

Seasonal variation in coyote feeding behaviour and mortality of white-tailed deer and mule deer

Susan Lingle

Abstract: Young ungulates are considered especially susceptible to predation in the initial weeks following birth. However, the timing of mortality can vary depending on the availability of alternative prey and the type of predator, and could vary depending on antipredator defenses used by prey. I used coyote (*Canis latrans*) scats, observations of coyote hunting behaviour, and mortality data for deer to examine seasonal variation in coyote feeding behaviour and mortality of sympatric white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) fawns. Coyotes captured the vast majority of deer they consumed, forming groups that hunted deer from June through March. Coyotes were observed hunting deer most often in winter when ground squirrels were not available, and an inverse correlation between the amount of deer and ground squirrel in coyote scat reflected this relationship ($r_s = 0.77$, $P = 0.004$). Fawns of both species had poor survival rates in 1994 (1 of 10 tagged whitetails survived to 1 year, none of 22 mule deer survived), improved survival rates in 1995 (33% of 15 whitetails, 25% of 24 mule deer), and most mortality appeared to be due to coyote predation. The season in which fawns of each species were most vulnerable differed. Tagged whitetail fawns had similar mortality rates in early summer, when they were less than 8 weeks old, as they did in winter, when they were 5–9 months old (35 and 37%, respectively, in 1995). In contrast, mule deer fawns had low mortality rates in early summer (4% in 1994, 17% in 1995), but high mortality rates in winter (100% in 1994, 53% in 1995). Changes in fawn:doe ratios and the examination of carcasses similarly indicated that coyotes captured more whitetails in summer and more mule deer in winter. The seasonal variation in mortality rates of the two species cannot be explained by physical prey characteristics, their relative abundance, or extrinsic factors, and may be due instead to species differences in antipredator behaviour.

Résumé : Les jeunes ongulés sont particulièrement susceptibles d'être victimes des prédateurs au cours des premières semaines après leur naissance. Cependant, cette situation peut varier, selon que d'autres proies sont disponibles, selon le type de prédateur, et pourrait varier aussi en fonction des manoeuvres anti-prédatrices des proies. J'ai examiné la variation saisonnière du comportement d'alimentation du Coyote (*Canis latrans*) de même que la mortalité chez les faons du Cerf de Virginie (*Odocoileus virginianus*) et les faons du Cerf mulet (*Odocoileus hemionus*) du même milieu, par analyse des fèces, par observation du comportement de chasse des coyotes et par examen des données sur la mortalité des cerfs. Les coyotes ont capturé la majorité des cerfs qu'ils ont consommés, formant des groupes de chasse de juin à la fin de mars. La chasse aux cerfs par les coyotes a été observée surtout en hiver alors que les spermophiles étaient absents et la corrélation inverse entre la quantité de cerf et la quantité de spermophile dans les fèces a confirmé cette relation ($r_s = 0,77$, $P = 0,004$). Les faons des deux espèces ont eu un taux de survie médiocre en 1994 (1 Cerf de Virginie sur les 10 marqués a survécu pendant 1 an, aucun des 22 Cerfs muets n'a survécu), un taux de survie plus élevé en 1995 (33% des 15 Cerfs de Virginie, 25% des 24 Cerfs muets) et la mortalité était semble-t-il due surtout aux coyotes. Les faons des deux espèces n'étaient pas tous vulnérables à la prédation au même moment. Les faons marqués du Cerf de Virginie ont eu des taux de mortalité semblables au début de l'été, alors qu'ils avaient moins de 8 semaines, et en hiver lorsqu'ils étaient âgés de 5 à 9 mois (35 et 37% en 1995). En revanche, les faons du Cerf mulet ont eu des taux de mortalité faibles au début de l'été (4% en 1994, 17% en 1995), mais élevés en hiver (100% en 1994, 53% en 1995). Les variations du rapport faons : biches et l'examen des carcasses ont révélé que les coyotes capturaient plus de Cerfs de Virginie en été et plus de Cerfs muets en hiver. La variation saisonnière de la mortalité des deux espèces ne peut s'expliquer par les caractéristiques inhérentes aux proies, ni par leur abondance relative, ni par des facteurs extrinsèques, mais est peut-être due aux différences dans le comportement anti-prédateurs des deux espèces.

[Traduit par la Rédaction]

Introduction

Young ungulates are known to be particularly vulnerable to predation, yet there is little information about when they

are most vulnerable and whether this time varies among species. They are generally considered most susceptible in the initial weeks following birth (Lent 1974). However, the timing of mortality can vary depending on prey abundance and

Received December 18, 1998. Accepted August 17, 1999.

