

Group composition and cohesion in sympatric white-tailed deer and mule deer

Susan Lingle

Abstract: White-tailed deer (*Odocoileus virginianus*) have been reported to live in smaller groups than mule deer (*Odocoileus hemionus*). Group size, however, generally varies with habitat conditions, and no comparison has been made between the social structures of the two species living in the same ecological conditions. I compared the size, composition, and stability of groups formed by sympatric whitetails and mule deer living in a prairie habitat in southern Alberta. Seasonal trends were similar for the two species. Females and fawns usually formed small groups during summer. Larger mixed-sex groups became increasingly common during winter, well after the breeding season. Despite the similar seasonal trend, mule deer were significantly more likely than whitetails to occur in relatively large groups composed of both sexes during winter, and whitetails were more likely to occur in small female groups. Mule deer groups were more stable than whitetail groups, and marked mule deer fawns developed strong associations with other known fawns. Habitat variation was limited and was not related to group size. These results show that the composition and cohesion of whitetail and mule deer groups differ, even when the species live in similar circumstances. The differences in grouping behaviour, larger more cohesive groups formed by mule deer than by whitetails, are consistent with those expected to result from the selection pressure of predation.

Résumé : Les cerfs de Virginie (*Odocoileus virginianus*), rapporte-t-on dans la littérature, vivent en groupes plus petits que les cerfs muets (*Odocoileus hemionus*). La taille des groupes varie, cependant, avec les conditions de l'habitat et il n'existe pas de comparaison de la structure sociale des deux espèces vivant dans les mêmes conditions écologiques. Il m'a été possible de comparer la taille, la composition et la stabilité des groupes formés par des cerfs de Virginie et des cerfs muets vivant en sympatrie dans un habitat de prairie du sud de l'Alberta. Les tendances saisonnières sont semblables chez les deux espèces. Les femelles et les daims forment généralement de petits groupes durant l'été. Des groupes plus grands comprenant des mâles et des femelles deviennent plus fréquents en hiver, bien après la fin de la saison de reproduction. Malgré les tendances similaires, les cerfs muets sont plus susceptibles que les cerfs de Virginie de se retrouver au sein de groupes relativement grands de mâles et de femelles durant l'hiver et les cerfs de Virginie ont plus de chances de se retrouver dans des petits groupes de femelles. Les groupes de cerfs muets sont plus stables que ceux des cerfs de Virginie et des petits cerfs muets marqués ont établi des liens très forts avec d'autres daims connus. La variation de l'habitat est limitée et n'est pas reliée à la taille des groupes. Ces résultats montrent qu'il existe des différences dans la composition et la cohésion des groupes de cerfs de Virginie et de cerfs muets, même lorsque les espèces cohabitent dans des conditions similaires. Les différences de comportement de regroupement, des groupes de plus grande taille avec plus de cohésion chez les cerfs muets que chez les cerfs de Virginie, sont compatibles avec les effets de la pression sélective de la prédation.

[Traduit par la Rédaction]

Introduction

White-tailed deer (*Odocoileus virginianus*; hereinafter whitetails) and mule deer (*Odocoileus hemionus*) are closely related species that are similar in size in northern locations (Mackie 1964; Wishart 1986). Whitetails are generally viewed as more solitary than mule deer (Geist 1981), although there has not been a direct comparison of the social structure of

the two species living in the same conditions to test this perception.

Both whitetails and mule deer have been reported to live mainly in small matrilineal groups consisting of a doe, her fawns, and possibly yearlings during summer (Hawkins and Klimstra 1970; Hirth 1977; Mathews and Porter 1993; Bowyer 1985; Schwede et al. 1993). Mule deer frequently form larger groups comprising both sexes during winter (Bowyer 1984, 1985). Hirth (1977) found considerable variation in group size and composition in whitetails living in different habitats during winter. In a wooded habitat, whitetails tended to occupy small family groups. In a more open habitat, whitetails commonly formed larger mixed-sex groups, similar to those reported for mule deer. Hirth's results, and similar variation in group size in many species (Estes 1974; Jarman 1974; Thirgood 1996; Stuwe and Hendrichs 1984; Hirth 1977; LaGory 1986; but see Bender and Haufler 1996), make it seem possible that the apparent variation between the social structures of whitetails and mule deer could

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simply reflect behavioural responses of individuals to the habitats in which they have been studied.

Whitetails and mule deer have similar productivity (Beasom and Wiggers 1984; Mackie et al. 1998), breeding systems (Hirth 1977; Kucera 1978; Geist 1981), and feeding habits (Martinka 1968; Krausman 1978) but are associated with different habitats. Whitetails tend to occupy gentle terrain with cover, whereas mule deer are found in more rugged and open areas (Swenson et al. 1983; Wiggers and Beasom 1986; Wood et al. 1989). Nevertheless, both species occupy a wide range of habitats and coexist in many areas (Anthony and Smith 1977; Kramer 1973; Swenson et al. 1983; Wiggers and Beasom 1986; Wood et al. 1989). I compared sympatric whitetails and mule deer to determine whether their social organization differs when they live in the same ecological conditions. Specifically, I compared the size, composition, and stability of their groups. This work was done with deer living in a prairie habitat in southern Alberta. The landscape was extremely open compared with most locations where these animals live and, consequently, should have been conducive to the formation of larger groups. Groups including females and fawns received the most attention because this work was done during a study of deer responses to predation to which fawns were most vulnerable (Lingle 2000; Lingle and Pellis 2002).

Materials and methods

Study site

The research was conducted on a 225-km² cattle ranch in southern Alberta (49°N, 112°W). A core study area of 20 km² (1996 ha) was identified in which censuses and most observations were conducted. Most habitat variation was topographical and this influenced distributions of the two species (Lingle 2002). In early summer, there was considerable overlap between the species, with the vast majority of whitetail and mule deer females rearing their fawns on slopes, avoiding gently rolling terrain (<5°). By autumn, whitetails left the steeper slopes and returned to more gentle terrain, while mule deer remained on the slopes. From autumn through winter, mule deer occupied the higher, steeper slopes (rising >60 m from the base, >10° in slope), whitetails occupied gently rolling or flat terrain (<5°), and both species used the lower, gentle slopes (<60 m high, <10°; for a map see Lingle 2000).

