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Anti-Predator Strategies and Grouping Patterns in White-Tailed Deer and Mule Deer

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Abstract

White-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) are closely related species of similar size that differ in their anti-predator behavior. White-tails flee from coyotes (*Canis latrans*), whereas mule deer typically stand their ground and attack this predator. I used observations of coyotes hunting deer to identify: (i) changes in group structure made in response to coyotes; and (ii) the relationship between group structure and the risk of predation for each species.

In response to coyotes, groups of mule deer merged with other groups and individuals bunched together. Predation attempts were more likely to escalate when groups split and individuals failed to bunch. Coyotes typically attacked mule deer that were in outlying positions, and these deer had to move to central positions to end attacks. Due to the high frequency of attacks on small groups as well as to the level of dilution of risk, individuals in small mule deer groups were at high risk of being attacked compared with those in larger groups. In contrast to mule deer, white-tails made no consistent changes in group size or formation, and coyotes attacked individuals in central as well as in outlying positions. Variation in aspects of group cohesion was not related to the vulnerability of white-tails, and there was no obvious difference in the risk of attack facing individuals in groups of different size. These results suggest that coyote predation selects for relatively large, cohesive groups in mule deer, apparently because this type of group improves their ability to deter coyotes. Coyote predation does not have similar effects on groups formed by white-tails, which use flight rather than deterrence to avoid predation. The benefits of responding cohesively, occupying certain positions within groups, and forming groups of a certain size can vary widely depending on the anti-predator strategies used by an animal.

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Introduction

In response to the same predator, animals belonging to one prey species flee while those from another species stay and defend themselves (Mech 1970; Kruuk 1972; Lima 1993). The type of group preferred by a species can be associated with its anti-predator strategy (Edmunds 1974; Jarman 1974; Treisman 1975). If animals try to avoid predation by hiding from predators, they may form small groups which are difficult to detect. If animals attempt to mob predators, they may be more successful in avoiding predation when they form larger groups.

The risk of predation can affect several group characteristics other than size. It may affect group cohesion if individuals are better at avoiding predation when they stay together (Magurran & Pitcher 1987; Watt et al. 1997). Predation can affect positions preferred by individuals; the center of a group is generally viewed as safer than the edge, although this may depend on the predator and prey species involved (Krause 1994). Predation risk can also affect group membership. For instance, individuals of different species can lower their risk of predation by banding together (e.g. Popp 1988; FitzGibbon 1990; Bshary & Noë 1997).

In attempts to understand why animals form groups, biologists have focused on the anti-predator benefits of increased group size, including shared vigilance (Lazarus 1979), dilution of risk (Foster & Treherne 1981; Morgan & Godin 1985), predator swamping (Clark & Robertson 1979), confusion of predators (Neill & Cullen 1974; Milinski 1977), and an increased ability to mob predators (Curio 1978). Less attention has been devoted to the ways in which group structure or cohesion affect or are affected by predation (Morgan & Godin 1985; Magurran & Pitcher 1987; Krause 1994; Watt et al. 1997), even though structural features of groups may determine whether or not it is beneficial for individuals to join a group rather than live solitarily (Pulliam 1973).

White-tailed deer (*Odocoileus virginianus*, hereafter white-tails) and mule deer (*O. hemionus*) are closely related species that are similar in size (Mackie 1964; Wishart 1986), overall morphology (Eslinger 1976; Wishart 1986), feeding habits (Anthony & Smith 1977; Krausman 1978), and reproductive capacity (Beasom & Wiggers 1984; Mackie et al. 1998). They differ in their habitat preferences; mule deer prefer more rugged and open habitats, whereas white-tails occupy gentler terrain with greater cover (Wiggers & Beasom 1986; Wood et al. 1989). However, both species occur in a wide range of habitats and coexist in many of these. White-tails and mule deer also differ in their basic responses to predators, and this variation occurs independent of habitat differences (Lingle 1992, 1998). Mule deer are more likely to hold their ground against coyotes (*Canis latrans*), and individuals that are attacked are typically defended by conspecifics (Lingle 1998). White-tails flee when attacked and individuals can avoid predation by outrunning coyotes.

The basic social organization of white-tails and mule deer is similar. Females tend to separate themselves when giving birth, but form groups with related females and their young in late-summer (Hirth 1977; Bowyer 1985). Animals of both species form larger groups, which may include both sexes, in autumn and winter (Hirth 1977; Bowyer 1985). Even though there is substantial overlap in the sizes of their groups, the median group size is larger for mule deer than for white-tails in winter (Lingle 1998). Mule deer groups are also very stable in winter, whereas white-tails frequently move in and out of groups.

One might expect differences in grouping patterns, both flexible responses shown during predator–prey interactions and enduring aspects of their social structure, to be associated with the differences in white-tail and mule deer anti-predator strategies. Since mule deer typically rely on other group members to defend them against coyotes when attacked, they might be particularly vulnerable when alone or in uncohesive groups. Being alone or in unstable groups might not disadvantage white-tails, because they are able to outrun coyotes. In this way, predation and differing anti-predator behavior could contribute to differences in the size and structure of mule deer and white-tail groups. To test this hypothesis, I used data collected during observation of coyotes hunting deer to: (i) identify changes in group structure made in response to coyotes; and (ii) examine whether the structure of white-tail and mule deer groups is related to their risk of predation. Specifically, I examined three aspects of group cohesion, namely, changes in the formation of groups, the stability of groups, and the position of attacked deer in a group. I also assessed the relationship between group size and the likelihood that an individual was attacked by coyotes.

