also those wounded seriously enough to die later as a result of the attack.

A running description of each interaction was recorded on audio-tape. For each encounter, several variables were noted: species, type of deer group (adult only, juvenile only, or mixed-age), group size, number of juveniles, age and sex of individual attacked, height of the group above the base of the slope, the closest distance to which coyotes approached the deer, prey responses, and the outcome of the interaction. Deer were grouped on the basis of distance, with a group separated by more than 50 m from another group (Clutton-Brock et al. 1982). The tape recorder was left on during attacks so their duration could be determined after the hunt using a stopwatch.

Exact group size was obtained for 69% of mule deer and 85% of white-tail groups that were encountered, including all groups having fewer than six deer (12 mule deer and 57 white-tail groups). In cases when it was not possible to make an exact count, the group was assigned to one of five categories: *x-small*, 1 adult with or without fawns, or fewer than three fawns with no adult; *small*, 2–5 deer, excluding *x-small* groups; *medium*, 6–10 deer; *large*, 11–20 deer; *x-large*, over 20 deer. The median value in the category was used for a group when exact size was not obtained to estimate per-capita attack and kill rates.

We identified prey behavior at each hunt stage as follows. Deer were considered alert if they adopted an alert posture (erect neck, both ears angled upward and facing coyotes), exhibited an alarm signal (e.g., tail flag), or simply moved away from the coyotes. A group was excluded from analyses when none of its members alerted to coyotes, although the effect of alert behavior on hunting success is considered in detail elsewhere (Lingle and Wilson 2001). Once alert, deer either fled, moved but then stopped and re-oriented to approaching coyotes, or stayed in place throughout the interaction. The behavior exhibited last during a particular hunt stage was used to describe the deer’s behavior for that hunt stage. When different members of a group behaved differently, the responses of the deer that were approached or attacked were used rather than the response of the deer that were ignored.

Finally, we recorded whether any individual in a group was aggressive to coyotes, either in self-defense or to defend other deer. Aggressive behavior was defined as approaching or confronting coyotes while exhibiting at least one element of a threat posture (ears held at right angles to the head with ear cups facing down or forward, preorbital glands or body fur flared) or overt aggression (striking a coyote).

Data analysis

When describing encounter rates and overall hunting success, the sampling unit was the individual hunt. Unless specified otherwise, all hunts were included, even if the beginning or end was not seen, to avoid biasing results against unsuccessful hunts (i.e., no capture), which might last longer and be more difficult to observe in their entirety.

We used the interaction with a single group of deer as the sampling unit when examining the risk facing deer. Characteristics of deer groups, including size and composition, changed frequently so were unlikely to be the same during more than one hunt. It was more important to avoid repeated observation of individuals at the attack stage, since this is the stage at which coyotes focused on one individual. Based on locations at which individuals were at-

tacked, physical differences among these individuals (age, sex, natural markings, and the presence of ear-tags on 20% of fawns), the outcome of attacks (some were killed so could not be observed a second time), and the small number of attacks that were observed, it was unlikely that more than one attack was observed on any individual. For these reasons, we do not believe that the data collected were biased by repeated observation of individual deer.

Coyotes were not seen making multiple kills in a single hunt and this seems unlikely to occur during winter unless circumstances were exceptional (e.g., see Patterson 1994). When different coyotes chased different deer simultaneously, they immediately abandoned their chase once a deer was killed by another coyote. Simultaneous pursuits were therefore treated as one event.

Data were restricted to the winter of 1995–1996, when coyotes were monitored throughout their hunts, to obtain an unbiased sample of the proportion of encounters resulting in attacks or kills. Predation attempts observed in previous winters or that were in progress when first seen were used to examine the duration of attacks, the frequency of wounding, and whether age or antipredator behavior was related to the probability of attack or capture.

Nonparametric tests were used to analyze data, because data involved frequencies or were not distributed normally. Williams's correction was applied to G -values when $df=1$. The overall G -value was not adjusted when $df>1$, but alpha was adjusted using the Bonferroni correction (α/k) in subsequent pairwise contrasts to maintain an experimentwise error rate of 0.05 (Sokal and Rohlf 1995). This correction was also applied to Mann-Whitney tests used for pairwise contrasts following a significant Kruskal-Wallis test. P -values shown are for two-tailed tests.