Both slopes and rolling terrain were open, with native fescue and mixed-grass prairie in 83% of the study area. Small stands of short shrub (*Symphoricarpos occidentalis* and *Rosa* sp.), typically <0.50 m high, were scattered throughout the native grassland. Other than two stands of tall shrub (*Prunus virginiana* and *Amelanchier alnifolia*), 1–2 m high and approximately 1 ha each, no large tracts of tall shrub or tree cover were present. The remaining 17% of the study area, a large field on gentle terrain, had been cultivated until the mid-1980s at which time it was reseeded with introduced grasses. This was the most open area due to the absence of any shrub. Due to the dry climate and strong Chinook winds, there was typically only 0 to 10 cm of standing snow during the two years of study.

Coyotes (*Canis latrans*) were the only predator of deer observed on the study site. There was no hunting of deer by

humans on the ranch, although deer that moved off the ranch were exposed to 12 days of rifle hunting in November.

Seasons

Six seasons corresponding to significant events in the annual life cycle of deer were identified. Transitions between seasons were identified depending on the age of fawns, seasonal changes in habitats used by deer, and changes in coyote feeding habits that could significantly affect deer (Lingle 2000). The seasons are early summer (5 June – 31 July), late summer (1 August – 30 September), autumn (1 October – 30 November), winter (1 December – 15 February, the approximate date when ground squirrels (*Spermophilus richardsonii*) start to emerge, which corresponds to a diet shift for coyotes), late winter (16 February – 31 March), and spring (1 April – 4 June). Early and late summer or winter and late winter were lumped when samples were too small to analyse them separately or when there was no reason to expect a substantial difference between the finer divisions.

Censuses

Data on group size and composition were obtained from biweekly censuses of the study area between June 1994 and September 1995 (once per week in June and November). The basic procedure was to walk or drive a certain route, stopping at predetermined vantage points to search for deer and travelling in the opposite direction on alternate censuses. It typically required 2 days to cover the entire study area. In summer (June–September), when distributions of whitetails and mule deer overlapped substantially, a major slope system was censused on one day and a river valley the next because there was little movement of deer between these areas. The species were more segregated following summer. From October through May, mule deer were censused on one day and whitetails on another, even though this meant covering most of the area twice.

All whitetails and mule deer observed within the study area during censuses were counted. Vegetation was lush enough to hide some deer in summer, particularly the most-concealed animals, which were whitetail females and fawns of both species. By October, vegetation was desiccated and unlikely to obscure deer completely. Rolling terrain or gullies undoubtedly concealed some animals throughout the year, although vantage points were selected to maximize opportunities to view into low-lying areas. The route and census procedures were planned to avoid repeated sightings of the same group or individual, and a group or individual was ignored when there was a possibility that it had been sighted previously.

Data were recorded for each group of deer seen during a census. A group was defined as an aggregation of animals in which each member had another deer within 50 m while being farther than 50 m from deer in another group (Clutton-Brock et al. 1982). Data included species, group type (female, adult male, mixed sex, yearling male, or juvenile; after Hirth 1977), group size, whether all animals in the group were assuredly seen, the number of animals of each age and sex class (adult male, yearling male, adult female, and juvenile), activity, and topography (slope or rolling). Yearling males were distinguished from older males by the smaller size of their bodies and antler configuration; yearling females were

pooled with adult females. Juveniles were distinguished from yearlings or adults until the June following the year in which they were born. Group type was recorded as “unknown adult” if one or more adults in a group could not be distinguished as females or males; groups were recorded as “unknown” if one or more animals could not be distinguished as adults, yearlings, or juveniles. Groups were excluded from the analysis of group type or size when it was possible that some members were overlooked due to topography or vegetation.

Sightings of marked fawns

Fawns were caught and ear-tagged during their first week of life to identify individuals. These included 24 mule deer and 17 whitetails born in June 1995. On average, individually marked mule deer fawns were resighted every 11 days during summer and whitetails every 8.5 days. Marked fawns of both species were resighted every 6 days, on average, during winter. When a marked fawn was sighted, the size and composition of its group and the fawn’s activity were recorded. The stability of a group, an indication of group cohesion, was evaluated by recording whether one or more animals joined or left a group (i.e., yes or no) during a 10-min observation period that began once a marked fawn was sighted. Lastly, other marked fawns in the same group were identified. Because of a high mortality rate, primarily from coyote predation, the sample of marked fawns was smaller in winter (mule deer, $n = 10$; whitetails, $n = 6$) than in summer. If disturbance related to the observer or another human interfered with a specific trait, for instance, group composition or stability, data were not recorded for that trait. This applied both to data on marked fawns and to census data.

Data analysis

Size, type, and stability of groups

Group size tends to be strongly skewed in social ungulates such as whitetails and mule deer, which tend to form a large number of small groups and a small number of large groups (Clutton-Brock et al. 1982; Jarman 1982). This poses a problem for a person trying to describe group size. Even though one recognizes that most animals are in large groups, most of the groups are small. Jarman (1982) tackled this dichotomy by distinguishing between “observer centred” and “animal centred” measures. Traditional (observer centred) means or medians reflect the most frequent size of group. Observer-centred measures are useful when considering how an outsider, such as a human or a predator, views the group, but they tell us little about the social environment that an individual animal experiences. In contrast, animal-centred measures (eq. 1 (after Jarman 1982), also called “typical group size”) can be used to identify the size of group in which most animals occur:

$$[1] \quad \frac{\sum_{i=1}^N g_i^2}{\sum_{i=1}^N g_i}$$

where N is the number of sampled groups and g_i is the size of each.

Both animal-centred and observer-centred measures were obtained from census data, although statistical tests rely on

the raw, observer-centred data. Data on the groups occupied by marked fawns are inherently animal centred so should correspond most closely to animal-centred census results.

The group was the sampling unit for census data. The individual fawn was the sampling unit for data collected on marked fawns. A single value for group characteristics was calculated for each fawn to avoid biasing results in favour of more frequently sighted animals. The proportion of times in which a marked fawn was sighted in a certain type of group was used to represent the type of group in which each fawn occurred. A median value was obtained for the size of groups in which each marked fawn was seen. The proportion of sightings of each fawn during which a group change occurred was used to examine group stability. For analyses involving marked fawns, data were only used for one twin when both were marked.

There are advantages and drawbacks to the use of data from censuses or sightings of marked fawns. Sampling the same animals during biweekly censuses could potentially result in a lack of independence of data. However, this should not be a problem because groups changed composition more frequently than censuses were done. Averaging data collected for one individual, which is commonly done to avoid problems with pooling (Machlis et al. 1985), poses a contrasting problem in that it can reduce biologically meaningful variation (Leger and Didrichsons 1994). I present results obtained using both the raw census data and the averaged data for fawn sightings to check whether the same trends are evident regardless of the method used and regardless of the year of study. Census data from June 1994 to May 1995 were used for the analysis of group type; census data from June 1995 to September 1995 were added to the group size analysis to increase the sample of mixed-sex groups, which are uncommon in summer. Data on marked fawns were from June 1995 to March 1996.