Coyotes are important predators of deer at the site where this study was conducted, relying on deer most heavily in winter (Lingle 2000). Fawns are more vulnerable than older deer. Fawns of both species are born at the same time in mid June and so are about 5 mo old as they enter their first winter. The results presented here are restricted to winter.

Study Site and Subjects

The research was conducted at a 20-km^2 study site on a 225-km^2 cattle ranch in southern Alberta (49°N, 112°W). Topography included slopes, rising about 150 m from their base, with gently rolling or flat terrain, $< 5°$ in steepness, elsewhere. Mule deer occupied the higher, steeper slopes, white-tails the flatter terrain, and both species occurred on the lower, gentle slopes (Lingle 2000). The landscape was open, with native fescue and mixed grass prairie in 83% of the study area. The remainder of the study area had been cultivated 10 yr before the study, but had since been re-seeded with introduced grasses.

About 250 white-tails and 135 mule deer occupied the study area in the winters of 1994–95 and 1995–96 (Lingle 2000). In summer, there were four coyote dens in this area with another three within 0.5 km of its boundary. These seven packs were observed hunting deer in the study area in winter. The results

presented here are based on 2000 hours of observation made between Nov. 1 and Mar. 1 in the winters of 1993–94, 1994–95 and 1995–96.

Methods

Definition and 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 in-line at a fast walk, 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 pausing 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).

In the winters of 1993–94 and 1994–95, I observed coyote–deer interactions that occurred while I was observing groups of deer or conducting focal observations of coyotes. I was rarely able to monitor coyotes throughout their entire hunt in the first two winters. By the winter of 1995–96, I was able to monitor coyote packs as they moved among different groups of deer, often for the entire hunt. I attempted to find packs of coyotes before they started to hunt deer, and remained at a vantage-point throughout the hunt. A relatively long observation distance (500–1000 m away) enabled me to view the entire route used by coyotes and most groups of deer they passed. I used 7×42 binoculars and a 20–45 Nikon ED II spotting scope to observe animals. Four main vantage points provided a view of most of the study area. Each provided views of white-tail habitats, three provided views of shared habitats, and two provided views of mule deer habitats. I adjusted my position in the vicinity of each vantage point to improve opportunities for observation during hunts.

Hunt Stages

Prey animals may use different tactics to terminate a predation attempt depending on the stage the attempt has reached (Endler 1986). It is therefore important to distinguish defenses used at different stages of a hunt. Here, I distinguish the stages of being passed, encountered, approached, pursued, attacked, and mortally wounded or killed. The stage of being passed only applied to deer on slopes. Coyotes usually followed a route that was roughly parallel to

the base of a slope. Coyotes were defined as passing groups of deer on slopes that were originally in front of the coyotes while they searched for deer, using a line drawn from the base to the top of the slope, at a perpendicular to the direction of the slope, to distinguish groups that were in front of coyotes from those behind them. A group of deer within this region was defined as being passed when the coyotes' main travel route (excluding sharp turns to approach a nearby group) was at its shortest distance to that group, regardless of the distance between the deer and the coyotes. If coyotes traveled directly up-slope, which was only observed for one short section of two hunts, they were defined as passing deer within 400 m.

An encounter was defined as any time during a hunt when coyotes appeared to detect a group of deer within 200 m. This distance was selected because I was able to monitor all groups within this distance and most approaches began at shorter distances. The first sign of interest in a group was termed an approach. Coyotes could stalk, walk or run to approach a group or an individual deer. If coyotes stopped once they were detected or after the deer's initial alert response, the predation attempt was considered as having stopped at the approach stage. The stages of encounter and approach were pooled in the analyses presented here.

Hunts escalated to a pursuit if coyotes continued to approach the deer after the deer reacted to them or after coyotes arrived within 2 m of the deer. Pursuits could be made on entire groups or they could consist of a short lope after an individual, possibly to 'test' it (e.g. Mech 1970; Kruuk 1972; Creel & Creel 1995). Once coyotes focused their efforts on one individual that appeared in immediate danger of capture, I considered the pursuit as having escalated to an attack. The form of attacks varied from a prolonged chase, a short committed chase with little distance separating the coyote and deer, a lunge if a coyote was within contact distance, or a prolonged attack in one location (e.g. repeated lunging at a deer that maneuvered around or fought coyotes but did not flee). An attack could be unsuccessful; or it could result in a mortally wounded deer or in immediate capture.

Group Characteristics

Groups were defined as aggregations of deer in which each member was within 50 m of another member, while the aggregation was over 50 m from another deer (Clutton-Brock et al. 1982). Several characteristics of deer groups were identified before or as coyotes encountered them (Table 1). These characteristics included the species, group size, the number of juveniles present, and the type of group (entirely adult or containing juveniles). Whether or not a group had a neighboring group within 100 m was also recorded.