Results

Sequence and outcome of hunts

Coyotes encountered 2.3 times more white-tail than mule deer groups per kilometer traveled (Table 1), which could be expected from differences in their abundance. White-tails were 2.5 times more common than mule deer and white-tail fawns 2.3 times more common than mule deer fawns in the winter of 1995–96 (Lingle 2000). Despite encountering more white-tails, coyotes made kills in a similar proportion of white-tail and mule deer hunts. A deer was killed in 2 of 18 hunts of white-tails (one fawn, one adult female), and in 2 of 17 hunts of mule deer (two fawns), restricting data to hunts for which the outcome was known. One of the mule deer that died was severely wounded during the attack, only dying a day later.

Of the groups of deer encountered, coyotes were significantly more likely to approach, pursue and attack mule deer than white-tails (Fig. 1a; approach, $G_{adj}=9.23$, $df=1$, $P=0.002$; pursuit, $G_{adj}=17.35$, $df=1$, $P=0.0001$; attack, $G_{adj}=13.35$, $df=1$, $P=0.0003$). They made an attack

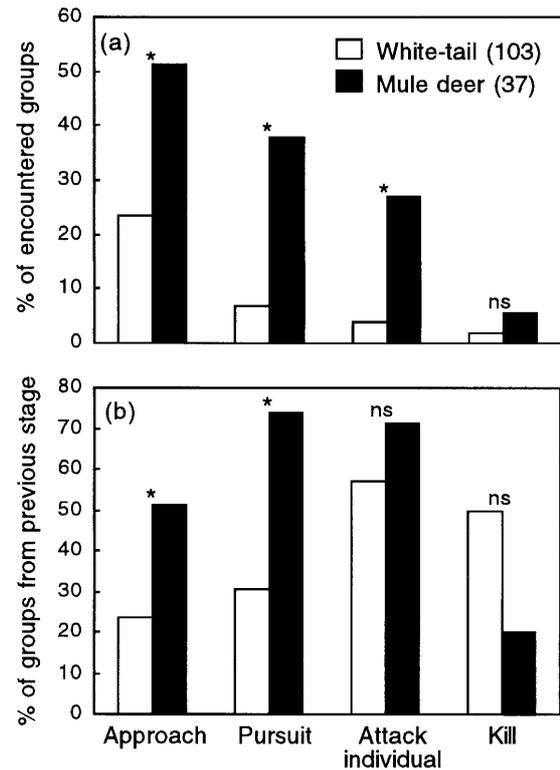


Fig. 1a, b Escalation of predation attempts with groups of white-tails and mule deer. *Significant difference between the species at a particular hunt stage; ns non-significant. **a** The percentage of groups that were encountered that were involved in subsequent hunt stages. **b** The percentage of groups from previous hunt stage involved at subsequent hunt stage

in 27% of encounters with mule deer, but in only 3.9% of encounters with white-tails. The difference in kill rate was not significant, with a kill in 5.4% of mule deer encounters and in 1.9% of white-tail encounters ($G_{adj}=0.89$, $df=1$, $P=0.35$). However, it is possible a difference would be detected if a larger sample of kills were obtained. Taking the small difference in group size between species into account (8.6 mule deer per group vs 7.7 white-tails), individual mule deer appeared 6 times more likely to be attacked (3.1% vs 0.51%), and 2.5 times more likely to be killed (0.63% vs 0.25%).

Adult and mixed-age groups were pooled in these analyses, because coyotes were no more likely to approach groups with juveniles than groups without for either species (white-tails, coyotes approached 3 of 22 adult groups, 20 of 80 juvenile groups; $G_{adj}=0.94$, $df=1$,

Table 1 Rate at which coyotes encountered white-tails and mule deer per hunt (*med* median, *IQR* interquartile ranges). Statistical comparisons: Mann-Whitney test: for groups, $Z=-3.61$, $P=0.0003$; groups/km, $Z=-2.45$, $P=0.01$; individuals, $Z=-2.92$, $P=0.003$

Species	<i>n</i>	Groups/hunt		Groups/km/hunt		Individuals/hunt	
		med	IQR	med	IQR	med	IQR
White-tail	19	5.0	3.0–7.8	2.5	1.5–5.0	40.0	18.0–59.3
Mule deer	20	1.5	1.0–3.0	1.1	0.2–1.5	14.5	5.0–22.0

$P=0.33$; mule deer, 1 of 5 adult groups, 17 of 30 mixed age groups, $G_{\text{adj}}=2.21$, $df=1$, $P=0.14$). The lack of a significant difference for mule deer may have been due to the small sample of adult groups. The effects of age on the likelihood of being attacked and antipredator behavior are considered further on in this paper.