S. Lingle.¹ Large Animal Research Group, Department of Zoology, University of Cambridge, CB2 3EJ, U.K.

¹Present address: Department of Psychology and Neuroscience, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada (e-mail: susan.lingle@uleth.ca).

the availability of alternative prey (Bowen 1981; Hamlin et al. 1984; Potvin et al. 1988; Huggard 1993a; Forbes and Theberge 1996), extrinsic factors such as snow depth (Huggard 1993b; Gese and Grothe 1995), and the type of predator (Ballard et al. 1991; Adams et al. 1995). The timing of mortality may also be associated with variation in anti-predator behaviour. Many ungulates appear to be particularly vulnerable when they are old enough to flush from hiding but still too young to outrun predators (Lent 1974; FitzGibbon 1990). It is possible that young animals of species that rely more on maternal defense than on their own ability to flee are better protected against predators in the initial weeks of life.

Year-round studies of moose (*Alces alces*) and caribou (*Rangifer tarandus*) report that calves are most vulnerable to brown bear (*Ursus arctos*) and wolf (*Canis lupus*) predation in their initial weeks of life (Ballard et al. 1991; Gasaway et al. 1992; Adams et al. 1995; Stuart-Smith et al. 1997). Similarly, elk (*Cervus elaphus*) calves are most susceptible to bear and coyote (*Canis latrans*) predation in the month following birth, and predation is rare in winter (Singer et al. 1997). Information is less clear-cut for deer fawns because studies have generally been restricted to one time of the year. Within summer, white-tailed deer (*Odocoileus virginianus*) fawns have been found to be most vulnerable to coyote, wolf, and bear predation in the few weeks following birth (Cook et al. 1971; Mathews and Porter 1988; Kunkel and Mech 1994), or when fawns are between 2 and 8 weeks of age (Carroll and Brown 1977; Nelson and Woolf 1987). Mule deer (*Odocoileus hemionus*) fawns at two sites were as, or more, vulnerable to coyote predation later in summer, when fawns were 6–15 weeks old (Steigers and Flinders 1980; Hamlin et al. 1984). Mule deer fawns also appear to suffer heavy predation in winter (White et al. 1987; Unsworth et al. 1999). Without a direct comparison of predation rates on the two species at the same location, it is difficult to know whether the variation in timing of mortality is due to factors that differ between sites or studies or to differences between the prey species themselves.

Little is known about the tactics coyotes use to hunt ungulates, and this hinders our understanding of their effect on ungulate populations. On the one hand, coyotes are generally viewed as being too small and not social enough to have a significant effect on ungulate populations, unless the prey are in poor condition, in marginal habitats, or the snow is deep (Gunson et al. 1993). In areas with larger predators, such as wolves, or with a large supply of hunter-killed carrion, coyotes appear to rely more on scavenged ungulate carcasses to obtain food than on hunting ungulates themselves (Bekoff and Wells 1982, 1986; Paquet 1992). On the other hand, coyotes are known to be a major source of mortality for neonatal ungulates (Cook et al. 1971; Barrett 1984; Hamlin et al. 1984) and can also be a significant source of mortality for older mule deer fawns in winter (White et al. 1987; Unsworth et al. 1999). Coyotes are also known to be capable of capturing adult deer and larger species of ungulates (Hilton 1978; Bowen 1981; Paquet 1992; Gese and Grothe 1995). Most reports of coyotes trying to capture ungulates have been observations of interactions between coyotes and individual groups of prey (young fawns, MacConnell-Yount and Smith 1978; Hamlin and Schweitzer 1979; Truett

1979; Wenger 1981; Byers 1997; older ungulates in winter, Bowen 1981; Bowyer 1987; Gese and Grothe 1995). No one has observed coyotes continuously to determine whether they hunt ungulates opportunistically and occasionally when certain conditions such as deep snow are present, or whether packs of coyotes engage in regular and extended hunts similar to those of wolves and other social canids (Estes and Goddard 1967; Mech 1970; Creel and Creel 1995).

Whitetails and mule deer are closely related species that are similar in overall morphology and nearly identical in size and mass in northern locations, including Alberta, Canada (Eslinger 1976; Wishart 1986). Although their habitat preferences differ, they have considerable overlap and coexist in many regions (Anthony and Smith 1977; Wiggers and Beasom 1986; Wood et al. 1989). At a site where whitetails and mule deer are sympatric, I used coyote scats, observation of coyote hunts, and mortality data for deer to address the following questions. (i) To what extent do coyotes consume deer in different seasons, and how does this correspond to their use of other foods? (ii) To what extent do coyotes capture the deer they eat and how? (iii) What are seasonal patterns in the mortality of whitetail and mule deer fawns? Factors that may underlie variation in mortality, including interspecific variation in anti-predator behaviour, will be addressed in the Discussion.

Materials and methods

Study site and subjects

This research was conducted on a 225-km² cattle ranch in southern Alberta, 50 km south of the city of Lethbridge. Censuses and focal observations of animals were conducted in a 20-km² core study site. The landscape was open prairie. Over 83% of the core study site had native fescue and mixed grassland. The remainder was cultivated until the mid-1980s and has since been reseeded with exotic grasses. Most habitat variation was topographical. There were two slope systems. The largest one was formed by the Milk River Ridge, with slopes rising from 30 to 150 m (Fig. 1). A wide river valley, the North Pothole Coulee, with 10- to 60-m slopes, also passed through the study area. The remainder of the study area consisted of gently rolling and flat terrain.