Exact group size was identified for 69% of mule deer and 85% of white-tail groups that were encountered, including all groups having fewer than six deer. When there was insufficient time to make an exact count, a group size category was recorded (Table 1, group size). The median value in the group size category was used for analyses when exact sizes were not available. To test whether group

Table 1: Characteristics of deer groups recorded during coyote hunts

Group size
Small: ≤ 5 deer
Medium: 6–10 deer
Large: > 10 deer.
Group type
Adult: groups consisting of adult females, males or yearlings.
Groups with juveniles: either mixed age or consisting entirely of juveniles.
Group formation (applies to groups having > 1 deer)
Bunch: Individuals move closely together, typically standing shoulder to shoulder, with 3–5 deer within 2 m of most individuals.
Move together: Spacing among individuals contracts.
Spread: Spacing among individuals increases.
No change.
Stability of group
Join: Group joins or is joined by another group.
Split: At least one individual leaves group.
Join & split: Part of group joins another group, part of group leaves.
No change: No change in group membership.
Position of attacked deer
Central: Individual has group members within 10 m of itself and within 180° from every angle.
Edge: Individual is < 10 m from other group members but has no other deer within 180° on one side.
Outlying: Individual is ≥ 10 m from other group members and has no other deer within 180° on one side.
Solitary: Individual has no other deer within 50 m.

size was related to the probability that a group was pursued or attacked, data were restricted to groups encountered during hunts observed in the winter of 1995–96, as long as I observed searching behavior before coyotes made an attack. Because I monitored coyotes throughout their hunts in the winter of 1995–96, this sample should contain an unbiased sample of group sizes that were passed and encountered. Additionally, mule deer appeared to occur in different-sized groups in the winter of 1994–95 than in 1995–96 and the vulnerability of deer differed as well (Lingle 2000), probably independently of group size. By restricting the analysis of group size to data from 1995–96, annual variation in vulnerability would not confound the effect of group size.

Three aspects of group cohesion were recorded during hunts, including changes in the spacing among individuals (group formation), the stability of groups with resulting changes in group size, and the position of attacked individuals (traits defined in Table 1). Changes in group formation and group membership, and also whether or not a group had a deer in an outlying position, were recorded at each hunt stage. The position of attacked individuals was recorded at the start of an attack, when coyotes quit an attack, and when they

wounded or killed a deer. Deer were classified as being in a central, edge, or outlying position within a group, or were classified as solitary if no other deer were in their group (Table 1).

Certain criteria were set before conducting analyses. Solitary deer were excluded from the analysis of group formation since it was not possible for them to have a formation. Solitary deer were included in the analysis of group stability, although their effect on the results will be considered since it was only possible for them to join groups and not to split into subgroups. Groups that did not alert when encountered by coyotes were excluded from analyses of group formation and group stability for the encounter stage, because the failure to detect coyotes could lead to increased vulnerability (Lingle & Wilson, 2001) independent of their grouping patterns. Alert behavior included orienting to coyotes with an alert posture (erect neck, 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 simply moving away if alerted by neighboring deer.

No difference was detected statistically between the probability of coyotes approaching adult groups and those with juveniles (either mixed age or entirely juvenile), although coyotes were more likely to attack juveniles than adults when encountering groups with both age of animal (Lingle 1998). Both types of groups were pooled in most analyses presented in this paper, with the goal of identifying overall behavioral patterns used by each species and the relationship of these patterns to deer vulnerability. When it seemed possible that group type or an animal's age could have confounded results, I carried out additional analyses with data restricted to groups containing juveniles or to juveniles that were attacked. There were insufficient data to conduct separate analyses for each group type.

Data Analysis

The sampling unit was a single group of deer, because coyotes encountered and pursued groups of deer. Pseudoreplication should not have been a problem, because groups changed in composition more often than I observed hunts in a particular area (about one hunt every 3 d at the most). Comparison of the number of deer in the study site with the number encountered during hunts also indicated that individuals were rarely present in more than one group that was observed: this averaged 1.6 times for mule deer that were encountered and 1.4 times for white-tails for all of winter 1995–96 (Lingle 1998). It was more important to avoid repeated observation of individuals at the attack stage, since this is the stage at which coyotes focus on one individual. Based on locations at which individuals were attacked, physical differences among these individuals (age, sex, physical markings such as the size of rump patches or tail coloration, and the presence of ear-tags on about 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 I observed more than one attack on any individual.

Data for a group were used as long as each group was involved in a separate interaction with coyotes. Groups were excluded if they joined another group being pursued or if they were joined by another group that was being pursued. In this way, behavioral events such as joining and bunching that might lead to a merged group or occur within it, respectively, were represented once rather than twice. If a group split, data were used for the part of the group involved in the most advanced hunt stage, for instance, for an individual that was attacked rather than for the rest of the group that was ignored. If members of a group responded differently during a hunt stage and there was no difference in the outcome, data were not used simply because too few groups showed a mixed response to include these in the analysis (e.g. five out of 102 white-tail and zero out of 52 mule deer groups had some individuals that split from a group, whilst others joined another group).

Non-parametric tests were used to analyze data, because data mostly involved frequencies or were not distributed normally. G-values were adjusted using the Williams's correction when $df = 1$. When more than two groups were compared, a G-test was used when all expected frequencies were > 5. The overall G-value was not adjusted in this case, but alpha was adjusted for subsequent pair-wise tests using the sequential Bonferroni correction to maintain an experiment-wise error rate of 0.05 (Sokal & Rohlf 1995). When more than two groups were compared and at least one expected frequency was < 5, a series of pair-wise tests was made using either G-tests or Fisher exact tests, depending on the expected frequencies, and alpha was also adjusted in these cases. The p-values presented in results are two-tailed.

