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Detection and Avoidance of Predators in White-Tailed Deer (*Odocoileus virginianus*) and Mule Deer (*O. hemionus*)

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Abstract

In this paper, we investigate the relationship between early detection of predators and predator avoidance in white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*), two closely related species that differ in their habitat preferences and in their anti-predator behavior. We used observations of coyotes (*Canis latrans*) hunting deer to test whether the distance at which white-tails and mule deer alerted to coyotes was related to their vulnerability to predation. Coyote encounters with both species were more likely to escalate when deer alerted at shorter distances. However, coyote encounters with mule deer progressed further than encounters with white-tails that alerted at the same distance, and this was not due to species differences in group size or habitat. We then conducted an experiment in which a person approached groups of deer to compare the detection abilities and the form of alert response for white-tails and mule deer, and for age groups within each species. Mule deer alerted to the approacher at longer distances than white-tails, even after controlling for variables that were potentially confounding. Adult females of both species alerted sooner than conspecific juveniles. Mule deer almost always looked directly at the approacher as their initial response, whereas white-tails were more likely to flee or to look in another direction with no indication that they pinpointed the approacher during the trial. Mule deer may have evolved the ability to detect predators earlier than white-tails as an adaptation to their more open habitats, or because they need more time to coordinate subsequent anti-predator defenses.

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Introduction

We generally expect species that differ in size and morphology to differ in the extent to which they rely on crypsis or on early detection (e.g. Heatwole 1968; Jarman 1974; Burger 1984; Sodhi 1991), but not species that are physically similar. However, differences in concealment and detection behavior can evolve among similar species as adaptations to different habitats. For example, different species of monkeys specialize in the detection of aerial or terrestrial predators, depending on the height of forest they typically occupy (Gautier-Hion et al. 1983; Peres 1993; Bshary & Noë 1997). Differences in detection abilities and alerting behavior could also arise in association with variation in anti-predator strategies. For instance, responses that take longer to coordinate may require longer alerting distances.

White-tailed deer and mule deer are closely related species with similar mating systems (Hirth 1977; Kucera 1978; Geist 1981), life-history patterns (mule deer refs in Wallmo 1981; white-tail refs in Halls 1984), and feeding habits (Martinka 1968; Krausman 1978). Despite these similarities, white-tails and mule deer prefer different habitats and rely on different methods of avoiding predators (Geist 1981). Even though the species coexist in many areas, white-tails tend to occupy more gentle terrain and wooded habitats, while mule deer prefer more rugged and open habitats (Swenson et al. 1983; Wiggers & Beasom 1986; Wood et al. 1989). When confronted with coyotes, white-tails tend to flee, while sympatric mule deer are more likely to make small adjustments in their position in the habitat, bunch together with other individuals, and attack the predators (Lingle 1998, in press). Geist (1981) suggests that mule deer may be better able to detect predators at longer distances than white-tails as an adaptation to their open-country lifestyle. Differences in their ability to detect predators might be expected. Despite being nearly identical in size and in their musculo-skeletal structure in the northern parts of their range (Mackie 1964; Eslinger 1976; Wishart 1986), white-tails and mule deer differ in specific perceptual features. Mule deer were named for their large external ears, measuring two-thirds of the length of their heads vs. half for white-tails (Anderson & Wallmo 1984), and they also have more laterally placed eyes (Wishart 1986; Wishart, unpubl. data).

In this study, we use data gathered during observations of coyotes hunting deer to test whether alert distance is related to the vulnerability of white-tails and mule deer, and whether this relationship differs for the two species. We then present data obtained during an experiment to test whether the two species differ in their ability to detect a human approacher. The study was conducted at a site where coyote packs hunted sympatric white-tails and mule deer. We were able to observe these hunts because of the open prairie landscape. Coyotes were a significant source of mortality from Nov. through Feb., primarily capturing fawns which were between 5 and 9 mos old at the time, but also killing some adults (Lingle 2000).

This study of predator detection is important for several reasons. Firstly, it provides data on detection abilities and alert responses that should be helpful in

understanding trade-offs which animals make when living in different habitats or when using certain anti-predator strategies. Secondly, biologists are recognizing that we need a better understanding of predator detection and alerting behavior in order to advance our understanding of vigilance (Lazarus 1979; Elgar 1986; Arenz & Leger 1997; Lima 1995a, b, 1999). Finally, despite the assumption that early detection is important to prey and the large volume of vigilance studies based on this assumption (review by Elgar 1989), relatively few studies have examined whether early detection or early response affects the outcome of predator–prey interactions (but see Mech 1970; Eaton 1974; Kenward 1978; FitzGibbon 1988).

Studies of predator detection have a significant methodological difficulty, because detection of a threat is typically inferred from a variety of alert behavioral responses (Dimond & Lazarus 1974; Lazarus 1979; Ydenberg & Dill 1986). In fact, animals may be aware of a problem but show no response; they may be aware of a disturbance and alert without locating the threat; or they may be aware, alert, and locate the threat (Dimond & Lazarus 1974; Lazarus 1979; Ydenberg & Dill 1986). Precautions were taken in this study to reduce the possibility that deer detected the approacher without responding. Furthermore, the form of alert response was identified and these data were used to address the question of whether deer showed a behavioral response at the moment of detection.

Study Site and Subjects

Research presented here was conducted on a 125-km^2 portion of a large cattle ranch in southern Alberta between Nov. and early Apr. 1993–1994, 1994–1995 and 1995–1996. Within this area, there was a core study site of 20 km^2 in which animals were censused and intensive observations of coyotes and deer were conducted. There were about 135 mule deer and 250 white-tails in the core study site in winter (Lingle 2000), with another approximately 350 mule deer and 200 white-tails in the larger area included in the detection experiment. Four coyote packs had dens within the core study area, with dens of another three packs within 0.5 km of its boundary.