About 250 Dakota white-tailed deer (*O. v. dacotensis*) and 135 Rocky Mountain mule deer (*O. h. hemionus*) occupied the core study site in the winters of 1994–1995 and 1995–1996. In early summer, the vast majority of female whitetail and mule deer reared their fawns on slopes or in the coulee (Fig. 1a). By winter, whitetails returned to flatter terrain, but mule deer remained on the slopes (Fig. 1b). There were four coyote dens in this area and another three within 0.5 km of its boundary. Coyote dens and movements appeared to be well distributed throughout the study area in both summer and winter. No other nonhuman predators of deer were present at the study site. There was also no hunting of deer by humans, but if deer left the ranch they were at times shot by hunters.

In the winter of 1994–1995, temperatures were mild and snowfall was below average (weather data were obtained from Agriculture Canada Research Centre and the McIntyre Ranching Company). The following winter was severe, with below-average temperatures and above-average snowfall. The strong chinook winds common to this region generally prevent snow from accumulating. As a result, there was generally no snow on the ground in the winter of 1994–1995 (monthly median of 0 cm for December, January, and February, from daily records). Despite additional snowfall in 1995–1996, there was usually less than 10 cm on the

Fig. 1. Distribution of whitetails, mule deer, and coyotes within the study site in summer (a) and winter (b). Deer areas were formed by outlining locations of deer recorded during censuses and focal observations. Four coyote packs had dens within the study site and another three packs had dens within 0.5 km of its boundary. Winter rendezvous sites are shown for all seven packs, including two sites for two packs. Dens and rendezvous sites having the same number are sites used by the same pack.