Results

Group Cohesion

Group formation

One of the most striking responses of mule deer was their tendency to bunch together. Individuals moved closer together in about 60% of mule deer groups that were encountered, pursued, or attacked by coyotes (Fig. 1), and in about 80% of interactions that did not escalate beyond each hunt stage. They not only moved closer together, but over 85% of these groups became tightly bunched. Similar to muskoxen (*Ovibos moschatus*), the formation could be an irregular circle or square, or a line abreast (Miller & Gunn 1984). White-tails were less likely to move closer together than were mule deer groups, and they were more likely to make no change in their spacing or to spread out (Fig. 1). A few white-tails moved closer to another individual when encountered by coyotes, and this was usually fawns moving near to their mothers. However, on no occasion did I see an entire group of white-tails bunch together as mule deer typically did.

Coyotes were significantly less likely to pursue and attack mule deer when individuals moved together than when they spread out (Fig. 2a). White-tails

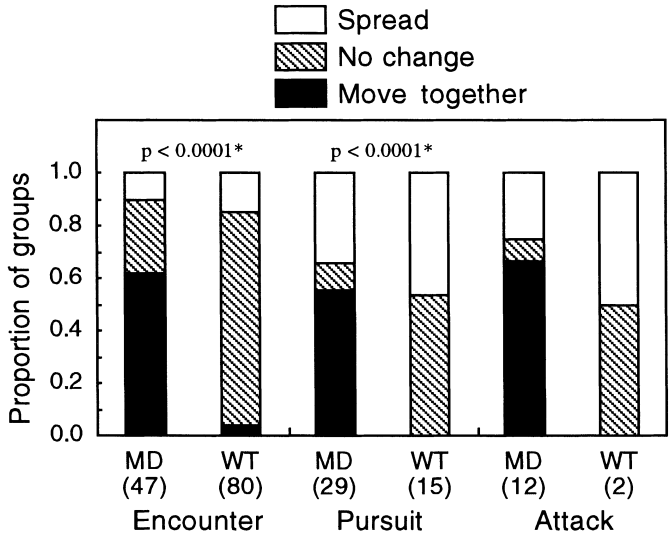

Fig. 1: Change in group formation in response to coyotes by mule deer (MD) and white-tails (WT). Species, sample sizes, and hunt stage (encounter, pursuit or attack) given below bars. G-tests used to compare frequency of response depending on species (encounter, $G = 55.3$, $df = 2$, $p < 0.0001$; pursuit, $G = 20.54$, $df = 2$, $p < 0.0001$; attack, insufficient white-tail data to test but existing data are consistent with differences seen at other stages). * indicates significant results

rarely moved closer together so it was not possible to test the effect of this formation on their vulnerability. Whether or not they spread out or made no change in spacing did not appear to affect the likelihood that they were pursued or attacked (Fig. 2b).

Stability of groups

The majority of groups of both species made no change in composition during their interactions with coyotes. However, mule deer that made a change usually joined another group, so that their groups were larger following the interaction (paired sign test: 18 groups became larger, four smaller, 40 groups did not change in size, $p = 0.004$). Groups with a neighboring group within 100 m were more likely to increase in size from merging than those without a neighbor ($G_{adj} = 6.64$, $df = 1$, $p = 0.01$). The tendency to increase in size rather than to make no change was not related to the original size of a group (40% of small groups, 40% of medium, and 50% of large groups increased in size when data are restricted to groups having neighbors, Fisher exact test, $p = 1.0$ for the three pair-wise tests).

White-tails showed no tendency to change their group size in a consistent direction (paired sign test: 10 groups became larger, 16 smaller, 87 did not change, $p = 0.33$). The tendency of mule deer to join other groups more often than