The landscape was open prairie. Over 83% of the core study area was native fescue or mixed grassland. The remaining 17% was used for cultivation until the mid-1980s when it was re-seeded with native and exotic forbs and grasses. Vegetation outside the core site was entirely native prairie, excepting exotic species that may have spread into isolated areas. Grassland consisted of short desiccated grass and forbs (<40 cm high in winter when observations were conducted), with small patches of similarly short shrub. Small stands of taller shrubs, 1–3 m high, occurred on sheltered slopes. Most variation in habitat was topographical. Previous analysis indicated that the higher steeper slopes (>60 m rise from the base of the slope) were primarily occupied by mule deer in winter, while gently rolling terrain, <5 degrees in steepness, was mostly used by white-tails (see map in Lingle 2000). Lower gentle slopes (<60 m high, <10 degrees in steepness) were used by both species.

Other than coyotes, there were no non-human predators of deer during winter. There was also no hunting of deer by humans on the ranch, although deer were exposed to hunting in Nov. if they moved outside the ranch.

Alert Distance and Vulnerability to Coyotes

Methods

Observation of hunts

Coyote packs went on regular and extended outings during which they hunted deer. The entire outing was considered a hunt, during which a coyote pack could encounter several groups of deer or none at all. In a hunt, an average of 4.4 coyotes traveled at a fast walk, walking in-line, following a leader who remained the same throughout the hunt (Lingle 2000). Coyotes appeared to search for deer by looking around as they traveled or when they paused on high points. Coyotes frequently encountered deer when engaged in other activities such as travel, hunts of small prey or when resting, but these encounters rarely led to predation attempts in winter (Lingle 1998). Hunts of small prey were distinguished from hunts of deer by a smaller number of coyotes, the absence of a fixed formation or leader if in a group, searching behavior in which coyotes used slower gaits, covered little distance, traveled in irregular directions and oriented their heads more steeply to the ground, and by different behaviors used to capture prey (Lingle 2000).

The seven coyote packs were observed hunting deer during 1600 h of observation between 1 Nov. and the end of Feb. 1994–1995 and 1995–1996, with another 400 h of observation in winter 1993–1994. In the first two winters, we opportunistically saw coyote packs make predation attempts on individual groups of deer. By the winter of 1995–1996, we were able to sit at vantage points and observe packs as they engaged in continuous group hunts. We observed hunts from distances typically ranging from 500 to 1000 m using a 20–45 × zoom ED spotting scope and 7 × 42 binoculars. This distance was maintained because coyotes were not habituated so would not hunt if we were closer and because we were able to view the entire route taken by coyotes as well as most groups of deer they passed from this distance. Data on coyote–deer interactions were recorded on audio-tape and transcribed afterwards. Encounters reported here include only those occurring when coyote packs were identified as hunting deer based on behaviors described above.

Hunt stages

Stages of a predation attempt were distinguished according to the intensity of interaction between the coyotes and deer. Deer that detected coyotes when the pack was starting to move but not yet traveling in their direction might *leave early*, thereby avoiding an encounter with the coyotes. A group was *encountered* when coyotes within 200 m appeared to detect it. This distance was selected

because we were able to monitor deer within this distance of coyotes and most approaches seemed to begin at shorter distances. Coyotes were considered as having detected a deer group if they looked at it, approached it, or if there appeared to be no obstructions between the coyotes and deer. Our priority was to monitor interactions between coyotes and deer groups they encountered, so we were unlikely to have seen all groups that left early after detecting coyotes.

Hunt stages ranging from the approach to the attack were defined broadly so that differences in prey behavior did not lead to spurious differences in classification. Because mule deer often held their ground, coyotes frequently attacked them by repeatedly lunging from less than 1 m away. Because white-tails typically fled, coyotes typically chased them during an attack, and the coyotes could be 2–10 m behind the deer. Classifications were therefore based on certain behaviors and the apparent intensity of interaction for coyotes and deer, not on the distance separating coyotes from deer. The first behavioral indication that coyotes adjusted their gait or route to move directly to a group was termed an *approach*. Coyotes could stalk, walk, or run to approach a group or an individual deer. Hunts escalated to a *pursuit* if coyotes continued to approach after the deer reacted to them or after coyotes arrived within 2 m of the deer. Pursuits could be chases made on entire groups or short casual 'testing runs' after an individual (e.g. Mech 1970; Kruuk 1972). An *attack* occurred when coyotes made an intense and committed effort to capture one individual. The form of attack could take several forms: a prolonged chase in which coyotes traveled at a fast gallop; a short committed chase; a lunge if a coyote was within contact distance and appeared to make an intense effort to capture a deer; or a prolonged attack in one location, e.g. repeated lunging at a deer that avoided coyotes by sudden maneuvers or fighting rather than by flight. The final stage was that of being fatally wounded or immediately *killed*.

Alerting data

The distance between the lead coyote and the closest member of a deer group was estimated when an individual in the group first showed any form of alert behavior. Alert behavior included orienting to the coyotes with an alert posture (erect neck, both ears angled upward and facing coyotes), looking in another direction with an alert posture, exhibiting other indications of alarm including anti-predator signals (e.g. tail flag) or an escape gait, or simply moving away if alerted by neighboring deer. A group could therefore detect coyotes or be alerted by another group during these observations.

Alerting distances were estimated and rounded using categories which were also used in the detection experiment (Table 1). Categories became larger when longer alert distances were involved because of the greater difficulty in estimating longer distances. Coyote routes and deer groups were plotted on a topographical map during hunts. We estimated distances by eye when coyotes and deer were less than 500 m from us and appeared to be within 200 m of each other, using the map when uncertain. We relied on the topographical map for help in estimating

Table 1: Group, habitat and climatic traits recorded during observation of coyote–deer encounters and the detection experiment. Type of variable includes continuous, ordinal or nominal