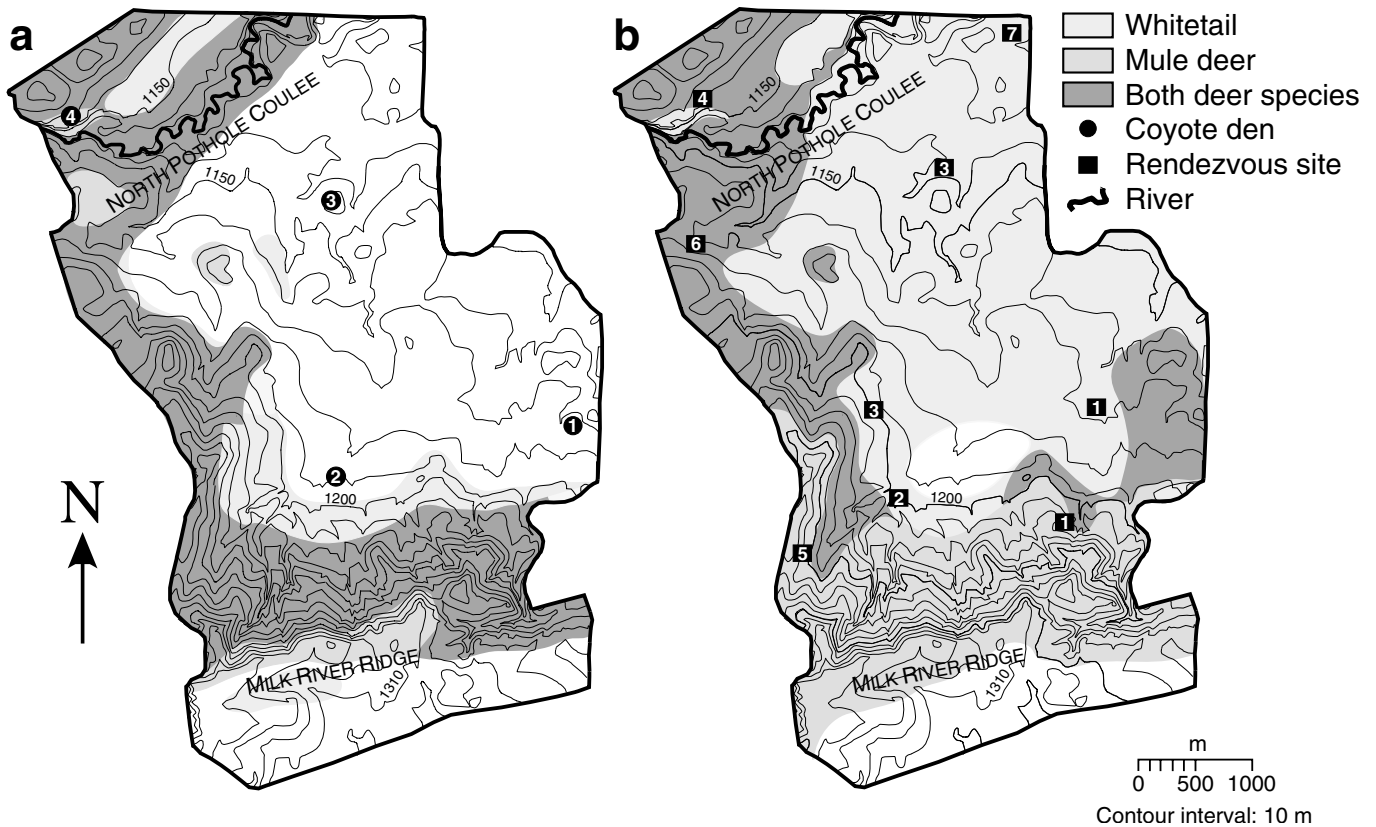


Table 1. Definitions of seasons, with major events occurring during each.

	Date	Fawn age at end of season (weeks)	Major events
Early summer	5 June – 31 July	5–8	Birth. Fawns in hiding. Most females on slopes
Late summer	1 August – 30 September	14–17	Fawns increasingly visible. Whitetail females and fawns return to flats
Autumn	1 October – 30 November	22–26	Fawns associate mostly with adult groups. Deer breed. Deer shift to winter range, when applicable. Last ground squirrel seen on 10 November 1995
Winter	1 December – 15 February	33–36	Ground squirrels in hibernation
Late winter	16 February – 31 March	39–42	Ground squirrels emerge; first one seen on 14 February 1996
Spring	1 April – 4 June	49–52	Initial plant growth. Coyote pups born

ground (monthly medians were <5 cm in December, 5–10 cm in January, and <5 cm in February).

Type and schedule of research

Animals in the study area were observed directly and intensively from September 1993 to early July 1996. I spent approximately 4000 h observing animals and field assistants worked for another 1425 h independently. The most intensive periods of observation were during summer and winter, with an average of 254 h/month of fieldwork carried out from June to the end of September in both 1994 and 1995, and 203 h/month of fieldwork from November to the end of February in the winters of 1994–1995 and 1995–1996. Most of the time in summer was spent conducting focal observations of tagged fawns and their mothers. Most of the time in winter

was spent conducting focal observations of coyotes. Four to 8 days per month were spent censusing animals in the study area or specifically looking for tagged individuals. I primarily worked from a vehicle until May 1995, but walked after that time to minimize damage to the prairie and because I found that I was more likely to see predation attempts when walking.

Seasons

Six seasons corresponding to significant events in the annual life cycle of deer were identified. Transitions between seasons were identified using the age of fawns, seasonal changes in habitat use by deer, and changes in coyote feeding behaviour that could significantly affect deer (Table 1). In particular, the dates on which ground squirrels (*Spermophilus richardsonii*) entered and emerged

Table 2. Behavioural traits of coyotes used to distinguish hunting for deer versus hunting for other prey or traveling.

Prey species or behaviour	Group size	Gait during search	Travel route	Head orientation during search or travel
Small prey (mostly voles, but also insects, eggs, or birds)	Usually one or two, but at times individuals in packs will hunt small prey simultaneously	Slow or normal walk with pauses	Vole: straight with turns, zigzag path, or wander locally with no distance covered. Frequently walk straight to patches of dense vegetation where they wander as they hunt locally, then walk to another patch. Digging for other prey tends to be in one spot	Down or at sharp angle to ground (e.g., <math><45^\circ</math>)
Ground squirrels	Usually one but occasionally two or three	Slow walk and slow-motion stalk	Overall route is usually straight, but may veer from side to side as they approach prey. Frequently double back after a few hundred metres and hunt along the same stretch	Head at moderate or close angle to the ground (approx. <math>45^\circ\text{--}60^\circ< math>)<="" td=""> </math>45^\circ\text{--}60^\circ<>
Deer (continuous group hunts) ^a	Typically three to eight. Rarely a pair	Mostly use a fast walk. Occasionally pause to scan as they enter new valleys	Travel at a given moment is straight, but tend to take an indirect route either to stay in low ground, follow topographical contours, or to encounter deer	Ahead or to deer as they encounter them
Travel	Most often one, sometimes two	Fast walk	Straight and directly between two points	Ahead

Note: Sources used for definitions of hunting for small prey and ground squirrels include Bekoff (1978) and Wells and Bekoff (1982), but the definitions were extended to cover travel between searches for prey, as well as the specific hunt events. Coyotes may hunt more than one prey species during the same outing, such as "small prey" and "ground squirrels" or "small prey" and "deer."

^aThe most common form of behaviour used to hunt deer in winter is described here; for variations see Lingle (1998).

from hibernation correlated strongly with the coyotes' use of deer for food and, consequently, with deer mortality rates (see Results). Based on coyote feeding habits alone, I would have identified the start of winter as a date in November when the last of the ground squirrels hibernated. To confine the effects of the breeding period of the deer and hunting by humans to one season, I instead defined winter as beginning on December 1, which followed the hunt and most rutting activity. The winter of 1994–1995 is referred to as winter 1994 and the following winter as 1995.