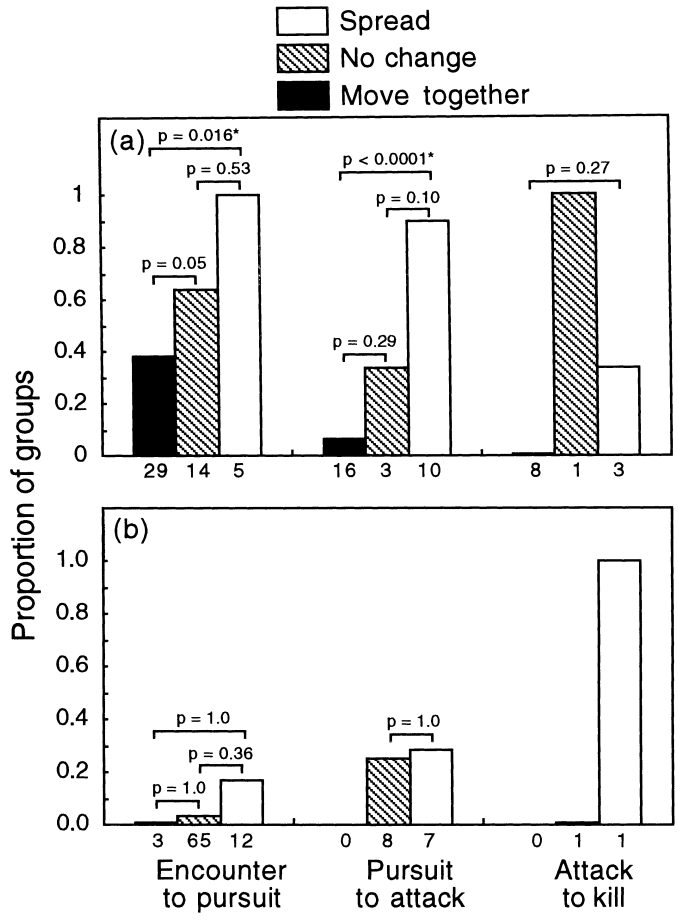

Fig. 2: Proportion of interactions that escalate depending on the formation of the group for (a) mule deer and (b) white-tails. Sample sizes given below data bars. When data are absent, the sample size is shown ($n = 0$) to distinguish these cases from those in which data were available but no attempts escalated. A series of pair-wise tests was made rather than one overall G-test for each hunt stage, because there was at least one cell with an expected frequency < 5 for each stage. The G-test was used when all expected frequencies were > 5 and the Fisher exact test when at least one expected frequency was < 5. Ends of brackets point to groups being compared, and * indicates significant p-values after alpha is adjusted using the sequential Bonferroni correction. Statistical tests were made as long as $n \geq 3$; however, readers should note that the small samples used in certain tests may have led to type II errors, that is, to the failure to detect differences that exist

white-tails was not due to a larger number of neighboring groups. White-tails were more likely to have conspecific neighbors (77% of 113 white-tail groups, 52% of 61 mule deer groups, $G_{adj} = 15.02$, $df = 1$, $p = 0.0001$). White-tails might also have been expected to be more likely to join other groups because they tended to occur in smaller groups (see Fig. 5) and a larger proportion of white-tails were

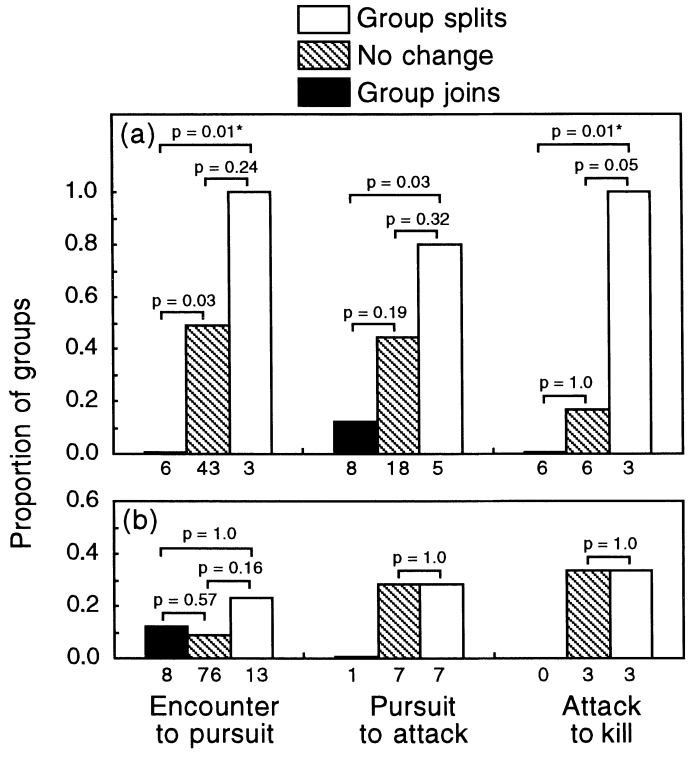

Fig. 3: Proportion of interactions that escalate depending on whether a group joins another group (or is joined), makes no change, or splits into subgroups for (a) mule deer and (b) white-tails. Sample sizes given below bars. When data are absent, the sample size is shown ($n = 0$) to distinguish these cases from those in which data were available but no attempts escalated. A series of pair-wise tests was made rather than one overall G-test for each hunt stage, because there was at least one cell with an expected frequency < 5 for each stage. The G-test was used when all expected frequencies were > 5 and the Fisher exact test when at least one expected frequency was < 5. Ends of brackets point to groups being compared, and * indicate significant p-values after alpha is adjusted using the sequential Bonferroni correction. Statistical tests were made as long as $n \geq 3$; however, readers should note that the small samples used in certain tests may have led to type II errors, that is, to the failure to detect differences that exist

solitary during these hunts (19% of 113 white-tail groups vs. 7% of 61 mule deer groups).

Coyote encounters with mule deer were significantly more likely to escalate to pursuits and attacks to kill after a group split than after a group joined another group, with a similar tendancy for pursuits to escalate to attacks (Fig. 3a). There was no relationship between the stability of groups and vulnerability of white-tails at any hunt stage (Fig. 3b). Few white-tails joined other groups when pursued or attacked, so it was only possible to compare groups that made no change with groups that split for those two hunt stages.