The difference in hunt sequence did not arise because coyotes attacked a fixed number of deer per hunt regardless of the number encountered. If so, mule deer would have appeared more vulnerable, because coyotes would be attacking a larger proportion of the less common species (mule deer). As long as coyotes encountered deer during a hunt, hunts of mule deer progressed further than hunts of white-tails (Mann-Whitney test, $Z=2.17$, $n_1=18$, $n_2=16$, $P=0.03$). For instance, at least one attack occurred during 56% of hunts in which mule deer were encountered but in only 22% of hunts involving white-tails.

The probability of escalation between successive hunt stages was examined to identify the exact stage at which white-tails and mule deer differed in their risk. Mule deer were at higher risk of an interaction escalating when encountered or approached (Fig. 1b; encounter to approach as above; approach to pursuit, $G_{\text{adj}}=7.78$, $df=1$, $P=0.005$). Once pursued, white-tails and mule deer were attacked at similar rates (pursuit to attack, $G_{\text{adj}}=0.38$, $df=1$, $P=0.54$). When attacked, in the winter of 1995–96, mule deer were quite successful in avoiding capture with only 2 of 10 attacks resulting in kills. The probability of being killed once attacked did not differ significantly (Fig. 1b; attack to kill, Fisher exact test, $P=0.52$); however, as with encounters resulting in kills, a larger sample is needed to test this with adequate power.

The mule deer's resistance to capture once attacked was evident in two other aspects of the hunt sequence. Attacks on mule deer lasted significantly longer than attacks on white-tails (median, interquartile ranges for white-tails=20 s, 12–52.5 s, $n=7$; mule deer=209 s, 51–541 s, Mann-Whitney $U=69$, $n=12$, $P=0.02$). Furthermore, predation attempts on mule deer that ultimately resulted in death were commonly interrupted after a deer was wounded. Two of the four encounters with mule deer that resulted in death were interrupted after the deer had been severely wounded. The final capture was made 3 h later in one case and over 24 h later in the other. Altogether, 12 mule deer were seen with wounds obviously inflicted by coyotes (mostly on the rump, hind limbs or sides of body). Ten of those were severely wounded fawns that died within a few hours or days. We did not observe white-tails that were wounded by coyotes but only died much later.

When both fawns and adults were present in a mule deer group, coyotes were more likely to attack fawns (binomial test, 9 of 9 attacks on fawns, mean proportion of fawns in attacked groups was 0.44, $P=0.002$). Mule deer adults were only attacked when fawns were not present (5 females and 2 males) or after they defended fawns (2 females). A difference in the probability of juveniles or adults being attacked was not as obvious for white-tails. Coyotes attacked fawns in three of five white-tail

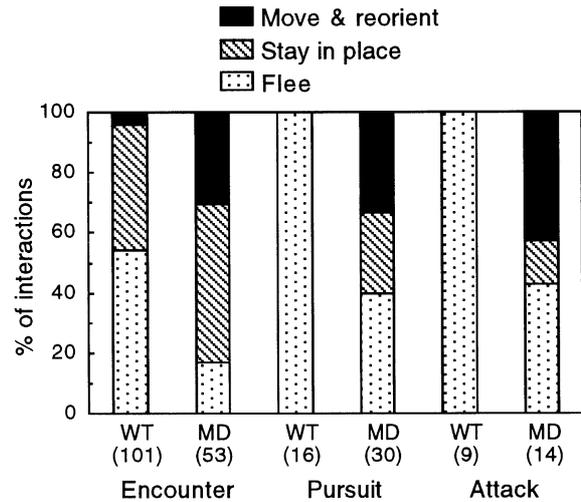


Fig. 2 Percentage of interactions in which deer fled, stayed in place, or moved and reoriented to coyotes at different hunt stages. Species (WT white-tails, MD mule deer), sample size and hunt stage below bars

groups when they had a choice (mean proportion of fawns in these groups was 0.38; $P=0.42$).