Variable (type)	Categories and definitions
Approach and alert distance: actual, then rounded (cont)	Distances < 5 m left at nearest meter; distances from > 5–30 m rounded to the nearest 5 m; > 30–50 m to the nearest 10 m; > 50–200 m to the nearest 25 m; > 200–400 m to the nearest 50 m, distances over 400 m rounded to the nearest 100 m.
Group type (nom)	Adult; mixed age (adults and juveniles, which are between 5 and 9 mos of age during winter).
Group size (nom)	Small, ≤ 5 deer; medium, 6–10 deer; large, over 10 deer.
Annual variation (nom)	Winter of 1993–1994, 1994–1995 and 1995–1996.
Activity of group (nom)	Rest; active; rest and active; travel.
Type of habitat (nom)	White-tail, mule deer, or shared. Areas used by each species identified during censuses and focal observations in winter.
Topography between approacher and deer (nom)	Up-slope; down-slope; cross-slope; across rolling or flat terrain.
Gain (cont)	Difference in height between approacher and deer (m).
Exposure of approacher to deer (ord)	Average, person viewed against background of vegetation; exposed, person viewed against background of snow, sky, or light prairie so should be highly conspicuous.
Topography of deer (nom)	Slope (part of main slope system); steep rolling (discrete hill ≥ 7.6 m in height and $5°$ in steepness); gently rolling (< 5 degrees).
Steepness (cont)	$\leq 5°$; 6–10°; 11–15°; 16–20°; $> 20°$ (determined using a map showing steepness of terrain).
Location of trial (nom)	Inside core study area; outside core study area.
Wind speed (cont)	km/h in 10 km intervals.
Wind direction (nom)	Deer upwind, crosswind or downwind of approacher. Data from days with no wind were pooled with upwind data.

distances when coyotes and deer were further from us or when the distance between them appeared greater than 200 m.

In addition to distance estimates and the outcome of the interaction (i.e. hunt stage), we recorded deer group size (small, medium, or large, see Table 1), deer group type (adult or mixed age), and the height of deer on slopes. Height was identified using a topographical map having 25-ft (7.6-m) contour intervals, and was converted to metric during the analysis. Heights above 50 ft (15.2 m) were recorded in 25-ft (7.6-m) intervals; under 50 ft (15.2 m), we estimated a group's height to the nearest 10-ft (3-m) interval. We were often able to identify the coyote pack that was hunting, or limit the possibilities based on rendezvous sites, pack

size and the presence of individuals with recognizable markings. However, our ability to distinguish packs was too limited to include pack effects in the data analysis.

Data Analysis

The individual group of deer was the sampling unit. This was because predators encounter groups of prey rather than individuals (Huggard 1993), and we gathered one value for alert distance per group. Pseudo-replication was unlikely to be a problem. Groups of deer changed frequently in size and composition so were unlikely to be the same during more than one hunt. Furthermore, the number of deer in the core study site and the number of deer encountered during hunts indicated that repeated observations of the same individuals were infrequent, averaging 1.6 times for mule deer that were encountered and 1.4 times for white-tails for all of winter 1995–1996 (Lingle 1998).

Data from a group were used as long as each group was involved in a separate encounter with coyotes. We did not use data for groups that either joined or were joined by another group already involved in a predation attempt. Data for groups containing fawns or females were included, while excluding groups composed solely of males. This was because coyotes primarily attacked fawns and females and the responses of animals in all-male groups appeared to differ from those of other deer. Too few all-male groups were sampled to examine the relationship between their responses and vulnerability systematically. Some males were present in groups having females and fawns.

An ordinal logistic regression (using JMP statistical software, available from SAS Institute, Inc.) was used to test whether alert distance and species affected the outcome of coyote–deer encounters (i.e. hunt stage), while controlling for other variables. Hunt stage, from the encounter to the kill, was treated as an ordinal variable. Groups that left early were excluded from the analysis, because data for this stage were too incomplete to justify comparing use of this tactic by the two species statistically.

Results

Groups of both species alerted to coyotes at shorter distances in predation attempts that reached more advanced hunt stages (Fig. 1). However, mule deer became involved in more advanced hunt stages when alerting at the same distance as white-tails. The regression analysis identified a significant interaction among species, alert distance and group size (Table 2). To examine the three-way interaction, we first tested whether species and alert distance, alongside other variables shown in Table 2, affected hunt stage within group size categories. Species and alert distance had strong independent effects for small and medium groups, but interacted for large groups (logistic ordinal regression: effect of species for small groups, $\chi^2 = 9.25$, $p = 0.002$, alert distance, $\chi^2 = 11.1$, $p = 0.0009$; medium groups: species, $\chi^2 = 8.80$, $p = 0.003$, alert distance,
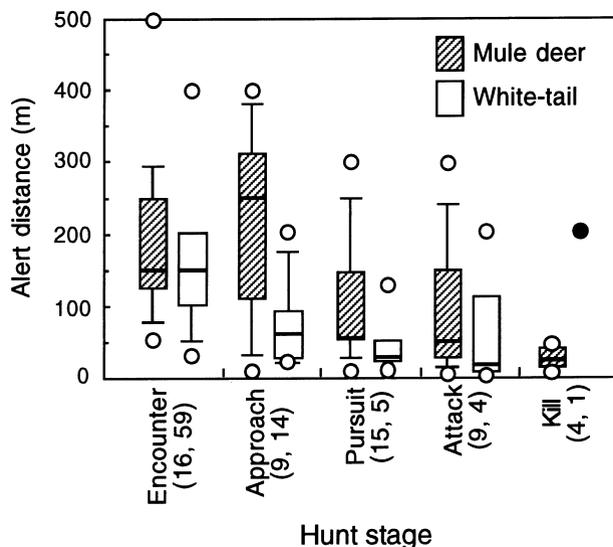
Fig. 1: Distance between coyotes and deer when first member of a group alerts to coyotes (alert distance) for interactions ending at different hunt stages. Boxes represent interquartile ranges, horizontal lines within boxes show medians, capped bars represent 10th and 90th percentiles, and open circles show range of data. Sample sizes (mule deer, white-tail) below hunt stages. When n < 6, 10th and 90th percentiles are not indicated. Seventy-fifth and 90th percentiles are identical for white-tail encounter; 25th percentile and median are identical for mule deer pursuit. There was only one white-tail kill for which the alert distance was known, and this point is plotted by itself (closed circle)

$\chi^2 = 15.4$, p = 0.0001; large groups, species × alert distance, $\chi^2 = 6.79$, p = 0.009, species, $\chi^2 = 11.20$, p = 0.0008, alert distance, $\chi^2 = 1.91$, p = 0.17).