Position of attacked deer

Mule deer that were attacked by coyotes were usually in outlying positions when attacked, that is, on the edge of the group and at least 10 m from another deer (Fig. 4). At the end of attacks which deer survived, most of these individuals had moved to central positions or other deer had moved to the attacked animal. Even though fawns in two attacks were still in outlying positions when coyotes quit attacking, their mothers stayed between the coyotes and fawns continuously, battling the coyotes, until the fawns were over 500 m from the coyotes. One adult female survived an attack even though she was separated from the group by 30 m, but coyotes continued to follow her afterwards. In contrast to mule deer that avoided capture, mule deer that were killed were still in outlying positions or solitary. As a result, mule deer were more likely to be in outlying positions or alone when an attack started or when an animal was killed than when coyotes abandoned an attack (Fig. 4, G-test: position of deer at start of attack vs. that when coyotes quit, $G_{adj} = 16.45$, $df = 1$, $p < 0.0001$; Fisher exact test: position of deer when killed vs. that when coyotes quit, $p = 0.03$). The same trends were found when data were restricted to attacks on juveniles (Fisher exact test: nine out of nine attacked deer outlying at start of attack vs. two out of six when coyotes quit, $p = 0.01$; kill

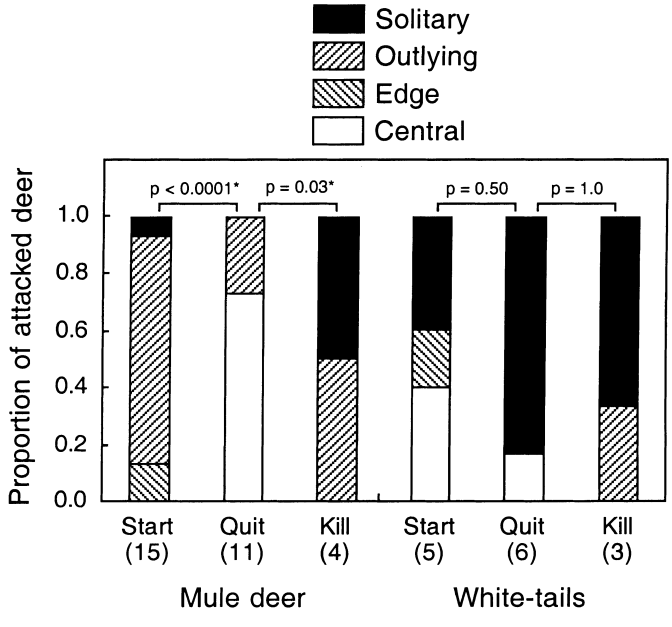

Fig. 4: Position of individuals that were attacked by coyotes at the start of an attack (start), when coyotes quit an attack (quit), or when coyotes killed an animal (kill). Sample sizes below bars. Deer in outlying positions were pooled with solitary deer and compared with central deer for statistical tests, and individuals on the edge of the group were excluded. Ends of brackets point to groups being compared, and * indicates significant p-values ($\alpha = 0.05$ for each test)

[four out of four outlying] vs. coyotes quit, $p = 0.08$). The lower significance levels for juveniles are probably due to reduced statistical power from the smaller samples.

Coyotes appeared to prompt deer into outlying positions by either running towards a group and surprising it so that the group fled and splintered ($n = 4$), or by making repeated rushes at a group until a juvenile appeared to panic and fled ($n = 3$). Only five of 12 groups in which attacks occurred had an outlying animal when initially encountered by coyotes (with data for another three groups unknown). Fourteen of these 15 groups had an outlying deer by the end of the pursuit. Coyotes rushed or circled 10 other mule deer groups that stood bunched together for periods lasting from 20 s to several minutes, apparently trying to prompt a deer into flight, without success.

Coyotes attacked white-tails that occupied central positions in a group as well as white-tails that were in outlying positions or alone, and white-tails did not need to move close to a group to end attacks (Fig. 4). In fact, individual white-tails often fled far from a group to escape, with five out of six white-tails being alone when coyotes aborted their attack. Consequently, no differences were detected in the positions of white-tails at different stages of the attack (Fig. 4, start of attack vs. coyotes quit, $p = 0.50$; coyotes quit vs. kill, $p = 1.0$). If a tendency exists, which may have been overlooked due to the small sample, it is for white-tails to move away from the group when attacked.

Group Size

Coyote hunting success

Group size was not related to the probability that a mule deer group was encountered once passed by coyotes on slopes, which ranged from 50 to 55% ($G = 0.14$, $df = 2$, $p = 0.93$), but it was weakly related to the likelihood that a group was attacked. Coyotes showed a non-significant tendency to attack mule deer in small groups more often than deer in intermediate-sized groups (Fig. 5a), and this tendency was stronger when data were restricted to groups having juveniles. Coyotes attacked juveniles in four out of seven small groups but in only one out of 14 medium groups (Fisher exact test, $p = 0.025$). A difference was not detected between the probability of attack for encounters with large vs. medium or small groups; however, the proportion of encounters with large groups resulting in attacks and kills appears to be more similar to data for small groups than to data for medium groups (Fig. 5a). Too few kills were observed to justify statistical analysis of this hunt stage, but it is important to note that data for this stage show the same visual trends as data for attacks.