Individual associations

The frequency of association between marked fawns was examined as another indication of social cohesion. This was calculated as the number of times two animals were seen together divided by the total of the number of times they were seen together plus the number of times each animal was seen separately (coefficient 2, after Clutton-Brock et al. 1982).

Statistical tests

Standard parametric and nonparametric tests were used to analyse data (Sokal and Rohlf 1995). G tests were used to compare the frequency of different types of groups from census data. G values were adjusted with Williams’s correction when $df = 1$. The overall G value was not adjusted when $df > 1$, but alpha was adjusted using the Bonferroni correction (α/k) in subsequent pairwise tests to maintain an experiment-wise error rate of 0.05 (Sokal and Rohlf 1995). Kruskal–Wallis and Mann–Whitney tests were used to compare the proportion of groups of certain types from data on marked fawns, and z values were reported for Mann–Whitney tests when n_1 or $n_2 > 10$; otherwise, U values were reported (Siegel and Castellan 1988). Dunn’s multiple comparison procedure was used following significant Kruskal–Wallis tests (Zar 1999). All tests were two-tailed.

Results

Numbers of deer

Roughly similar numbers of whitetails and mule deer were present in the first year of the study, although each species was more common at certain times of year and in certain locations (Lingle 2000). More mule deer were seen during summer censuses, with 126 ± 23.3 (mean \pm SD) mule deer (49% female) and 96 ± 15.6 whitetails (46% female) observed in late-summer censuses of 1994 ($n = 3$ censuses). More whitetails were seen in winter, due to an influx to the study area in October and November: 225 ± 16.0 whitetails (52% female) and 160 ± 23.5 mule deer (46% female) were observed during winter 1994–1995 censuses ($n = 5$). The disparity between the species increased the following winter, with 270 ± 28.5 whitetails and 106 ± 35.5 mule deer ($n = 3$) in the 1996-ha study area.

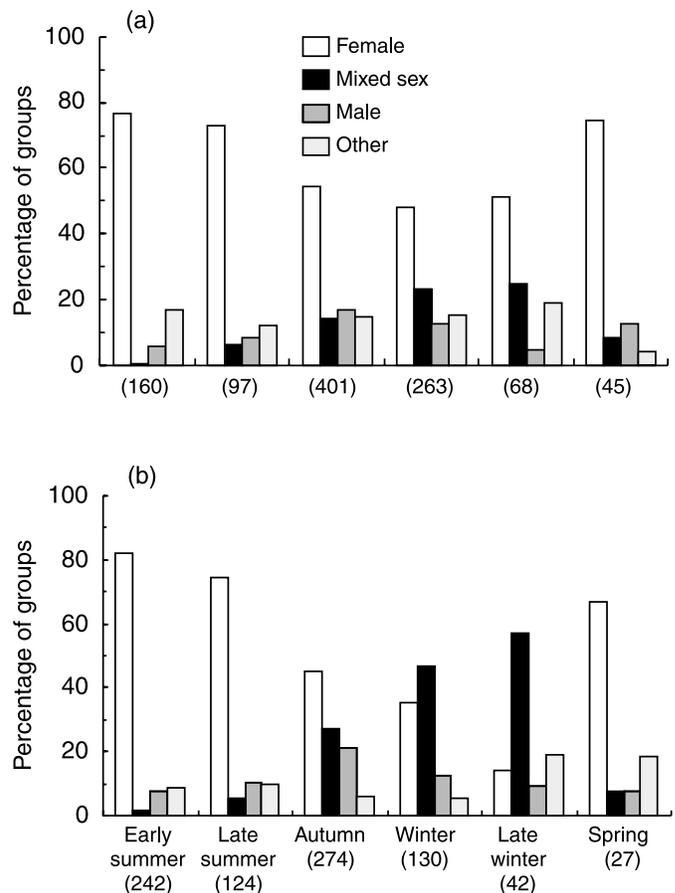
Group type

The type of group occupied by a deer was influenced by its species, with a similar seasonal trend observed for both species. Female groups were most common in spring and summer after which the proportion of mixed-sex groups increased (Fig. 1). The proportion of mixed-sex groups did not peak during the autumn rut, as might be expected if these associations were simply due to courtship activity, but continued to increase over winter for both whitetails and mule deer, declining sharply in spring. Mixed-sex groups constituted 25% of whitetail groups and 57% of mule deer groups in late winter. Those values underestimate the exact values because a substantial proportion of groups were classified as “unknown adult” or “unknown” in late winter (Fig. 1): some of those groups undoubtedly had both males and females. The proportion of female or mixed-sex groups differed significantly among the seasons for both species (Fig. 1) (effect of season on frequency of female or mixed-sex groups: whitetails, $G = 70.80$, $df = 3$, $P < 0.0001$; mule deer, $G = 202.70$, $df = 3$, $P < 0.0001$, with the two parts of summer and two parts of winter combined; for both species, female groups were more likely to occur in summer, and mixed-sex groups were more likely to occur in all other seasons). Male groups appeared relatively common during autumn (Fig. 1), which may be due to the presence of single males travelling among different groups during the rut as they search for receptive females.

Despite the similar seasonal trend, mixed-sex groups were more common in mule deer and female groups were more common in whitetails from autumn through winter. There was no difference in the type of groups formed by whitetail and mule deer females during spring or summer (Fig. 1) (effect of species on frequency of female or mixed-sex groups: summer, $G = 0.0$, $df = 1$, $P = 0.99$; autumn, $G = 19.28$, $df = 1$, $P < 0.0001$; winter, $G = 27.38$, $df = 1$, $P < 0.0001$; spring, $G = 0.0$, $df = 1$, $P > 0.99$).