Coyote feeding habits

Data on coyote feeding habits were collected by identifying food items in scats and observing the coyotes' foraging behaviour.

Collection and analysis of coyote scats

Coyote faeces were collected and analyzed to determine the amount of deer consumed relative to other prey items in different seasons. Approximately 30 coyote scats were collected each month from November 1994 until February 1996, excluding April 1995, when I was away.

Equal numbers of scats were collected from four portions of the study site to increase the probability that the scats were deposited by a cross section of coyotes from different packs. Mule deer were

dominant in one area in which scats were collected, whitetails were dominant in one area, and the two species shared the remaining two areas. I tried to collect fresh scats along the main walking or driving trails (15 km long), and I collected most scats during the last 2 weeks of a month to increase the probability of their being from that month. I found fewer scats on the main trails in spring and summer, so I had to search for additional scats away from trails at those times.

Scats were sent to the Big Sky Laboratory in Florence, Mont., for analysis. After scats were autoclaved and washed, the contents were distinguished using characteristics of fur, teeth, bones, or structures such as hooves or claws (G. Haas, personal communication). The fur of most species could be identified by eye; scale impressions were made when this was not possible. Deer remains could not be reliably distinguished as either whitetail or mule deer, so they were simply classified as deer. Items present in each scat were classified into major (over 40% of volume by a visual estimate), minor (over 5%), or trace items.

Coyote foraging behaviour and identification of deer hunts

From June 1994 to March 1995, I recorded data from all coyote groups that I saw and conducted focal observations of coyotes engaged in any type of activity, paying particular attention to various forms of hunting and travel. By May 1995, I developed a cluster

Table 2 (*concluded*).

Group formation during search	Approach or capture behaviour	Type of vegetation during search or travel	Use of high or low ground (relative to 15 m diameter around individual)
Usually alone, but no fixed formation if with others. Leader tends to change while individuals wander off-course while hunting in local areas, unless pups are following parent	Vole: pounce and head shake. Other prey: digging; short rush, and head-thrust	Vole: mostly moderate height and density. May travel across short vegetation to patches of taller denser vegetation where prey is sought. Digging for other prey tends to be on dirt with no vegetation	Average: no particular use of high or low ground
Usually alone, but no formation if with others	Freeze and orient to prey followed by short rush	Very short, thin vegetation	Average: no particular use of high or low ground
In line with fixed leader	Varied: walk, run, or lunge	Short, thin vegetation. Basic travel is still in short vegetation in summer, but may enter denser vegetation when searching for hiding fawns	Low: tend to follow low ground or gullies, with occasional spotting from high points
In line, usually alone or with one other coyote	Not applicable (unless catch a small prey item opportunistically during travel)	Short, thin vegetation	Usually average, but commonly travel along ridges

of traits that I could use to distinguish hunts of deer from hunts of small prey (mostly voles, *Microtus pennsylvanicus*, but also insects, eggs, and birds), hunts of ground squirrels, and travel (Table 2). These patterns were identified after I repeatedly saw coyotes capture prey using these techniques. Behaviour patterns previously described for hunts of small prey were fully applicable and used here (Bekoff 1978; Wells and Bekoff 1982), although the group's formation and the coyotes' route of travel between specific predation sequences were incorporated in these definitions to distinguish these from hunts of deer. From May 1995 to March 1996, I used the resulting behavioural definitions to identify activities of 895 coyote groups sighted on 185 days and while conducting focal observations of hunting behaviour. In this paper, data from observations of coyotes will be presented descriptively (i) to provide information that may be useful to others who are interested in identifying coyotes which are hunting deer and (ii) to identify dates on which coyotes were observed hunting or eating certain foods.

Causes and rates of deer mortality

Data on causes and rates of mortality were collected by (i) monitoring survival of tagged fawns; (ii) monitoring changes in the age structure of the population using censuses; and (iii) examining deer carcasses.

Sightings of tagged fawns

Fawns were found and caught in June of both 1994 and 1995 when they were 1–7 days old; these included 28 whitetails and 47 mule deer. Each fawn was tagged with one or two plastic ear tags, using the colour of the tags to distinguish individuals. Tagged fawns were resighted in several ways. When I conducted focal observations of individual fawns in summer or coyotes in winter, I had the opportunity to look for tagged fawns in the same area. This was especially useful for finding fawns in summer, when they spent most of their time in hiding. Censuses provided a systematic opportunity to resight tagged fawns in the study area. In three censuses conducted between July and September, 27–55% of tagged whitetail fawns and 38–74% of tagged mule deer fawns were sighted. In four censuses conducted between October and March, 62–72% of tagged whitetail fawns and 74–93% of tagged mule deer fawns were seen. The median date on which fawns were first resighted was 11 days after capture for mule deer and 14 days for whitetails. In early summer (capture to the end of July), tagged mule deer fawns were seen every 11 days on average, and whitetail fawns every 8.5 days. Sightings were more frequent in other seasons; for example, individual fawns of both species were seen on average every 6 days in winter.