The interactions were examined further by correlating alert distance and hunt stage within group sizes for each species. Alert distance had a similar and

Table 2: Logistic ordinal regression used to test effect of alert distance and species on outcome of coyote encounters (hunt stage) while controlling for other variables

Variable	df	χ^2	p
Species × Group size × Alert distance	2	9.73	0.008
Alert distance × Group size	2	19.32	0.0001
Group size × Species	2	6.93	0.03
Alert distance × Species	1	0.22	0.64
Species	1	26.91	< 0.0001
Alert distance	1	12.75	0.0004
Group size	2	3.05	0.22
Height	1	14.85	0.0001
Group type	1	1.80	0.18

Model $\chi^2 = 99.69$, n = 132, p < 0.0001, $r^2 = 0.30$.

relatively strong correlation with hunt stage for all sizes of mule deer groups (Spearman rank correlation for mule deer: small, $r_s = -0.52$, n = 14, Z = -1.87, p = 0.06; medium, $r_s = -0.60$, n = 23, Z = -2.83, p = 0.005; large, $r_s = -0.58$, n = 17, Z = -2.30, p = 0.02). The effect of alert distance was less consistent for white-tails. Alert distance was significantly correlated with hunt stage for small and medium groups, but not for large groups, apparently explaining the two- and three-way interactions obtained in the regressions (white-tails: small, $r_s = -0.39$, n = 43; Z = -2.49, p = 0.01; medium, $r_s = -0.62$, n = 23, Z = -3.17, p = 0.002; large, $r_s = -0.31$, n = 17, Z = -0.31, p = 0.92).

Habitat differences were controlled by including height in the model. This was because height and topography were the main characteristics distinguishing the habitats of white-tails and mule deer, and these features were also associated with their vulnerability to coyotes (Lingle 1998). It was sufficient to include height in the model because this subsumes topography: animals on flat or rolling terrain had a height of 0 m.

There was considerable variation in the relationship between alert distance and hunt stage for both species (Fig. 1). A few factors may be responsible for this variation and deserve further attention. Firstly, deer within a group did not become alert simultaneously. Individual fawns in three mule deer groups did not appear to detect coyotes until the predator was within 2 m and attacked them, even though other members of their group detected coyotes earlier, at distances of 250 m for one and 25 m for the other two groups. The latter distances were used in the data (Fig. 1; Table 2). Secondly, coyotes seemed to use different hunting tactics, at least when hunting white-tails, which may affect the importance of early detection for the prey. At times, coyotes walked stealthily to white-tail groups and appeared to abandon these approaches once detected. At other times, coyotes ran conspicuously into large groups of white-tails even though deer were alert. Despite all the deer being alert and running, coyotes often continued these pursuits, switching from one deer to another. Consequently, white-tails alerted to coyotes at distances under 30 m in seven pursuits or attacks which involved stalking, but became alert at comparatively long distances of 125–200 m in three other attacks in which coyotes ran into their groups even though the deer were alert.

Further evidence of a difference in the role of early detection for the two species include six mule deer groups that left the area after detecting coyotes that were beginning to hunt, but were still over 500 m away and not moving in their direction. This tactic was not observed in white-tails. Coyotes were also more likely to approach mule deer than white-tails that failed to detect them. Of 12 white-tail groups that did not alert when encountered within 200 m, coyotes approached three groups, simply ignoring the other nine. (The nine groups that did not alert could not be included in Fig. 1 or Table 1 since there were no alert distances for them). In contrast, coyotes approached all seven mule deer groups that did not alert when encountered (two-tailed Fisher exact test, p = 0.003). These mule deer were not more vulnerable than the white-tails because of habitat differences. Even though most of these mule deer groups occurred in low habitats

in which they were most vulnerable (Lingle 1998), the nine white-tail groups were still lower on slopes or on gently rolling terrain.

Detection of an Approaching Human

Methods

A detection experiment was conducted in which we compared the distance at which animals belonging to each species and age group (adult or juvenile) alerted to a human approacher. This experiment was carried out over 130 h on 28 d between Nov. and early Apr. 1994–1995 and 1995–1996.

Alert distance

Certain conditions had to be met before approaching a group to sample alert distances. Deer were only approached when they had an unrestricted view of the person, and the approacher had an unrestricted view of all deer in the group throughout the trial. Because this was difficult to achieve when moving across the rolling terrain found in the study area, we accepted temporary gaps in view amounting to less than 10% of the distance covered if an approach was made from over 200 m. Groups were not used if they were alerted by another group or disturbed by a coyote, other humans, vehicles or anything else.

Once a group was selected, the approacher walked directly toward it at a steady pace of about 1 m/s. Data were quietly recorded on audio-tape when the approacher was over 400 m from the deer, and brief notes were made on paper without stopping when at a closer distance. A deer was considered as having become alert when it either oriented to the approacher with an alert posture (head erect, head and ears facing observer), oriented in another direction with an alert posture, moved away with some form of alert response (as indicated by the position of head, gait, or anti-predator signals), or followed another deer that was alert. Deer that remained in place were considered alert when they maintained some form of alert response for 10 s. Because the first deer to alert in nearly all groups oriented directly to the approacher (46 out of 47), it was clear that the deer were reacting to the approacher or, for subsequent deer, to the responses of other group members to the approacher.

The approacher recorded the distance at which the group was first sighted and from which it was approached (*approach distance*), and the distance at which the first and last deer of each age/sex class exhibited an alert response (*alert distance*). Distances were estimated using a combination of a visual estimate, a range-finder, and a topographical map. Distances were rounded to categories used when observing coyotes (Table 1). There was one common exception to use of the categories identified in this table; if deer detected the approacher within a short distance of the start of the approach, a more precise interval was recorded, for instance, 5, 10 or 20 m less than the estimated approach distance, depending on the distance the approacher had covered. Both of us made these 'detection walks', each working alone. However, we practiced together before conducting

the experiment, in areas where we did not gather data later and continued to practice estimating distances throughout the study.