Similar results were obtained for marked fawns (Fig. 2, Table 1). Fawns of the two species were usually spotted in female groups in summer. Whitetail fawns were seen in mixed-sex groups in winter and in late winter more often than in summer (Fig. 2, Table 1a). Mule deer fawns were seen in mixed-sex groups more often from autumn to late

Fig. 1. Percentage of groups of different types observed during censuses of whitetails, *Odocoileus virginianus*, (a) and mule deer, *Odocoileus hemionus* (b). “Other” group types include yearling male, juvenile, unknown adult, and unknown. The following group types comprised $>4\%$ of groups classified as other. Whitetails: yearling male groups, 10.6% in early summer, 4.7% in autumn; unknown adult groups, 7.4% in late winter; unknown groups, 11.0% in winter and 11.8% in late winter. Mule deer: juvenile groups, 5.6% in late summer; unknown adult groups, 19.0% in late winter.



winter than in summer. Despite the similar seasonal pattern, mule deer fawns were significantly more likely than whitetail fawns to occur in mixed-sex groups from autumn to late winter, and whitetail fawns were more likely to occur in female groups in winter and late winter (Fig. 2, Table 1b). Marked whitetails were sighted in mixed-sex groups 36% of the time in winter, declining slightly to 30% in late winter. Marked mule deer were sighted in mixed-sex groups 63% of the time in winter, with this increasing to 85% of the time by late winter.

Whitetail fawns were also sighted in female groups more often than were mule deer fawns during summer (mean = 90.2 vs. 76.2% of sightings) (Table 1b). However, this was not because mule deer fawns were in mixed-sex groups at that time. Instead, mule deer fawns were spotted in juvenile groups, having no adults, more often during summer than were whitetails (mean = 13.8 vs. 5.1% of sightings, $z = -1.96$, $P = 0.04$).

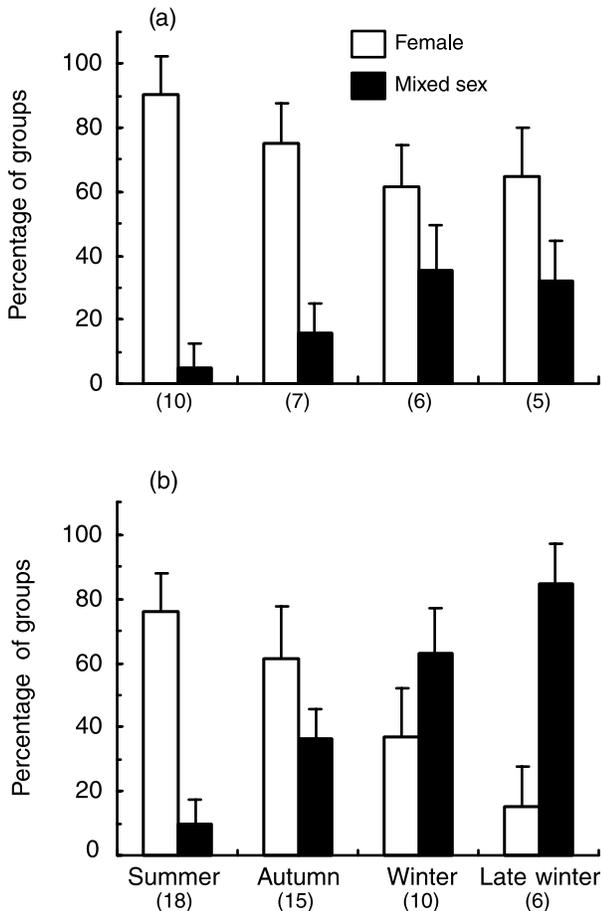
Table 1. Statistical comparison of factors affecting the type of groups occupied by marked fawns of whitetails, *Odocoileus virginianus*, and mule deer, *Odocoileus hemionus*.

(a) Effect of season on group type, tested within species.			
Species and group type	<i>H</i>	<i>P</i>	Significant contrasts
Whitetail female	14.66	0.002	Summer ≠ winter and late winter
Whitetail mixed sex	18.78	0.0003	Summer ≠ winter and late winter
Mule deer female	27.91	<0.0001	Summer and autumn ≠ winter and late winter
Mule deer mixed sex	35.09	<0.0001	Summer ≠ autumn, winter, and late winter; autumn ≠ late winter

(b) Effect of species on group type, tested within season.								
Group type	Summer		Autumn		Winter		Late winter	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>
Female	-2.36	0.02	-1.69	0.10	49.5	0.02	30.0	0.006
Mixed sex	-0.84	0.41	-2.61	0.009	63.5	0.005	30.0	0.006

Note: Kruskal–Wallis (*H*) was used to test for seasonal effects (*df* > 1), and Mann–Whitney (*U* or *z*, depending on sample size) was used to test the effect of group type and species (*df* = 1) (*z* values reported for Mann–Whitney tests when either *n*₁ or *n*₂ > 10; otherwise, *U* values reported). See Fig. 2 for samples sizes.

Fig. 2. Mean ± SD percentage of sightings of marked fawns in female or in mixed-sex groups: whitetails (a) and mule deer (b).



Group size

Groups with females (female and mixed-sex groups combined) and groups with marked fawns increased in size from summer to late winter (Figs. 3a and 4a, respectively). More specifically, groups were smallest in June and largest in Feb-

ruary (Fig. 3b). This seasonal pattern was most obvious for mixed-sex groups but also applied to female groups (Figs. 3c, 3d, and 4b) and was statistically significant for both (Tables 2a and 3a). Although mule deer female groups declined in size from December to March in the winter of 1994–1995 (Figs. 3c and 3d), this was due to the extremely high mortality of fawns that year. The number of adults in these groups remained steady during the same period (observer-centred median = 2.0).

Mixed-sex groups were significantly larger than female groups in all seasons for both species (Figs. 3c, 3d, and 4b, Tables 2b and 3b). Male groups seen during censuses were small for both species, with an observer-centred median of one or two animals throughout the year. Some locations regularly used by males in spring and summer outside the study area were not censused, so these data may not fully represent characteristics of male groups in those seasons.

Mule deer were observed in significantly larger groups than whitetails from autumn through winter, both during censuses (Fig. 3a, Table 2c) and during sightings of marked fawns (Fig. 4a, Table 3c). The difference was most pronounced in winter, when marked mule deer fawns occurred in groups with a median size of 13.5 and 21.5 (winter and late winter, respectively) and whitetail fawns in groups with a median size of 6.0 and 8.0 (Fig. 3a). Even though whitetails tended to form the smallest groups, they also formed a few large, loose aggregations that were some of the largest groups of all.