Comprehensive searches both inside and outside the study area were made for fawns that had not yet been seen during a particular

month at the middle and end of the month. At most times of the year, I was able to observe tagged fawns frequently and long enough to know whether their mother was alive, whether they were nursing or part of a social group, and whether they had any obvious signs of poor health. I attempted to find physical markings in order to recognize mothers, twins, or common associates of tagged fawns. By the end of summer, I could recognize associates of 50% of tagged whitetails and 59% of mule deer born in 1994, and 44% of whitetails and 100% of mule deer born in 1995. I could generally find a specific fawn on a given day if I set out to look for it any time after mid-July. There were a few times when it was difficult to identify the probable cause of disappearance or death. Fawns were difficult to monitor during the first month of life because of the initial lag in resighting them and because they spent most of their time hiding in vegetation. Fawns were also difficult to monitor if they moved outside the ranch during a seasonal shift in range, which primarily occurred in autumn.

A fawn that disappeared was presumed to have died if (i) the fawn had been relocated regularly until its disappearance; (ii) the fawn's disappearance did not coincide with range shifts made by other deer; (iii) I found and examined, on several occasions, several groups of deer in the area which the fawn inhabited and in areas where it seemed that the fawn could possibly have moved to; and (iv) the fawn had recognizable family members or associates that were located on several occasions without the fawn.

The disappearance of a fawn was attributed to one of the following causes, each listed with its associated observations. (1) *Coyote predation*: either predation was observed or a carcass was found with clear signs of a kill having been made (e.g., coyote and deer tracks merging with their tracks leading to a carcass; fur and blood found away from the carcass, indicating that contact between coyotes and deer occurred prior to death; or puncture wounds on the carcass). (2) *Probable coyote predation*: a fawn was seen regularly with no obvious signs of poor health before its disappearance and there was no other likely cause, such as a human hunter or a seasonal range shift; mother, twin, or associates were still seen after the fawn disappeared; if the fawn had no known associates, many deer still occupied areas previously used by the fawn. (3) *Death from unknown cause*: fawn exhibited slightly unusual behaviour (e.g., failure to travel with mother and twin) prior to its disappearance and may have died from poor health, an accident, or predation; mother, twin, or associates were still seen after the fawn disappeared. (4) *Early death from unknown cause*: fawn was never resighted or only seen during the first week, so it may have been abandoned, died from an early health problem, or been killed by coyotes. (5) *Hunting*: fawn was reported shot by hunters. (6) *Coyote predation or hunting*: fawn was healthy before it disappeared, was known to move into hunted areas in November, and disappeared during the time of the November hunt; mother, twin, or associates were still seen after the fawn disappeared. (7) *Disappearance from unknown cause; dead or range shift*: fawn disappeared at a time when range shifts were occurring and the fawn had moved toward the northern edge of the ranch before it disappeared (animals generally moved north of the ranch when they shifted their range). (8) *Range shift*: fawn was seen moving through and beyond the study area; fawn was resighted periodically outside the study area; or fawn left the study area in winter but returned in spring.

To avoid a bias against survivors (White and Garrott 1990), fawns that moved outside the study area where they could not be relocated regularly were excluded from the base number of tagged fawns entering that season as of the season they moved, even if they returned the following summer.

Age-structure data obtained from censuses

Data on the age structure of the whitetail and mule deer populations were obtained from censuses and used to assess trends in fawn mortality. During a census, I drove or walked along a 12-km

route, stopping at certain vantage points to search for deer, and I traveled in the reverse direction on alternate censuses. I attempted to sight and record all deer in the study area during a census. This required 2 days in many cases, because censuses took about 12 h in winter and 18 h in summer when animals were in a larger number of smaller groups. To lessen the possibility of censusing the same animal more than once in winter censuses, I covered the predominantly mule deer area on one day and the predominantly whitetail area on the other. In summer, when the distributions of whitetails and mule deer had considerable overlap, I covered the Milk River Ridge slope system on one day and the North Pothole Creek river valley on the other because there was relatively little movement between these areas. There were few obstructions to my view in winter, so the number of deer sighted was considered a reliable indication of the number present. In contrast, vegetation was lush enough to conceal most fawns and many adults between June and September. Censuses were conducted biweekly from June 1994 to July 1995 (once per week during the June fawning and the November–December breeding periods). From July 1995 to June 1996, censuses were conducted at the start and end of seasons.