Because the main goal was to compare detection abilities of the two species, we attempted to minimize variation in habitat, climate, social structure, and behavior. Most detection walks were conducted outside the core study site where deer were not accustomed to seeing people on foot, or in parts of the core study area where we seldom walked, to lessen the possibility that deer detected the approacher but did not respond behaviorally. We mostly tested groups that were first sighted at distances between 100 and 500 m, because deer might have been less inclined to show a response if they detected a person approaching from a longer distance.

Deer in all groups had an unrestricted view of the approacher, and the approacher always walked through short (<40 cm), desiccated grassland. We attempted to minimize variation in background matching that could affect the deer's perception of the approacher by wearing clothes of the same color and brightness (forest green coat, tan trousers) and by avoiding approaches in which the person was silhouetted against the sky or snow. Most approaches were conducted with no snow cover, so the person would be viewed against the brown prairie grass. We approached groups across flat or rolling terrain or across slopes, avoiding routes that involved a large differential in height such as from directly above or below. Such routes could result in earlier detection distances which might bias results for longer mule deer distances because they use slopes more often than white-tails. Furthermore, those routes of approach are rarely used by coyotes (Lingle 1998). The detection experiment was planned to test the ability of deer to detect disturbances across unrestricted views, not the ability of deer to detect disturbances when topography restricted visual detection or when detection was complicated by effects of wind. We therefore tried to minimize the effects of wind by conducting approaches on days with low or moderate wind speeds (<30 km/h) and by approaching deer from down-wind.

Finally, we attempted to select groups having less than 10 deer, and groups in which all deer were active (it was more difficult to identify alert behavior when deer were resting). Even though we attempted to limit variation experimentally in the ways explained here, possible effects of the remaining variation in habitat, climatic and group characteristics on alert distances were controlled statistically while testing the effect of species, using variables and categories presented in Table 1.

Order of detection and form of alert response

During detection walks, we tried to record the order in which all members of each age/sex class became alert as well as the distance at which the first member became alert. The form of alert response was identified for individuals within groups when the order of detection was obtained. While other studies examined the general response (e.g. the tendency to stay or to flee) of deer that were encountered by a person (LaGory 1987; Smith 1991), we identified the form of

alert response at the fleeting moment when the deer first showed an indication of being alert. A deer either (a) oriented to the observer with an alert posture as its first response or after glancing in another direction for <1 s; (b) oriented to another deer in the group or in another direction with an alert posture; or (c) simply moved away in response to another deer in the group becoming alert. We also noted the number of deer of each age/sex class that appeared to pinpoint the approacher at some time during the trial, as indicated by their looking directly at the person, however briefly, within 30 s of the time that the last deer became alert.

Data analysis

With the large number of deer present (approximately 500 mule deer and 400 white-tails) and the variety of locations in which detection walks were conducted, it was unlikely that any group sampled during the detection experiment had the same composition as another group. Routes used during these walks were recorded on maps, and travel within a particular area was limited to two occasions. Certain individuals may have been present in more than one group, but even this would have been infrequent. Within the core study area, about 20% of mule deer fawns and 16% of white-tail fawns were tagged (Lingle 2000). We did not observe any of the marked fawns in more than one group sampled during the detection walks and over 60% of marked deer were not observed. These points indicate that pseudo-replication was unlikely to be a problem with data from the detection experiment.

The general linear model feature of JMP was used to test whether species was related to alert distance while controlling for approach distance and other variables that were potentially confounding. A logarithmic transformation was applied to alert distances to meet assumptions of parametric tests. Non-parametric tests were used for univariate analyses because data were often highly skewed or involved measurements of rank. The median rank for order of detection by adult females and by juveniles was identified when the order of detection was known for all individuals in a group. Median ranks of females and juveniles were compared using a paired sign rank test.

The main reasons for identifying the form of alert response were to consider how detection spreads through a group and to collect information that could help us evaluate whether the alert response was a useful indication of the moment of detection. The alert response of the first animal in a group was distinguished from the responses of other group members, because it would otherwise interfere with our ability to see how other deer became alert in groups of different size. This is because the first detector appeared constrained to alert by orienting directly to the approacher (see results), whereas other group members appeared to respond to the alert behavior of other deer as well as to the approacher. The response of the first detector would have a larger effect on small than on large groups because the first detector is a larger proportion of animals in small groups, and so could artificially lead to the conclusion that deer in small groups were more likely to orient directly to the approacher.

The median test was used to test whether age or species affected the form of alert response, and whether these effects could be due to variation in the animal's perceived level of danger (indicated by the distance at which the group first became alert to the approacher) or in the type of habitat (white-tail, mule deer, or shared). The median test was needed because values for alert responses were often truncated to the limit of possible values, making the more common Mann–Whitney or Kruskal–Wallis tests inappropriate (Siegel & Castellan 1988). G-tests with Williams's correction (after Sokal & Rohlf 1995) and the Fisher exact test were used to compare the frequency of values falling above or below the median. p-values are two-tailed and α is 0.05 for each test.

Results

Alert Distance

Mule deer alerted to the approacher at longer distances than white-tails, even after controlling for approach distance and other variables (Fig. 2; Table 3). Mule deer alerted shortly after the approach started with approach distances ranging from 70 to 1000 m (Fig. 2). White-tails were slower to detect the approacher across all distances from which they were approached. The statistical analysis was restricted to groups in shared habitats, because initial analyses within each species indicated that being in a shared or exclusive habitat affected alert distances for both species. Other variation in habitat, climate, social structure and behavior that could potentially affect detection behavior was minimized experimentally, and the analysis indicated that variation remaining in these factors did not affect
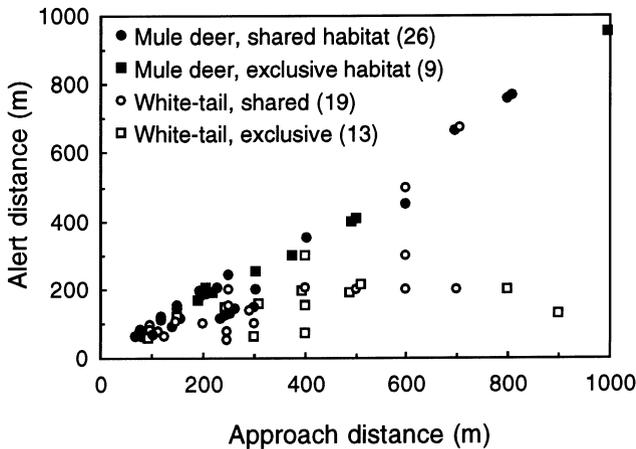