There was little difference in the size of whitetail and mule deer groups when groups of the same type were compared (Figs. 3c, 3d, and 4b). Statistical analysis of data for marked fawns supported the conclusion that mule deer groups were larger than whitetail groups of the same type, but analysis of census data did not (Tables 3c and 4c). Two differences were evident in the census data: mule deer female groups were larger in autumn and whitetail female groups were larger than mule deer female groups in late winter (Figs. 3c and 3d, Table 2c). These differences can be attributed to the larger proportion of mule deer fawns alive in autumn 1994 and to the larger proportion of whitetail fawns alive in late winter (Lingle 2000). These differences

Fig. 3. Size of whitetail (Wt) and mule deer (Md) groups observed during censuses conducted between June 1994 and September 1995: animal-centred medians and interquartile ranges for all groups with females (female and mixed-sex groups combined) (a), animal-centred monthly median for groups with females (b), observer-centred medians for female groups and for mixed-sex groups (c), and animal-centred medians for female groups and for mixed-sex groups (d). See Table 2 for sample sizes; see text for definition of observer-centred and animal-centred group size.

disappear when the analysis is restricted to the number of adults in the group (Table 2c) (female groups in autumn, $z = -0.56$, $P = 0.58$; female groups in late winter, $z = -0.60$, $P = 0.55$).

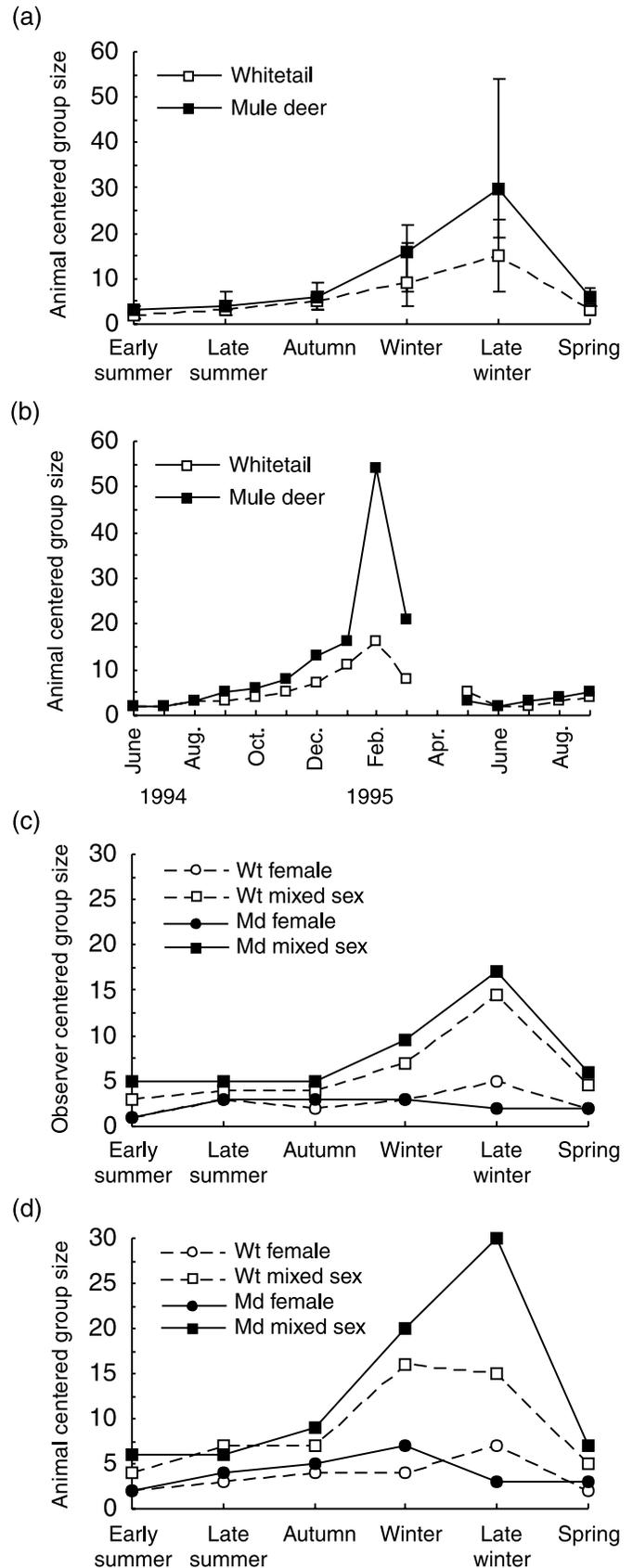
Habitat variation did not appear to affect the size of deer groups at this site. Group size did not differ between groups sighted on the slopes and those sighted on rolling terrain in winter (1994–1995 census data: whitetails, Mann–Whitney $z = -0.392$, $n_1 = 185$, $n_2 = 22$, $P = 0.69$; mule deer, $z = -0.328$, $n_1 = 33$, $n_2 = 68$, $P = 0.74$). Whitetail groups spotted in the seeded field, which was the most open habitat because it had no shrub, were no larger than groups in undisturbed prairie (Mann–Whitney $z = -0.259$, $n_1 = 80$, $n_2 = 127$, $P = 0.80$). It is important to note that variation in cover was limited due to the absence of any extended tracts of woodland.

Group stability

Whitetail groups with marked fawns were less stable than mule deer groups with marked fawns in winter and late winter (Table 4) (Mann–Whitney: winter, $U = 65$, $n_1 = 7$, $n_2 = 10$, $P = 0.003$; late winter, $U = 30$, $n_1 = 5$, $n_2 = 6$, $P = 0.003$). This difference is not attributable to species differences in group size or group type. Despite parallel changes in group size and group type over winter, the stability of whitetail and mule deer groups diverged: mule deer groups became more stable, whereas whitetail groups became more fluid (Table 4). Although seasonal effects were only significant for mule deer (Kruskal–Wallis: whitetails, $H = 1.04$, 2 df, $P = 0.60$; mule deer, $H = 6.81$, 2 df, $P = 0.60$), they were sufficient to lead to an interspecific difference in stability in winter, whereas there was none in autumn (Mann–Whitney: autumn, $z = -0.97$, $n_1 = 7$, $n_2 = 15$, $P = 0.33$). Data on group stability were recorded as simple occurrence data. Focal observations and larger samples would be useful to consider aspects of group stability more delicately.