Antipredator behavior

At all stages of the hunt sequence, white-tails were more likely to flee than mule deer (Fig. 2; G -test: encounters, $G=32.06$, $df=2$, $P<0.0001$; pursuits, $G=21.53$, $df=2$, $P<0.0001$; attacks, stay pooled with move and reorient, Fisher exact test, $P=0.007$). Indeed, once it became clear that they were the target of a hunt, white-tails only responded by fleeing. In contrast, mule deer exhibited a mixed strategy. They could flee or they could stand their ground. Even though mule deer juveniles were more likely to flee during attacks than adults, at times they also stayed in place (6/9 juveniles fled vs 0/4 adult females, Fisher exact test, $P=0.07$). Furthermore, mule deer were frequently aggressive to coyotes, whereas white-tails were never aggressive during the observed hunts (mule deer were aggressive in 27% of 53 encounters, 66% of 29 pursuits and 73% of 15 attacks; white-tails in none of 104 encounters, 16 pursuits or 9 attacks; G -test: encounters, $G_{\text{adj}}=31.74$, $df=1$, $P<0.0001$; pursuits, $G_{\text{adj}}=23.04$, $df=1$, $P<0.0001$; attacks, Fisher exact test, $P=0.0006$).

Mule deer were primarily aggressive to defend their companions, although self-defense was also observed. The most common form of aggression was observed when coyotes encountered or pursued a group. Depending on the size of the group, one to a few females would walk or trot toward the coyotes, assuming a threat posture, to keep the coyotes away from the group, which was typically bunched together at the time (Lingle 2001). When interactions escalated and coyotes attempted to lunge at or run after a deer, females stotted after the coyotes, striking them with their fore limbs. As long as

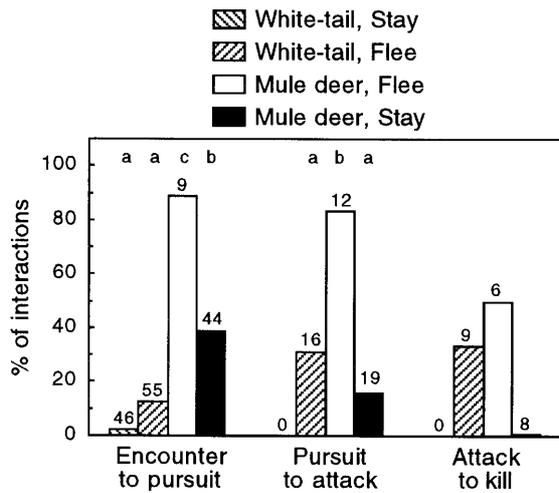


Fig. 3 Percentage of interactions that continued to a more advanced hunt stage for deer that fled or stayed in place in response to coyotes (G -test: encounter to pursuit, $G=43.48$, $df=3$, $P<0.0001$; pursuit to attack, $G=15.29$, $df=2$, $P=0.002$). Deer that moved but then reoriented to coyotes were pooled with deer that stayed in place. Sample sizes given above bars. When data were not available, the sample size is shown ($n=0$) to distinguish between these cases and those in which data were available but no interactions escalated. Different superscripts indicate significant differences between groups. Due to differences in behavior and vulnerability of adults and fawns at the attack to kill stage, statistical tests were restricted to attacks on fawns when sample size justified a test and are presented in the text. Data shown here include attacks on adults as well as fawns

adult females were present, juveniles left the aggressive defense to the females. When alone, juveniles tried to defend themselves, as evidenced by two isolated mule deer fawns that were aggressive to coyotes despite being badly wounded. Adult females that were attacked were similarly defended by other females but they also defended themselves (7/7 juveniles defended by females with no self-defense versus 3 females were defended by other females but also defended themselves, Fisher exact test, $P=0.008$).