Fig. 2: Distance at which first deer in white-tail and mule deer groups alerted to a human approacher (alert distance) plotted against distance at which the observer first sighted and began to approach the deer (approach distance). Data for groups in habitats shared by the two species distinguished from data for groups in exclusive habitats. Identical points were staggered at a diagonal to make them visible

Table 3: General linear model used to test the effect of species on alert distance while controlling for other variables

Variable	df	SS	F	p
Approach distance	1	5.90	64.51	< 0.0001
Species	1	1.16	12.70	0.002
Group type	1	0.39	4.28	0.06
Group size	2	0.33	1.81	0.19
Activity	3	0.33	1.20	0.34
Topography of deer	2	0.07	0.39	0.69
Location	1	0.02	0.24	0.63
Steepness of deer	1	0.003	0.04	0.85
Wind speed	1	0.24	2.58	0.12
Wind direction	2	0.10	0.56	0.58
Topography between deer and approacher	2	0.21	1.13	0.34
Gain	1	0.10	1.05	0.32
Exposure of approacher	1	0.09	1.03	0.32
Year	1	0.16	1.77	0.20

Full model: $F_{20,20} = 8.14$; $p < 0.0001$; $r^2 = 0.89$.
Interactions between species and approach distance, species and group size, and species and group type were not significant.

alert distances significantly (Table 3). Group size was not related to alert distance (Table 3), and this result was based on groups ranging in size from one to 33 members (median 5.0) for mule deer and from one to 22 members (median 3.0) for white-tails.

Adult females of both species alerted sooner than conspecific juveniles. The average female detected the approacher sooner than the average juvenile in all 16 mule deer groups for which a comparison could be made (paired sign rank test: 16 out of 16, p <0.0001). The average female detected the approacher sooner than the average juvenile in most white-tail groups (paired sign rank: 14 out of 17, p = 0.01, with three ties). The difference is more obvious when looking at the individual that detected the approacher first, although this does not control for the number of each age group present. Adult females detected the approacher first in 20 out of 21 mule deer groups having both females and fawns, with a male first in the remaining group (males were present in five groups). Adult females detected the approacher first in 21 white-tail groups, a juvenile in one, a female and fawn were simultaneous in two, and a male first in the remaining trial (males were present in six groups).

Alert Responses

The first deer that became alert, in 22 mule deer groups and in 24 out of 25 white-tail groups, oriented directly to the approacher with an alert posture. In the one exception, three white-tail females in a large group became alert when
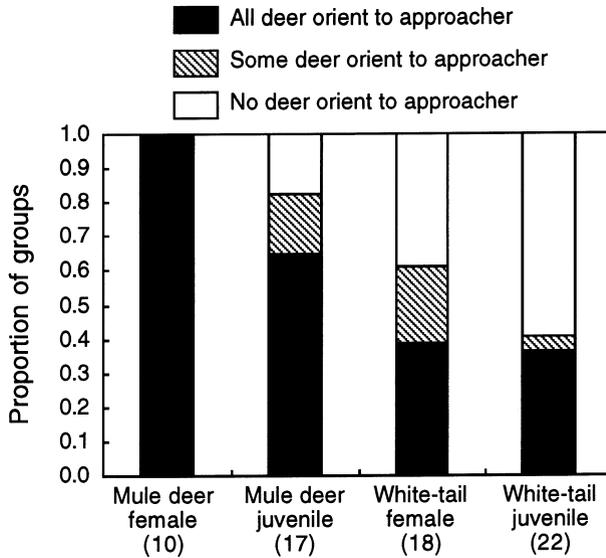
Fig. 3: Initial alert responses of juvenile and adult female white-tails and mule deer. Proportion of groups in which all, some, or no members of a particular age/species class oriented directly to the approacher as their first response. Sample size given below bars. Animals that did not orient to the approacher either oriented in another direction or moved away. The response of the first animal in a group to become alert is excluded from these data

downwind of the approacher on a day with a moderate breeze (30 km/h). Even though they were 700 m from the approacher, these deer sniffed the air several times, then walked away with flagged tails without orienting to the approacher, and were followed by the rest of the group.

Alert behavior shown by additional deer in the group was more varied and was affected by species and by age. The majority of mule deer of both age classes oriented to the approacher as their first response; however, juveniles were more likely to orient in another direction (Fig. 3; Table 4). Species comparisons were made within age groups because of age differences in response for mule deer. White-tails were less likely to orient to the approacher as their first response, with females more likely than mule deer females to look in a direction other than at the approacher. White-tail fawns were more likely than mule deer fawns to flee as their initial alert response, with adult females showing a similar but non-significant tendency. Nearly all mule deer, adult and juvenile, appeared to pinpoint the approacher at some point during the trial, as indicated by their orienting directly to the person, and this behavior did not differ by age group (Table 4). White-tail females were less likely than mule deer females to orient to the approacher during the trial, with fawns showing a similar but non-significant tendency when compared with mule deer fawns.

Habitat effects did not explain the species differences in alert behavior. Whether or not the trial was conducted in a shared or single species habitat did

Table 4: Statistical comparisons (median tests using G-values, df = 1) of the form of alert responses[a] of adult female and juvenile white-tails (WT) and mule deer (MD)

Comparison (n)	Orient to approacher		Orient other direction		Flee		Pinpoint approacher	
	G	p	G	p	G	p	G	p
Age comparisons								
WT fem (18) × juv (22)	1.57	0.21	0.17	0.68	0.44[b]	0.51	0.17	0.68
MD fem (10) × juv (17)	5.95	0.01	5.95	0.01		1.52		0.22
Species comparisons								
WT × MD females	12.66	0.0004	6.84	0.009	3.41	0.06	8.14	0.004
WT × MD juveniles	4.43	0.04	0.39	0.53	8.54	0.004	3.08	0.08

[a] Behavioral categories defined in text.