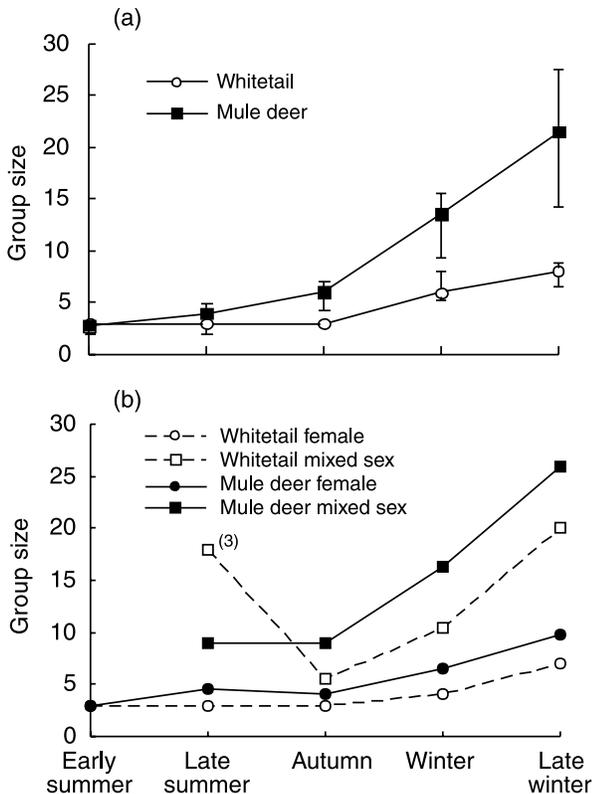
Individual associations

Most mule deer had at least one close associate among the other marked mule deer, with a median maximum association (i.e., the median association when using each fawn's closest associate) of 33.0% of sightings (interquartile range (IQR) = 14.3–45.0%, $n = 16$ fawns). The main exceptions, with no associations over 0% in autumn, were two fawns that were geographically isolated from other marked mule deer. Mule deer fawns had more frequent associations with an increasing number of fawns as winter progressed, so that fawns surviving winter had a medium maximum association of 44%. For instance, one fawn that died in December had been spotted with another marked fawn 11% of the time, but its twin that survived the winter was seen with the same fawn 33% of the time. As another example, two marked



fawns were observed together 44% of the time between December and late March but 91% of the time after 1 February. The extent of association among marked mule deer fawns

Fig. 4. Group size for individually marked whitetail and mule deer fawns: group size (median and interquartile ranges) for all group types combined (a) and median group size for female groups and for mixed-sex groups (b). Results are combined for early and late summer because fawns rarely occurred in mixed-sex groups in summer. The high median value for whitetail mixed-sex groups in summer is viewed as unreliable due to the small sample size: only three whitetail fawns were seen in mixed-sex groups during summer with one sighting for each compared with eight mule deer fawns with a few sightings for each. See Table 3 for sample sizes.



corresponded closely to their geographic relationship (Lingle 1998).

Whitetails did not have similarly strong associations with other marked fawns (median maximum association = 2.65%, IQR = 0.95–3.3%, $n = 8$ fawns). There were only four non-zero whitetail dyads, and all of these resulted from single sightings, three of which involved fleeting associations. The home ranges of each marked whitetail fawn overlapped with the range of at least three other marked fawns, so they had opportunities to associate with other marked fawns.

Discussion

Group composition and cohesion

Seasonal trends in group composition were similar for the two species. Females and fawns formed small groups during summer. Large mixed-sex groups became increasingly common over winter. These results confirm the tendency of both whitetails and mule deer to form large mixed-sex groups outside the rut in an open habitat (Hirth 1977; Bowyer 1985). However, those and most studies of ungulates (Geist and Petocz 1977; Bowyer 1984; Bleich et al. 1997; Thirgood

1996) reported the largest proportion of mixed sex groups during the breeding season, although Bowyer (1984) reported another, slightly smaller peak in the proportion of mixed-sex groups in April (~35% of groups in April versus ~40% during the breeding season 4 months earlier). Mackie et al. (1998) reported a slight increase of mixed-sex groups in mule deer, from about 10 to 14%, following the breeding season. At the present location, mixed-sex groups were considerably more common in late winter, comprising at least 25% of whitetail groups and 57% of mule deer groups versus 14 and 27%, respectively, during the rut. Mackie et al. (1998) attributed the greater proportion of mixed-sex groups and larger groups following the rut to the limited availability of winter habitat. This explanation seems unlikely to apply to the present situation: there was little to no snow cover between January and February 1995 that restricted access to food and no obvious concentrations of food resources used by deer during winter. In fact, group size peaked in February and declined in March. Food resources did not appear to improve until April when the spring flush usually occurs.

Despite the similar seasonal trend, mule deer were significantly more likely than whitetails to occur in relatively large groups composed of both sexes during winter, and whitetails were more likely to occur in small female groups. The tendency for mule deer to form larger groups was associated with their tendency to form mixed-sex groups. When groups of the same type, female or mixed sex, were considered, there was little or no difference in the size of whitetail and mule deer groups.

Group size increased at the same time as the proportion of mixed-sex groups increased for both species. The increase in mixed-sex groups seen in both species over winter, and the greater number of mixed-sex groups in mule deer than in whitetails, could be the simple consequence of the tendency to form larger groups. Conradt (1998a) pointed out that, if the two sexes associate at random, mixed-sex groups would be the natural consequence of increased group size in species such as deer that typically have skewed sex ratios. The results show that male whitetails are less likely than mule deer males to occupy groups with females. Further analysis is needed to establish whether the degree of sexual segregation in these species differs independently of group size.

The results obtained from the sample of marked fawns and from census data were equivocal as to whether mule deer groups of a certain type were larger than whitetail groups of the same type. The sample of marked fawns, which indicated that mule deer groups of a given type were larger, forms a more homogenous data set with less noise because data were restricted to groups having productive females. On the other hand, it is possible that biologically meaningful variation in group size was reduced when averaging data points for individual fawns to avoid problems with pooling (Leger and Didrichsons 1994). It was my impression from focal observations of these individuals that mule deer females banded together, forming larger groups than whitetails, once fawns were a few weeks old (S. Lingle, unpublished data).

Whereas the two species showed similar trends in group size, they showed opposing trends in group stability: mule deer groups became more stable as winter progressed but whitetail groups became more fluid. This is surprising given

Table 2. Statistical comparisons of factors affecting the size of groups in which females occurred using census data.