Antipredator behavior and the risk of predation

The different defensive tactics of mule deer influenced their vulnerability. Mule deer that fled when encountered were more likely to be attacked than those that stood their ground (Fig. 3). Only three of six mule deer fawns that fled when attacked survived, whereas all three that stayed in place did so. It is important to note that the three fawns that survived after fleeing did not do so by outdistancing coyotes during the chase. They survived because their mothers intervened and drove coyotes back while the fawns managed to get several hundred meters away.

Aggression was effective in ending attacks on mule deer. Groups that were pursued were actually more likely to be those that responded aggressively when encountered (Fig. 4). However, this is certainly an artifact of

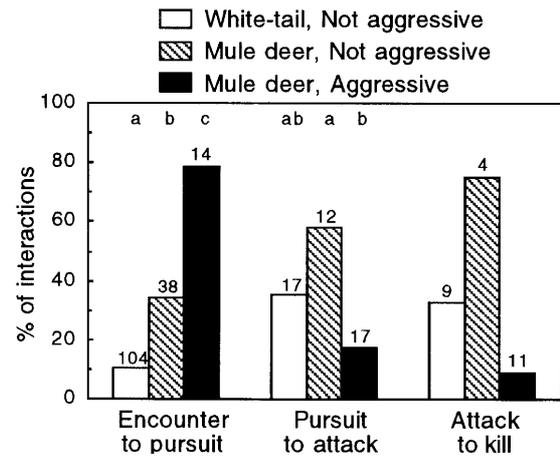


Fig. 4 Effect of aggression on outcome of interactions. Percentage of interactions that escalated to a more advanced hunt stage for white-tails, non-aggressive mule deer and aggressive mule deer (G -test: encounter to pursuit, $G=32.51$, $df=2$, $P<0.0001$; pursuit to attack, $G=5.22$, $df=2$, $P=0.07$). Different superscripts indicate significant differences between groups. Due to differences in behavior and vulnerability of adults and fawns at the attack to kill stage, statistical tests were restricted to attacks on fawns when sample size justified a test and are presented in the text. Data shown here include attacks on adults as well as fawns

coyotes being closer to these groups (median, IQR=5 m, 5–5 m for aggressive groups vs 75 m, 20–162 m for non-aggressive groups; Mann-Whitney $Z=-4.51$, $n_{agg}=11$, $n_{not\ agg}=37$, $P<0.0001$). Pursuits of aggressive mule deer were less likely to escalate to attacks and attacks to kills (Fig. 4). All three undefended fawns, but only one of seven defended fawns were killed (Fisher exact test, $P=0.03$).

Aggression also appeared to explain the long duration of attacks on mule deer and the occurrence of wounding. Coyote attacks lasted longer when they involved aggressive mule deer than non-aggressive mule deer or white-tails (aggressive mule deer, median, IQR=330 s, 127.5–630 s, $n=9$; non-aggressive mule deer=30 s; 9.8–33.8 s, $n=3$; white-tails=20 s; 12–52.5 s, $n=7$; Kruskal-Wallis $H=12.47$, $P=0.002$). In six cases when coyotes attempted to capture an animal they had already wounded, aggression by companions or by the wounded animal itself prevented coyotes from killing the deer for hours or days.

Regardless of prey response, coyotes pursued more mule deer than white-tail groups that were encountered (Figs. 3, 4). Once pursued, the proportion of groups attacked or captured was lowest for mule deer that held their ground or were defended. Of the deer that fled, coyotes were more likely to attack fleeing mule deer than fleeing white-tails. Unlike mule deer, white-tails that fled and survived did so by outrunning coyotes without assistance from other deer. Overall, 0.01 of encounters with mule deer groups resulted in a capture when they

held their ground or were defended, which was comparable to the 0.01 of encounters with fleeing white-tail groups that led to capture. The proportion of encounters resulting in capture was greatly augmented for mule deer that fled (0.37 of encounters with groups) or were undefended (0.15).

The species differences in antipredator tactics did not arise from differences in size of deer groups or from the size or identity of coyote packs. Both species formed small, medium and large groups. Irrespective of group size, white-tails were never observed to stand their ground or behave aggressively towards coyotes. Mule deer did so at all group sizes. The size of coyote packs hunting white-tails was similar to those hunting mule deer (mean \pm SD for white-tails=4.2 \pm 1.2, $n=19$; for mule deer=4.5 \pm 1.3, $n=23$; unpaired $t_{40}=0.68$, $P=0.50$). The identity of packs also did not explain the species differences in behavior or risk. Five of seven packs resided in areas where they could, and appeared to, hunt either white-tails or mule deer. Deer showed similar behaviors regardless of where they lived even though they were encountering different coyote packs. Furthermore, species-typical responses were seen when coyotes encountered or attacked mixed-species groups (Lingle 2001).