[b] There was no difference between the tendency to flee for mule deer females and juveniles: no animals from either group fled as their initial alert response. This meant that there were 0 df, making it impossible to calculate a G-value for this comparison.

not affect the alert response of white-tail females or juveniles or mule deer juveniles (median test using two-tailed Fisher exact test: p > 0.99 for all forms of alert response for the three groups). There was no variation in the responses of mule deer females, regardless of whether they were in a shared or single species habitat. Habitat effects were not expected to affect the alert response, since all animals were in full view and had an unobstructed view of the approacher during these trials.

Even though group size had a weak relationship with the alert responses of white-tails, it did not explain the species difference in alert response. As the size of white-tail groups increased, a larger proportion of females fled and a larger proportion of both age groups did not appear to pinpoint the approacher during the trial (Spearman rank correlation between group size and each form of alert response: proportion of individuals orienting to approacher as their first response, females, $r_s = -0.500$, $Z = -2.06$, $p = 0.04$; juveniles, $r_s = -0.35$, $Z = -1.6$, $p = 0.11$; proportion fleeing, females, $r_s = 0.537$, $Z = -2.21$, $p = 0.03$; juveniles, $r_s = 0.34$, $Z = 1.5$, $p = 0.12$; proportion pinpointing approacher, females, $r_s = -0.547$, $Z = 2.25$, $p = 0.03$; juveniles, $r_s = -0.49$, $Z = -2.24$, $p = 0.03$). White-tails did not occur in larger groups than mule deer, as would be necessary for this factor to explain why white-tails were more likely to flee without locating the approacher. The median size of white-tail groups in this sample was 4.0 (interquartile range, 2.0–5.0, n = 25) and 5.0 for mule deer (interquartile range, 3.0–8.0, n = 19), which did not differ significantly (Mann–Whitney test: $Z = -1.24$, $p = 0.22$). Furthermore, no relationship was detected between group size and the form of alert response for mule deer (p > 0.16 for all aspects of alert responses of mule deer juveniles, and no variation in responses of mule deer females).

Species differences in alert behavior also did not reflect the fact that white-tails detected the approacher at shorter distances, which could have led them to perceive a higher degree of danger and leave more quickly. Mule deer females were still more likely to orient to the approacher and tended to be more likely to locate the approacher when data were restricted to groups alerting within 300 m (median test using Fisher exact test: orient to approacher, $n_{wt} = 16$, $n_{md} = 7$, $p = 0.008$; locate approacher, $p = 0.06$). The reduced significance levels obtained in these tests are probably due to the smaller sample sizes used in the restricted data sets.

Discussion

Importance of Early Detection

Both white-tails and mule deer were safer when alerting to coyotes at longer distances. However, coyote encounters with mule deer progressed further than encounters with white-tails that alerted at the same distance. The observations of coyote–deer interactions should not be used to compare whether white-tails or mule deer detected coyotes sooner, because there were differences in the visibility of coyotes to deer and differences in the way in which deer groups became alert.

What these observations suggest is that mule deer need to alert to coyotes at longer distances than white-tails for interactions to end at the same hunt stage. The longer distance at which mule deer alerted to the human approacher indicates they have developed the ability to detect predators early compared with white-tails.

Early detection was more than an advantage to mule deer; it was also a tactic. Several mule deer groups detected coyotes early and left the valley where a hunt subsequently took place. This behavior was not observed in white-tails; however, it may have been overlooked because our priority was to monitor groups that were encountered. Additional observations are needed to determine how often mule deer use this tactic and whether white-tails ever use it.

We consider the results obtained from observation of coyote–deer interactions preliminary, because several aspects of deer alert behavior were not examined that may affect their vulnerability more than the distance at which the first member of a group becomes alert.

(1) At times there was a considerable lag between the time at which the first and last individual in a group became alert, and the latter may have a stronger relationship with the vulnerability of the prey (see results for examples).

(2) The moment at which a deer moves or signals, which may alert other group members, may have a stronger relationship with vulnerability than the moment at which the first deer simply stands alert, as was measured in this study.

(3) The way in which deer become alert may also affect the success of their evasion. Some groups or individuals saw coyotes; others became alert from the movement of neighboring deer without seeing the coyotes themselves.

(4) Observations also indicated that coyotes used two different strategies to hunt white-tails: in one they stalked a group, abandoning an approach if detected, and in the other they entered large groups in which deer were already alert and running and made testing chases after different individuals (see Kelsall 1968 for description of similar variation in wolf hunting tactics). This type of variation in hunting tactics could explain why alert distance was not related to the vulnerability of large white-tail groups even though it was related to the vulnerability of small white-tail groups.

In future work, it would be useful to confirm whether coyotes use these two hunting tactics and, if so, whether the importance of early detection to white-tails is related to the form of coyote hunting behavior and the size of white-tail groups.

It is possible that coyote packs differed in specific tactics or success, although their overall hunting methods appeared to be similar. Five of the seven packs were seen hunting both species at different times, so we do not think that differences among packs led to the observed difference between white-tails and mule deer. There was no difference in the size of packs hunting white-tails or mule deer (unpubl. data).

Mechanisms Affecting Detection

Mule deer detected the approacher sooner than white-tails across all distances from which deer were approached. This study examined alert responses

in conditions that emphasized long-distance visual or auditory cues by only approaching deer when they had an unobstructed view of the person. Further work should be carried out to investigate whether conditions more typical of closed habitats favor white-tails, for instance, when obstructions prevent visual detection, when predators appear at very short distances, or when deer are downwind of the approacher. Specialization for detection of predators in aerial or terrestrial predators has been reported for coexisting primate species (Gautier-Hion et al. 1983; Peres 1993; Bshary & Noë 1997).