Data recorded for each group included the following: species, group size, group composition, whether all animals were assuredly seen, location (Universal Transverse Mercator coordinates), and other social and habitat traits. Juveniles were distinguished from adults until June of the year after they were born. I was not able to classify all individuals during censuses. Groups having over 20% of individuals of unknown age or sex were excluded from calculations of age structure. I excluded all members of these groups from the analysis to avoid biasing results toward a larger number of easily recognizable individuals, e.g., males with large antlers. Nevertheless, I accepted groups with 20% unclassified individuals in the results in case the age structure of larger groups, which seemed more likely to have unclassified deer, differed from that of smaller groups.

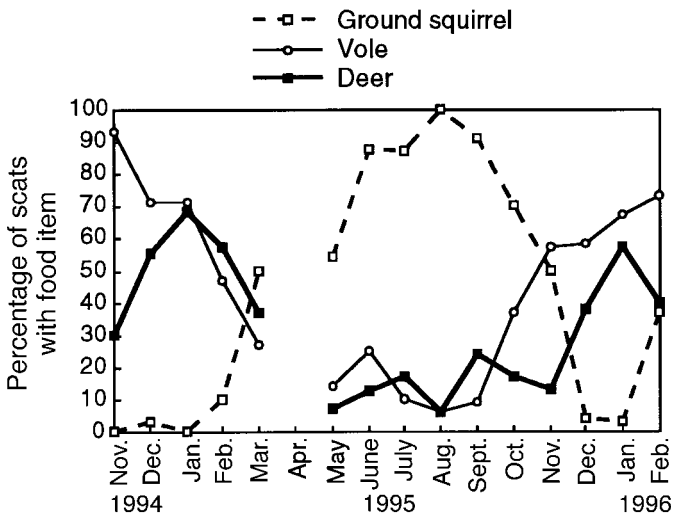
The ratio of juveniles to adult females (≥ 1 year) was calculated for censuses conducted between October 1994 and early February 1995 and for censuses from the following year. I found it difficult to distinguish adult females from males between mid-February and the end of March 1995. Therefore, I also calculated the ratio of juveniles to all adults in 1994 so that a value could be obtained for the end of winter. The effects of factors that can affect age ratios, including female productivity, movement, and adult mortality (Caughley 1974), were considered before drawing conclusions about fawn mortality from these data.

Examination of carcasses

Carcasses were examined to identify the species, age, and apparent cause of death for these deer. I used fresh carcasses (estimated <24 h) that were spotted from the main trails in winter. Most were found by seeing coyotes kill or eat a deer. On the desiccated vegetation or snow present in winter, it was relatively easy to determine whether coyotes had killed the deer. Signs of predation included bite wounds, blood and fur where contact was made prior to death, and tracks showing the animals' paths merging and leading to the kill site.

It was more difficult to find fresh carcasses from the main trails in summer than in winter, because of the denser vegetation and shorter time required for coyotes to consume the smaller fawns. I identified the species, age, and apparent cause of death for all carcasses found, not just fresh ones, at this time of year. This method seemed an acceptable method of comparing numbers of carcasses for the two species in summer, because whitetails and mule deer use the same general habitat during the fawning season (Fig. 1a), and I divided my observation time relatively equally between the two species. Inclusion of older carcasses meant that the cause of death was less obvious for carcasses found in summer.

Fig. 2. Percentages of coyote scats containing ground squirrel, vole, and deer. Scats were not collected in April. There was a significant negative correlation between ground squirrel and deer ($r_s = -0.768$, $n = 15$, $P = 0.004$) and between ground squirrel and vole ($r_s = -0.903$, $n = 15$, $P = 0.0007$).



Density of deer

The density of deer, particularly fawns, was calculated to determine whether the relative abundance of white-tail and mule deer carcasses was explained by the relative abundance of each species. To estimate density in the winter of 1994, I first calculated the average number of deer seen during censuses for each month (December, January, and February) and then used these three values to calculate an average population size for the whole winter. For the winter of 1995, I averaged the prewinter (1 December 1995) and late-winter (1 February 1996) results. To estimate the density of fawns in winter, I used the proportion of fawns among deer that I was able to classify by age to calculate the number of fawns among all deer that were counted during a census. This method assumes that the proportion of fawns in the classified and unclassified populations was the same. As in the procedure used for estimating density of all deer in winter 1994, I obtained an average number of fawns for each month before calculating an average for the entire winter.

The relative density of whitetail and mule deer fawns at the start of the summer of 1995 was estimated using data on tagged fawns. I first calculated the mean proportion of fawns that were tagged of fawns counted during three summer censuses. I then divided the number of fawns that were originally tagged by this proportion to estimate the number of fawns originally present in the study area after fawning. This method assumes that tagged and untagged fawns within each species died or otherwise disappeared at the same rate. Too few whitetails were tagged in 1994 for this method to be used to estimate the original number of whitetail fawns.