Lastly, the species differences in behavior and vulnerability cannot be explained by habitat variation. Most mule deer groups that were encountered (33 of 37) stood low on slopes, in habitats often shared with white-tails, because coyotes tended to travel on gentle terrain when they hunted deer (Lingle 2002). It was not only mule deer occupying rugged terrain, where white-tails did not occur, that held their ground. Mule deer groups encountered at all heights tended to hold their ground rather than flee (7 of 9 groups ≤ 30 m; 6 of 9 groups 31–61 m, and all 9 groups >61 m; height refers to height of a group above the base of a slope).

Discussion

Effectiveness of alternative antipredator tactics

Mule deer can be distinguished into high and low risk groups depending on their response to coyotes. They were at high risk of being attacked and captured when they fled and when other deer failed to defend them, and at low risk when they held their ground and confronted coyotes. There are other components to the mule deer's response that appear to increase their ability to deter coyotes. Mule deer tend to move to rugged terrain or high points and to bunch closely together with companions before reorienting to coyotes (Lingle 2001, 2002). As long as they stand close together, coyotes are unlikely to single out an individual for attack.

These results are consistent with Bowyer's (1987) report that coyotes were more likely to pursue mule deer that fled than those that stand their ground. While the main contribution of that paper was to show that larger groups of coyotes were more likely to show serious pre-

datory behavior toward deer, his conclusions about prey behavior warranted further attention because non-predatory encounters may have been included in the sample. If one wants to know how prey behavior affects a predator's hunting success, it is important to restrict analyses to interactions in which the predator is hunting that type of prey. Otherwise, two things can happen. If deer hold their ground when they encounter coyotes that are traveling or hunting small prey, it might appear that they are safe from standing their ground when it is possible that the deer simply recognized the coyotes posed no threat. Moreover, when non-predatory encounters are included, the outcome of interactions will rarely escalate beyond an encounter regardless of the prey animal's behavior.

White-tails always fled when pursued or attacked by coyotes. At these stages of the hunt, white-tails faced a risk of attack and capture intermediate between the high and low risk mule deer groups, that is, mule deer that fled versus those that held their ground and mule deer that were not defended versus those that were. However, because fewer white-tails were pursued when encountered in the first place, their overall risk of capture once encountered was similar to that of mule deer that confronted coyotes. This means that, on average, mule deer do more poorly in winter when encountered by coyotes than white-tails. They are only as good as white-tails when they confront coyotes and they often fail to do so. These results are consistent with data showing higher mule deer mortality during winter (Lingle 2000), and they raise a few questions. Why are white-tails but not mule deer able to evade coyotes by fleeing? If mule deer are so vulnerable when they flee, why do they use this antipredator strategy at all? Finally, why have different forms of antipredator behavior arisen in these species?

The fundamental difference that seems to let white-tails flee successfully but not mule deer seems to be speed. Unlike mule deer fawns, white-tail fawns were faster than coyotes when chased (Lingle 1998). The only reasons for a difference in speed that have been identified to date are also behavioral in nature, and these are differences in the timing and form of their gaits (Lingle 1992, 1993). As yet, no physical differences between the species have been found to explain the difference in their gaits or speed (Eslinger 1976). Rather than offering speed, the mule deer gaits provide greater maneuverability. The longer suspension of the mule deer gallop compromises its speed but can be helpful for jumping obstacles (Lingle 1992, 1993). Mule deer use the even greater maneuverability of the stot to attack coyotes and dodge their lunges (Lingle 1998).

In this study, there was no situation in which fleeing mule deer moved faster than coyotes during a chase, unless another deer blocked the predator. Mule deer were not able to outdistance coyotes when traveling up-slope any better than when traveling cross-slope (Lingle 1998). There was little broken ground available to determine whether mule deer could stot faster than coyotes could run across this type of terrain. It is possible that flight would be an appropriate response against a different type

of predator. However, we would expect slow speeds attained by mule deer to be even more limiting against large coursing predators such as wolves, which overtake prey in shorter distances than do coyotes (Paquet 1992). On the other hand, when faced with a large stalking and sprinting predator such as a mountain lion (*Felis concolor*), a sudden jump to dodge a predator's lunge followed by flight might be more effective than confrontation.