(a) Effect of season on group size, tested within species and group type.								
Species and group type	<i>H</i>	<i>P</i>	Significant contrasts					
Whitetail female and mixed sex	137.42	<0.0001	Early summer ≠ all other seasons; late summer and autumn ≠ winter and late winter					
Whitetail female	140.89	<0.0001	Early summer ≠ all other seasons; late summer, autumn, and spring ≠ late winter					
Whitetail mixed sex ^a	26.77	<0.0001	Summer and autumn ≠ winter and late winter					
Mule deer female and mixed sex	156.97	<0.0001	Early summer ≠ all other seasons; late summer ≠ winter and late winter; autumn ≠ late winter					
Mule deer female	138.29	<0.0001	Early summer ≠ late summer, autumn and winter					
Mule deer mixed sex ^a	21.72	<0.0001	Summer and autumn ≠ winter and late winter					
(b) Effect of group type (female vs. mixed sex) on group size, tested within species and seasons.								
Species	Summer		Autumn		Winter		Late winter	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>
Whitetail	-4.46	<0.0001	-4.04	<0.0001	-6.33	<0.0001	-3.70	0.0002
Mule deer	-8.23	<0.0001	-3.18	<0.002	-4.88	<0.0001	-2.82	0.005
(c) Effect of species (whitetail vs. mule deer) on group size, tested within group types and seasons.								
Group type		Early summer	Late summer	Autumn	Winter	Late winter	Spring	
Female and mixed sex	<i>z</i>	-0.66	-0.05	-2.91	-2.89	-0.79	-0.09	
	<i>P</i>	0.51	0.96	0.004	0.004	0.43	0.93	
Female ^a	<i>z</i>	-0.58	-0.52	-3.45	-1.03	-1.72	-0.19	
	<i>P</i>	0.56	0.61	0.0006	0.30	0.09	0.85	
Mixed sex ^b	<i>z</i>	—	-2.24	-1.12	-0.12	-0.26	—	
	<i>P</i>	—	0.025	0.27	0.26	0.80	—	

Note: Kruskal–Wallis used to test for seasonal effects ($df > 1$), and Mann–Whitney used to test the effect of group type and species ($df = 1$). Sample sizes were as follows. Whitetail, female groups: early summer, 208; late summer, 125; autumn, 205; winter, 119; late winter, 34; spring, 34. Whitetail, mixed-sex groups: early summer, 5; late summer, 13; autumn, 47; winter, 56; late winter, 14; spring, 4. Mule deer, female groups: early summer, 299; late summer, 157; autumn, 104; winter, 41; late winter, 5; spring, 14. Mule deer, mixed-sex groups: early summer, 19; late summer, 14; autumn, 64; winter, 52; late winter, 17; spring, 2.

^aWhen the number of adults per group was compared, there was no difference in the size of female groups in autumn ($z = -0.56$, $P = 0.58$) or in late winter ($z = -0.44$, $P = 0.66$).

^bEarly- and late-summer data were combined for mixed-sex groups owing to the small sample size and for both group types to enable comparison of summer group size in Table 2b. Too few mixed-sex groups were seen in spring to justify statistical comparisons.

that mule deer were more likely to be found in large groups containing both sexes. By itself, the difference in group size and composition would have led to the expectation that mule deer groups would be less stable. The different activity rhythms of male and female ungulates have been shown to contribute to the instability of mixed-sex groups, thereby contributing to sexual segregation in sexually dimorphic species (Conradt 1998b; Conradt and Roper 2002; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2002).

The cohesiveness of mule deer groups was also evident in the strong associations developed among marked fawns. Most mule deer fawns associated frequently with at least one other marked fawn, and the number and frequency of their associations increased during winter. More information is needed to determine whether these associations reflect individuals choosing to associate with certain individuals or are simply the natural consequence of the size and stability of their groups and habitat characteristics that influence their movements (“environmental funnelling”, after Lott and Minta 1983). Mule deer would be expected to have higher levels of association given that they occurred in groups with larger numbers of fawns and there were also fewer mule deer than whitetail fawns in the winter of 1995–1996.

Whitetails have been reported to have strong associations among close female relatives, including sisters or a doe and her yearling offspring, but these tend to end abruptly by the time the youngest doe is 3 years old, thereby setting an upper limit on group size (Hawkins and Klimstra 1970). Even though females stop associating within groups, their geographical relationship changes little. The type of social structure described by Hawkins and Klimstra appears to be compatible with observations made here. Whitetail fawns did not form stable social associations with other fawns to the extent that mule deer did, but then the smaller groups in which they occurred and the instability of their groups would tend to prevent strong associations from occurring. The small sample of marked deer would have precluded identification of a few close associates, some of which were identified using natural markings during focal observations.

Why do whitetails and mule deer differ in their grouping behaviour?

Information on the physiology and feeding habits of whitetails and mule deer is inadequate to determine how these factors contribute to the social organization of these species. Their similar body size in northern locations

Table 3. Statistical comparisons of factors affecting group size for marked fawns.

(a) Effect of season on group size, tested within species and group type; seasons include summer (early and late summer combined), autumn, and winter (winter and late winter combined).

Species and group type (<i>n</i>)	<i>H</i> or <i>U</i>	<i>P</i>	Significant contrasts
Whitetail female (10, 8, 8)	6.58	0.037	Summer ≠ winter
Mule deer female (17, 15, 10)	15.83	0.0004	Summer and autumn ≠ winter
Whitetail mixed sex (7, 5) ^a	19.5	0.18	None
Mule deer mixed sex (17, 15, 12)	15.83	0.0004	Summer and autumn ≠ winter

(b) Effect of group type (female vs. mixed sex) on group size, tested within species and seasons.

Species	Summer		Autumn		Winter	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>U</i> or <i>z</i>	<i>P</i>
Whitetail ^a	—	—	51.5	0.005	34.5	0.009
Mule deer	-3.33	0.001	-4.00	0.0001	-3.81	0.0001

(c) Effect of species (whitetail vs. mule deer) on group size, tested within group type and seasons.

Species	Summer		Autumn		Winter	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>U</i> or <i>z</i>	<i>P</i>
All group types ^{b,c}	-1.55	0.12	-3.03	0.003	-3.31	0.001
Female	-2.58	0.01	-2.20	0.03	69	0.008
Mixed sex ^a	—	—	-1.49	0.14	-1.96	0.05

Note: Mann–Whitney or Kruskal–Wallis tests presented, depending on whether there were two or more groups, respectively.

^aComparisons were not made using whitetail mixed-sex groups in summer owing to insufficient sample size. The effect of season on size of whitetail mixed-sex groups was compared between autumn and winter.

^bSample size (*n*) for all group types (in order of whitetail, mule deer): summer, 10, 17; autumn, 98, 15; winter, 5, 13; other sample sizes listed under seasonal comparisons.