The relationship between group size and the escalation of predation attempts could be the result of differences in group cohesion if small groups are more likely to split or to produce an outlying individual. Consistent with this suggestion was a non-significant tendency for small mule deer groups to produce more outlying animals than larger groups when approached within 25 m by coyotes (four out of

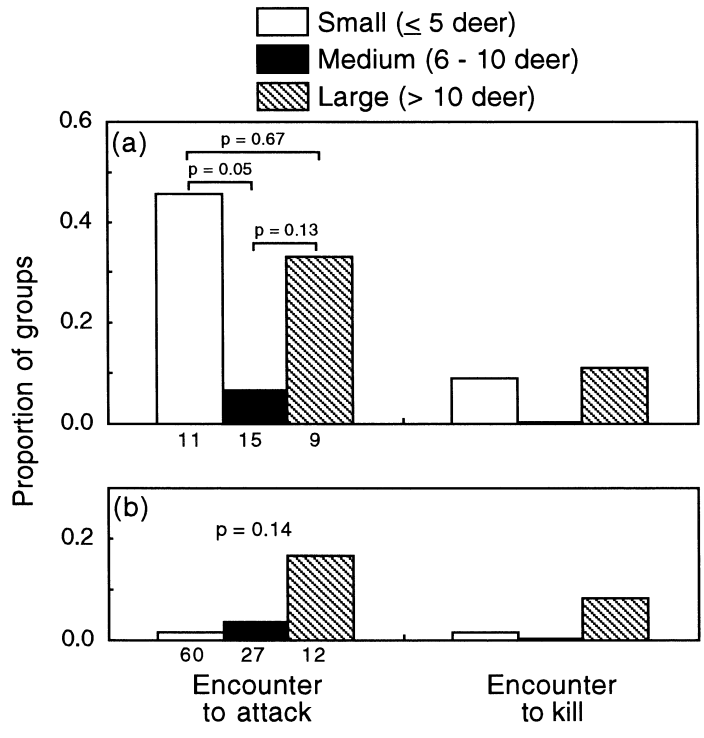

Fig. 5: Proportion of encounters that escalate to attacks and to kills depending on the size of a group for (a) mule deer and (b) white-tails. Sample sizes given below bars for attacks. The same sample of encounters was used for kills. For mule deer, a G-test was used to compare the frequency of attack on small vs. medium groups, and Fisher exact tests were used for the other two pair-wise comparisons. The ends of brackets point to groups being compared. None of these tests were significant after alpha was adjusted using the sequential Bonferroni correction. For white-tails, a G-test was used to compare the frequency of attack among the three group size categories. Due to the small number of kills that were observed, statistical tests were not conducted for that hunt stage for either species

five small groups vs. two out of 10 medium and large groups, Fisher exact test, $p = 0.09$).

The size of white-tail groups was not significantly related to the likelihood of an attack occurring within a group, using the small sample of attacks that were observed on white-tails ($G = 3.97$, $df = 2$, $p = 0.14$). In contrast to their hunting behavior on mule deer, any tendency was for coyotes to make more attacks on large white-tail groups than on small or medium groups (Fig. 5b).

Per capita risk

As would be expected by the high rate at which coyotes attacked small mule deer groups, individuals in these groups faced a much higher per capita risk of being attacked than those in larger groups (Table 2). White-tails in small groups

Table 2: Probability of attack per individual (p_{attack}) once encountered for deer in groups of different size. gs, mean size of groups that were encountered for each group size category

	Small		Medium		Large	
Species	p_{attack}	gs	p_{attack}	gs	p_{attack}	gs
Mule deer	0.165	2.7	0.008	8.0	0.019	17.1
White-tail	0.007	2.5	0.005	7.4	0.008	21.6

Probability of attack per individual calculated as probability of attack per group for each size category (from Fig. 5) divided by mean group size.

did not appear to be at high risk compared with mule deer in small groups, and there was also no obvious difference in the rate at which individuals were attacked in white-tail groups of different size (Table 2). A larger sample of attacks and kills is needed to compare the risk facing mule deer in medium and large groups and to compare the risk facing white-tails in all three sizes of groups more precisely.

Mixed-Species Associations

White-tails and mule deer responded in species-typical ways when in mixed species groups or when they had a heterospecific group within 100 m. Coyotes approached six mixed associations within 100 m, leading these associations to split into single species groups with no heterospecific neighbors. White-tails from these mixed groups left the area as coyotes approached, whereas mule deer either remained in place or moved and then reoriented to coyotes while the predator was still approaching, responses reported to be typical of each species (Lingle 1998). In four cases, mule deer joined neighboring groups of mule deer and, in five cases, individual mule deer bunched closely together. The last mixed group had only one mule deer, an adult male, which stayed in place.

Discussion

The grouping patterns of white-tails and mule deer appear to be closely associated with their anti-predator strategies. Individual white-tails can outrun coyotes (Lingle 1998), and the size and cohesion of their groups does not appear to have strong effects on their safety. Mule deer, at least juveniles in their first winter, cannot outrun coyotes. The relatively large, cohesive groups formed by mule deer and their aggressive response (Lingle 1998) provide an alternative form of protection by enabling them to deter coyotes rather than to outrun them. Coyotes typically made short rushes at bunched groups of mule deer, but they did not enter these groups, probably because of the implicit or explicit threat of aggression. In contrast, coyotes frequently ran into the middle of white-tail groups while chasing individuals in the groups.

Alternative anti-predator benefits of larger groups such as improved detection (Lazarus 1979) or confusion (Neill & Cullen 1974; Milinski 1977) of

predators seem unlikely or, at most, less important for mule deer. So far, there is no evidence that large groups of mule deer detect predators sooner (Lingle & Wilson 2001). Mule deer usually stay in place rather than flee, and are less successful if do they flee. They therefore do not use larger groups to confuse predators during flight.