There was no indication that different strategies were best for different individuals (Pettifor et al. 1988). Mule deer frequently varied their behavior during interactions, fleeing after standing in place or stopping after a period of flight. Encounters usually escalated to attacks after an animal fled, and were brought to a halt by the animal stopping. Flight, however, appeared useful as a temporary tactic that enabled deer to improve their position in some way. If a mule deer stood in place, but was alone, coyotes were likely to attack it (Lingle 2001). Individuals would therefore move to join a group and groups moved to join another group or to get to rugged terrain, and then stopped after reaching these locations. Flight may also be important to fawns in summer. When flushed from hiding spots, several fawns with no female nearby fled until they could get to a new source of cover which they used to escape from the coyotes' view.

A mule deer's decision to stay in place or to flee appears further complicated, because it could depend on the willingness and ability of other deer to stay with the animal and defend it, as well as on the individual's ability to defend itself. In three cases, fawns that were alone with their mothers fled after being repeatedly rushed by coyotes. These mothers then overtook and drove the coyotes back during heated battles lasting about 10 min, while the fawns managed to get several hundred meters in front of the coyotes and near other groups. It is possible that this response, flee while your mother fights, is more effective than staying in place when there are no additional deer present. However, if no female follows the fawn to defend it, the risk of capture is high. More commonly, rather than flee, these very small groups moved to larger groups or other deer came to them. In larger groups, only a few adult females came forward to attack coyotes. This means that the composition of a group and the location of certain individuals could affect another animal's tendency to stay or flee.

Finally, deer in good physical condition may be more willing to respond aggressively. It was our impression that mule deer defended other deer less readily as winter progressed and in years in which they might be expected to be in poor condition due to forage conditions. Contextual issues such as these could explain why mule deer maintain a mixed strategy with elements of flight as well as confrontation.

So why has a different form of antipredator behavior evolved in these species? One possibility is that flight, even by white-tails, is less effective than confrontation in rugged terrain, a habitat used more often by mule deer (Wiggers and Beasom 1986; Wood et al. 1989). Because white-tails avoided steep, rugged habitats in winter, we

have no data with which to address this hypothesis. Another possibility is that confrontation is more effective than flight during the season following the birth of fawns and – for some unknown reason – the species specialize in defense against predators in different seasons. This seems a likely explanation given that mule deer fawns are less vulnerable to coyote predation than white-tail fawns in the first few months of life (Whittaker and Lindzey 1999; Lingle 2000) and, overall, behavioral differences observed in winter persist in summer. Even though white-tail mothers will aggressively defend their own fawns in summer (Smith 1987; Lingle, unpublished data), mule deer mothers respond aggressively more habitually than white-tails and they also cooperate to defend fawns (Lingle, unpublished data). Females of species that defend fawns in this way may be more effective in protecting their fawns during the first few months of life, a period when most ungulates are too small and slow to outrun predators.

Mule deer are considerably smaller than other ungulates, such as eland (*Taurotragus oryx*) or musk oxen (*Ovibos moschatus*) reported to stand their ground and attack predators on a regular basis outside the post-parturition period (Tener 1954, Kruuk 1972). In fact, mule deer are over three times smaller than elk (*Cervus elaphus*), which typically flee to avoid coyotes (Gese and Grothe 1995). The highly social nature of mule deer defenses seems to enable mule deer to use a strategy of confrontation to deter coyotes despite their relatively small size. In ungulates that are similar in size to mule deer, reports of aggression as a standard defense against medium to large predators have been restricted to maternal defense of young in the weeks or months following birth (white-tails, Smith 1987; bighorn sheep (*Ovis canadensis*), Berger 1978; pronghorn (*Antilocapra americana*), Lipetz and Bekoff 1980; mountain goats (*Oreamnos americanus*), Cote et al. 1997), with rare use of aggressive defense in other seasons (bighorn sheep, Shank 1977; white-tails, Nelson and Mech 1985, 1994; Gese and Grothe 1995). White-tails have been reported to respond aggressively to predators rarely outside the fawning season (Nelson and Mech 1985, 1994; Gese and Grothe 1995). In 2,000 h of observation during which coyotes were frequently observed within 50 m of deer several times a day, we only observed two instances in which white-tail bucks chased single coyotes, and this was not when coyote packs were hunting deer. Mule deer continued to attack coyotes during non-predatory encounters, for instance, when the coyotes rested, traveled or hunted small prey. One thing that could theoretically influence the decision to flee or fight is snow depth, given that it is more difficult to outrun predators in deeper snow (Paquet 1992). There was little snow cover throughout this study due to strong chinook winds (monthly medians ranged from 0 to 10 cm for the winters of 1994–1995 and 1995–1996). It is possible that white-tails would be more likely to respond aggressively if snow is deep enough to restrict their ability to flee.