^cSize of whitetail and mule deer groups, using all group types, differed significantly in late summer ($z = -2.61$, $n_1 = 10$, $n_2 = 17$, $P = 0.009$) but not in early summer ($z = -0.54$, $n_1 = 10$, $n_2 = 17$, $P = 0.59$).

Table 4. Percentage (median and interquartile ranges (IQR)) of sightings of marked fawns during which changes in group membership occurred during a 10-min observation period.

Season	Whitetail			Mule deer		
	<i>n</i>	Med	IQR	<i>n</i>	Med	IQR
Autumn	7	21	17–23	15	14	0–27
Early winter	7	30	18–40	10	9	0–17
Late winter	5	38	15–45	6	0	0–0

(Mackie 1964; Wishart 1986) should lead to similar metabolic requirements (Gwynne and Bell 1968). The whitetail's more frequent association with agricultural and riparian habitats has led to the perception that they are more selective feeders (Hoffman 1985) and are better able to utilize high-quality succulent foods (Mackie et al. 1998) than are mule deer. However, I am not aware of data supporting this perception of their feeding habits. These associations may simply reflect the whitetail's greater use of gentle terrain, as was found to explain their greater use of native grassland (Wood et al. 1989). People who examined the feeding habits of sympatric whitetails and mule deer concluded that differences in diets were determined by the availability of foods in certain habitats and not by different preferences (Martinka 1968; Krausman 1978). Nonetheless, managers of captive deer find mule deer more difficult to sustain (R. Hudson, personal communication), so there is likely a difference in dietary requirements or another aspect of their physiology that has not been identified.

Many animals aggregate in large numbers to obtain food that is high in quality or quantity (Borkowski and Furubayashi 1998; Brashares and Arcese 2002). Vegetation was homogeneous throughout most of the study site, with both whitetails and mule deer occupying native prairie grassland. There were no locations or obvious food sources inside the study area that attracted large concentrations of deer to feed.

Some ungulates form larger groups when at higher density (Borkowski 2000; Ruckstuhl and Festa-Bianchet 2001; Hebblewhite and Pletscher 2002). Density cannot explain the larger groups formed by mule deer than by whitetails in winter because mule deer were at lower densities than whitetails in both winters.

Reproductive status influenced the size of groups for both species, with females of both species forming smaller groups following parturition than at other times of the year. Productive females of many species isolate themselves at parturition, while yearling or nonproductive adult females remain in larger groups (Lent 1974; Clutton-Brock et al. 1982; Bergerud et al. 1984; reviewed by Main et al. 1996). A species difference in the number of productive females did not explain the species difference in group size. The analysis of groups with marked fawns was focussed on groups formed by productive females: the mothers of the fawns. The timing of reproductive events also does not explain the differences between the species because the two species breed and give birth at the same times.

Animals of both species formed relatively large groups compared with deer in other locations (Hawkins and Klimstra 1970; Hirth 1977; Bowyer 1985). This was proba-

bly a facultative response to the landscape, which was extremely open compared with other locations where these species live and have been studied. The formation of larger groups in open habitats is usually viewed as an adaptation to predation (Jarman 1974) but may also be the consequence of the increased ability to see conspecifics in open habitats (Gerard and Loisel 1995).

In contrast, the species difference in group composition did not seem to be a facultative response to habitat variation. Half of the 20-km² study site was shared by the two species, and existing variation in vegetation and terrain had no apparent effect on group size. It is nevertheless possible that whitetails and mule deer evolved different grouping patterns in their typical habitats and that these adaptations do not relax completely when occupying the same habitat (regardless of whether they originally evolved due to predation, feeding behaviour, or another factor).

The tendency of mule deer to form larger, more stable groups than whitetails is consistent with differences expected from observations of their interactions with predators (Lingle 2001; Lingle and Pellis 2002). Mule deer typically bunched together and confronted coyotes; coyotes were more likely to attack and kill an individual when groups split and an individual became isolated. The cohesiveness of a group had a more powerful effect on risk than its size, although group size was related to a mule deer's risk. Coyotes were more likely to attack mule deer in small groups (<6 deer) than in intermediate (6–10) or large (>10) groups, resulting in a high level of risk to individuals in small groups (16.5% per capita risk of attack once encountered versus 0.8 and 1.9% for intermediate and large groups, respectively). Group size and cohesion were not similarly related to predation risk for whitetails (per capita risk of attack for small, medium-sized, and large groups were 0.7, 0.5, and 0.8%, respectively). Whitetails effectively avoided predation by independent flight with no direct assistance by other deer. These findings indicated that mule deer can lower their risk by forming relatively large, cohesive groups (Lingle and Pellis 2002).

Similar to females and fawns, mule deer males seemed to find safety in larger groups. Males that were alone when attacked frequently moved to a large group, which could consist of males, females, or both sexes; coyotes usually persisted in attacking a male until it got to a group. Females, not males, were actively aggressive when coyotes first approached a mixed sex group and females also actively defended individuals that were attacked (Lingle and Pellis 2002). Even though males rarely defended other individuals, they did defend themselves when attacked (S. Lingle, unpublished data). It is not clear whether males benefit from the presence of females in a group that are willing to confront coyotes or simply benefit from the increased size and cohesion of a group, regardless of whether the group contains males or both sexes.

In fact, it could be argued that adult males of both species might try to avoid groups with fawns because fawns were the most vulnerable and most likely to attract coyotes looking for deer to attack (Lingle 2000; Lingle and Pellis 2002). Many people have suggested that predation risk contributes to sexual segregation because females with young seek safer

habitats (reviewed by Ruckstuhl and Neuhaus 2002). Another hypothesis has been overlooked: predation risk could contribute to the behavioural segregation of males and females with no concurrent habitat segregation, if males try to avoid groups having fawns that are more likely to attract predators.

In summary, the composition and cohesion of whitetail and mule deer groups differed in an area where they live sympatrically. The observed differences were consistent with those expected to result from the selection pressure of predation, which has different effects because of the contrasting antipredator strategies used by the two species. Another possibility, which is not exclusive of the predation hypothesis, is that the two species evolved differences in grouping behaviour in response to the amount of cover in their typical habitats, and these behavioural adaptations persist even when they live in the same conditions. The emphasis on the difference between the species should not conceal their seasonal similarities. Females of both species split into the smallest groups when rearing young fawns in early summer. In contrast with most studies, deer of both species were more likely to occupy large groups consisting of both sexes as winter progressed, well after the breeding season. Insufficient information is currently available on the comparative physiology and feeding behaviour of whitetails and mule deer to determine how those factors could affect grouping behaviour in these species.

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