Coyote predation appears to select for cohesive groups in mule deer. Mule deer were more vulnerable when individuals spread out rather than bunched together, and when a group split rather than merged with other groups. Similarly, individuals occupying outlying positions were at high risk of being attacked and killed: there are fewer outlying than central deer in a group, yet most mule deer that were attacked were outliers. Deer that avoided capture were more likely to have moved to central positions than those that were killed. These aspects of group cohesion were obviously related: groups that spread out and then split tended to result in outlying or solitary animals.

The apparent effect of group size on vulnerability of mule deer may be due to differences in the cohesiveness of groups that differ in size. Results that support this idea are: first, group size was more weakly related to coyote hunting success than were aspects of group cohesion; and second, there was a tendency for small groups to produce more outlying individuals than larger groups, which may be the reason why they are vulnerable to coyote attacks. If intermediate-sized groups of mule deer are more cohesive than smaller or larger groups, as has been reported for musk-oxen, which form defensive formations similar to mule deer (Miller & Gunn 1984), they may be more effective in deterring predators than smaller or larger groups. This could explain why intermediate-sized groups appeared to be attacked less than both smaller and larger groups.

Even if the size of a mule deer group had a relatively small effect on coyote hunting success, predation appears to select strongly against mule deer that occupy small groups. Individuals in small groups had a 16% risk of being attacked once encountered by coyotes compared with a 0.8 to 1.9% risk for individuals in larger groups, due to the high number of attacks on these groups and to the small number of deer present to dilute the risk. Although few kills were observed, there is no evidence that deer in smaller groups were better at avoiding capture.

Coyotes also had an indirect effect on group size by prompting mule deer to form larger groups in their presence, an anti-predator behavior that has been reported for other species (Caraco et al. 1980; Magurran & Pitcher 1987). The behavioral effects of predators can be important selective mechanisms on prey animals in addition to or even in the absence of predation on those animals (Sih 1987). Too little is known to say why joining other groups matters to mule deer. Groups could merge with other groups to form a certain size of group that is safest. However, one might then expect small groups to be more likely to join neighboring groups than larger groups since they have the most to gain, and this was not the case. Deer in all sizes of group could benefit by merging if the risk of attack per individual is diluted with continuous increases in group size. The results presented here provide no evidence that mule deer are safer in larger than in

intermediate-sized groups; however, this conclusion is based on a small sample and deserves further attention. Rather than being dependent on group size, merging with other groups could simply be another indication of the cohesiveness of individuals within the groups, and could reflect their tendency to bunch with nearby deer and their ability to avoid splitting.

The results give no indication that characteristics of white-tail groups affect coyote hunting success or that coyotes select for white-tails to occur in groups of a certain size or structure. White-tails did not exhibit social defenses or cohesion in their anti-predator behavior: groups split as often as they merged and individuals did not bunch together. Moreover, individuals can outrun coyotes without being defended by other group members (Lingle 1998). Being in an outlying position in the group did not appear to be as risky for white-tails as it did for mule deer. The failure to select against white-tails in certain types of groups through predation may enable white-tails to occupy a broader range of group sizes and less stable groups than mule deer. The effects of predation are consistent with differences between white-tail and mule deer groups. In winter, mule deer occur in larger, more stable groups than white-tails (Lingle 1998).

Although these results did not uncover a relationship between group characteristics and vulnerability in white-tails, other traits should be examined. A notable feature of white-tail social organization was a high number of conspecific neighbors in certain locations. It is possible that white-tails are alerted by the movements of their neighbors without actually detecting the predator (i.e. the Trafalgar effect, Treherne & Foster 1981), which could be beneficial if it results in an earlier response, or disadvantageous if animals fail to pinpoint the predator's location (Treisman 1975; Lazarus 1979; Trail 1987).

There are several reports of animals lowering their risk of predation by banding together with other species (Popp 1988; FitzGibbon 1990; Bshary & Noë 1997). In contrast to these examples, mixed groups of white-tails and mule deer split into single species groups, with each species moving to different terrain (Lingle 1998) and responding in different ways. The species were observed to move apart once encountered or pursued by coyotes. It is possible that one or both species benefit by banding together at earlier hunt stages, for instance, in detecting predators.

As illustrated by the two species of deer, the anti-predator benefits of responding cohesively, occupying certain positions in a group, or forming groups of a certain size can vary widely depending on the anti-predator strategies used by an animal. While other studies have reported variation in the effects of group size (cf. Cresswell 1994a, b; Uetz & Hieber 1994; Krause & Godin 1995), and the position of individuals (Krause 1994) on predation risk, this study is unusual in that such variation was found between two sympatric prey species which are closely related, physically similar, and hunted by the same predator.

Selection by coyotes appears to influence the type of groups formed by white-tails and mule deer. However, other selective pressures that can affect their grouping patterns have not been examined. Even though mule deer in outlying positions are at high risk of being attacked, it is possible that they find it

advantageous to feed in these positions if this reduces competition or enables them to find dispersed food items, particularly when they occur in larger groups. It would be useful to consider the interaction among group size, group cohesion, and position of individuals during both feeding and predator–prey interactions to investigate the trade-offs made by these species when forming groups.

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