It is surprising that white-tails and mule deer use contrasting antipredator strategies, given they are closely related and similar in size, morphology and armor (Mackie 1964; Eslinger 1976; Wishart 1986). Even though the larger hearts and lungs of mule deer (Wishart 1986) may help them withstand longer attacks than white-tails, these features do not explain why mule deer are more aggressive. Superior aerobic capacity could have been applied to flight rather than to aggression. For example, pronghorn (*Antilocapra americana*) use their superior respiratory capacity for long distance running (Lindstedt et al. 1991).

Implications for studies of predatory behavior

The present study is unusual among reports of coyote-ungulate interactions in that it restricts data to observations made of coyote packs engaged in behavior typical of deer-hunting. Furthermore, it reports the rate of escalation for a relatively unbiased sample of encounters occurring during these hunts. Two authors reviewed coyote-bighorn sheep encounters reported in the literature, but noted that these accounts were probably biased toward more advanced interactions: people are unlikely to report interactions in which predators simply pass a prey animal with neither responding (Berger 1991; Bleich 1999). This bias probably explains why the rate at which juveniles were killed in those reports (33% of encounters with juveniles, 22% for males, and none for females) was high compared with results in this study. Unlike those studies, Bowyer (1987) reported all cases in which coyotes were within 50 m of mule deer. His observation of 4 pursuits, 2 attacks and 1 kill in 25 encounters may be lower than results in this paper (14 pursuits, 10 attacks, and 2 kills in 37 encounters for mule deer within 200 m of coyotes, with coyotes within 50 m in 17 of these encounters), because coyotes may not have been hunting deer in many of those encounters.

While these results provide information that should be considered when measuring a predator's hunting success, some important limitations need to be specified. We did not address the earliest hunt stage: whether coyotes were more likely to hunt white-tails or mule deer in the first place. It would also be helpful to have a more direct measure of the rate at which individuals or groups are encountered, for instance, by using focal observations of individuals. Furthermore, information on the costs of hunting is needed to compare the coyotes' efficiency hunting these species (Creel and Creel 1995). The coyotes that wounded a mule deer were not necessarily the same individuals that consumed the deer after it died a day or a week later. There may be substantial differences in the energetic costs of hunting each species, given that mule deer occupy more rugged terrain and attacks on them lasted longer.

The vulnerability of mule deer to pursuit once encountered, but not to capture when attacked, illustrates the importance of sampling all hunt stages and prey be-

havior when measuring hunting success. Differences between the behavior and speed of white-tails and mule deer seem to explain why coyotes pursued more mule deer they encountered, and also why mule deer were resistant to capture once attacked. Because mule deer either fled at a relatively slow speed or stood in place, coyotes could easily get near them regardless of the deer's response. This proximity gave coyotes continued opportunities to single out an individual for attack. The flight response and superior speed of white-tails can make it difficult for coyotes to find conditions in which they have a good chance to get near enough to a white-tail to attack it, which may be why so few encounters led to pursuits. The way in which the mule deer's aggression increased their resistance to capture once attacked is more obvious, because it is revealed by the longer and less successful attacks on aggressive mule deer compared with non-aggressive mule deer or white-tails. These examples illustrate the value of including prey behavior in models of hunting success in so far as prey defenses may not be fully represented by differences in size and morphology.

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