There is a strong possibility that perceptual differences between white-tails and mule deer led to the difference in their detection abilities. The longer ears (Anderson & Wallmo 1984) and more laterally placed eyes of mule deer (Wishart 1986; Wishart, unpubl. data) may enable them to detect predators at longer distances. The difference in detection abilities cannot be due to a conspicuous physical difference such as height (e.g. FitzGibbon 1990), because white-tails and mule deer are nearly identical in size in this region (Mackie 1964; Wishart 1986). The mule deer's ability to detect disturbances was also not due to a higher level of visual scanning; White-tails had higher levels of scanning, even though they were slower to detect the approacher (Lingle 1998). It is still possible that the species scan different portions of the habitat or that white-tails lift their heads for some reason other than to look for predators.

Relationship between Detection and Alert Response

One could ask whether mule deer detected the approacher sooner than white-tails or just revealed an alert response earlier. It is impossible to rule out this possibility completely without physiological indications of the moment of detection (Dimond & Lazarus 1974; Lazarus 1979). However, certain precautions were taken to avoid this problem and certain results suggest that it was not a problem. Firstly, we tried to avoid testing habituated deer, which would be less likely to respond after detecting a person, by conducting trials in areas where humans were generally not present. When practice trials were conducted in areas where deer regularly encountered humans, the deer reacted by looking at the person after which they returned to eating. This sequence of behavior was not observed during detection walks. Secondly and more importantly, mule deer are widely known to habituate more readily than white-tails (Geist 1981) and should have been more likely to detect the approacher without responding behaviorally.

Finally, the difference between the alert response of the first detector and that of subsequent animals provides a useful clue to evaluate whether alert responses are likely to coincide with the moment of detection. If individuals had already detected the approacher before showing a behavioral response, the first deer to show an alert response should have showed varied forms of alert behavior, for instance, moving away without orienting to the observer. Instead, the first deer to alert appeared constrained to orient to the approacher. These points suggest that the deer's alert response was a good indication of the moment they became aware of the disturbance.

Animals that are alert may or may not identify the nature of a threat or pinpoint its location (Lima 1995b). White-tails were more likely than mule deer to flee or to look in a direction other than at the approacher as their first response and were less likely to look at the approacher at any time during the trial. Even though the lateral placement of ungulate eyes should help them detect stimuli at their side, the consistent response of first detectors indicates that they, nevertheless, oriented their heads directly to the disturbance once alerted. It follows that animals that never glanced at the approacher were less likely to have pinpointed the nature or location of the disturbance than animals that glanced at the approacher, however briefly, during the trial. The white-tail's apparent failure to identify the type or location of a threat before fleeing could lead an individual to respond to false alarms or to select a poor escape route, even if it has the possible advantage of saving time when a predator appears at a short distance. The inverse correlation between group size and the tendency to pinpoint the approacher suggests that white-tails in larger groups might suffer from these problems more than animals in smaller groups (as suggested by Treisman 1975; Lazarus 1979; Trail 1987). The idea that individuals may benefit from increased group size by detecting predators earlier has received considerable study (Pulliam 1973; Lazarus 1979; Elgar 1989; Lima 1995a). Possible costs of increased group size for predator detection and evasion deserve more attention.

Why do White-Tails and Mule Deer Differ in their Detection Abilities?

Early detection was shown to be an anti-predator tactic for both species, because both white-tails and mule deer were disadvantaged when detecting coyotes late. The similarity in other aspects of their biology – mating systems, life-history patterns, feeding habits, body size and morphology (see introduction for references) – reduces the likelihood that these factors contribute to the species' differences in detection abilities. The difference in the detection abilities of white-tails and mule deer could be related to their anti-predator behavior in a few ways.

Mule deer may have developed superior abilities to detect predators as an adaptation to their more open habitats (Geist 1981). Animals occupying open landscapes have opportunities to detect predators sooner, and they may also be under pressure to do this because predators can also detect them sooner (Elton 1939; Lazarus & Symonds 1992). White-tails and mule deer may be making a trade-off between concealment and detection (e.g. Gotmark et al. 1995), given that white-tails tend to rely on concealment more than mule deer (Lingle 1998). However, this hypothesis is not sufficient to explain why coyote interactions progressed further with mule deer that alerted late when compared with white-tails living in the same habitat.

Mule deer may have a greater need for early detection than white-tails because of interspecific differences in anti-predator behavior. Mule deer are less likely to be encountered or attacked when in rugged rather than gentle terrain,

and they show strong tendencies to move into rugged terrain in response to predators (Lingle 1998). Early detection may enable them to move into these safe habitats or to leave the area completely. Unlike mule deer, white-tails did not use rugged areas to avoid coyotes; in fact, they moved to more gentle habitats in response to this predator.

Once encountered, mule deer still seem to require more time to coordinate subsequent defenses than do white-tails. One might initially suspect that mule deer would need a shorter alert distance if they stand their ground against coyotes rather than flee like white-tails. In fact, there are several components to the mule deer's response that require time to employ, even if these occur within a small geographical area. Once alert to coyotes, mule deer typically move short distances to raised spots in the ground, bunch closely together and, then, reorient to coyotes after which some individuals may attack the predator (Lingle 1998, in press). If mule deer fail to accomplish all these steps before being encountered, coyotes are likely to attack or kill a deer. If mule deer flee rather than hold their ground, they are even more likely to be attacked or captured because they cannot outdistance coyotes (Lingle 1998).

In contrast to mule deer, white-tails flee when pursued by coyotes and they can easily outdistance this predator (Lingle 1998). They can employ this tactic instantaneously and individually, so seem to need a relatively short detection distance for flight to be effective. Coyotes were more likely to ignore white-tails than mule deer that were encountered, even when data were restricted to deer that appeared to detect them (Lingle 1998). Coyotes may recognize that they need to be much closer to white-tails than to mule deer before pursuit is worthwhile because of the superior speed of white-tails.

These behavioral or habitat explanations of why mule deer are superior at detecting threats are not mutually exclusive. Social defenses similar to those seen in mule deer have been reported in mammals and birds using open habitats but not in species in closed habitats (Mech 1970; Kruuk 1972; Lima 1993). Cross-specific comparisons and observation of predator–prey interactions in other species can help us find out whether the variation in detection abilities and the consequences of late detection are associated with the amount of cover, with certain anti-predator strategies, or with other aspects of their biology.

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