Statistical tests

Nonparametric statistical tests (following Siegel and Castellan 1988; Sokal and Rohlf 1995) were used because data involved frequencies or were not distributed normally. Spearman's rank-order correlation coefficient was used to test for a relationship between the occurrence of different prey items in coyote scats. G tests with Williams' correction and Fisher's exact test were used to analyze frequency data, including mortality rates, age ratios from censuses, and the relative abundance of whitetail and mule deer carcasses

from different seasons. A binomial test was used to test whether juveniles were more abundant among carcasses found in the winter of 1995 than was expected from their availability in the population. Age ratios from the two winter 1995 censuses were used to calculate the expected probability that each carcass was a juvenile if coyotes captured individuals from different age groups at random. Probabilities given in the Results are two-tailed.

Results

Coyote feeding habits

Scat results

Coyotes relied on three main foods: ground squirrel, vole, and deer. Together these composed 87% of all animal food items ($n = 460$) and 93% of major animal food items ($n = 326$) found in 333 scats over 1 year, between March 1995 and February 1996. Ground squirrel composed 43%, vole 25%, and deer 20% of all food items (56, 20, and 17% of major items, respectively). The use of other foods was minor or restricted to short seasons. The next most common animal food was cattle by-products or cow (*Bos taurus*), constituting 4% of all and major food items. These were primarily consumed during the calving season (in 29% of May scats), when coyotes scavenged by-products of birth such as placentas, or consumed calves that appeared to die of non-predatory causes (R. Thrall, III, personal communication), but cow carrion was also an important food item for a short time in autumn (in 10% of October and November scats).

Deer were consumed in all months, but composed the largest part of the coyotes' diet in winter. Deer was found in 15% of scats during the postparturition period, June and July, but in 55% of scats in December and January. The amount of deer increased once the last of the ground squirrels hibernated in November and decreased once the first of the ground squirrels emerged in mid-February (Fig. 2). The relationship between these prey items was reflected in a strong negative correlation between the amount of ground squirrel and deer in scats ($r_s = -0.768$, $n = 15$, $P = 0.004$). Use of vole by coyotes followed a similar pattern to their use of deer: there was a strong and significant inverse correlation between the amount of ground squirrel and vole in scats ($r_s = -0.903$, $n = 15$, $P = 0.0007$).

Coyote foraging behaviour and identification of deer hunts

Observations of coyote feeding behaviour corresponded well to results obtained from scats. Coyote hunts of ground squirrels were last seen on 10 November 1995. The first ground squirrel hunts of 1996 were observed on 14 February, after which they were seen daily. Deer hunts were observed from June to March, but most frequently in July and in winter (23 hunts between June and September, with 16 of those in July, but coyotes were observed less in June; 11 hunts in October and November; 49 hunts between 1 December and 28 February). The daytime schedule of deer hunting varied seasonally. Eighty-three percent of 23 summer hunts and 63% of 11 autumn hunts were observed shortly after dawn (before 08:00 in summer and 09:00 in autumn) or late in the evening (after 19:00 in summer and 16:00 in autumn). Nine percent of both summer and autumn hunts were observed during the midday period (10:00–17:00 in summer and 11:00–14:00 in autumn). In contrast, the

Table 3. Causes of disappearance and mortality of tagged fawns.

Group ^a	No. tagged ^b	No. disappeared ^c	Early (abandoned, health, or coyote)	Coyote or probable coyote predation	Hunt	Coyote or hunt	Unknown death (health, coyote)	Unknown disappearance (dead or shifted range)	Shifted range
Whitetails									
1994	11	10	1	2	3	1	0	2	1
1995	17	12	3	7	0	0	0	0	2
Total	28	22	4	9	3	1	0	2	3
Mule deer									
1994	23	22	1	18	0	0	2	0	1
1995	24	18	1	16	1	0	0	0	0
Total	47	40	2	34	1	0	2	0	1

^aThe year is that in which the fawns were born.

^bNumber of fawns that were tagged originally.

^cNumber of fawns that disappeared during the first year of life, either from death or a shift in range.

largest proportion of winter hunts were observed at midday (55% of 49 hunts started between 11:00 and 14:00), and only 6% of winter hunts were crepuscular (before 09:00 or after 16:00). Differences in the timing of hunts were not explained by variation in the time of observations. In summer, 30% of observation time was during the crepuscular periods and 37% was at midday. In winter, 39% was during the crepuscular periods and 24% was at midday.

I observed coyotes using two other food sources in autumn, when ground squirrels became scarce. From 20 October to 20 November 1995, coyotes ate and fully consumed four cow carcasses that had lain untouched since June. This was reflected in the increase of cow in their scats in October and November. Coyotes were never seen attempting to capture cows or calves (personal observation). There was also a limited amount of deer carrion from the November human hunt held outside the ranch. An adult male whitetail died or was killed by coyotes a few days after being severely wounded by a human hunter and was consumed by coyotes; at least two other adults had serious limb injuries from hunting and may have died over the next few months.

The most common method by which coyotes hunted deer in both summer and winter was termed a continuous group hunt (see Methods and Table 2). In a continuous group hunt, coyotes traveled at a fast walk, with group members in line with 5–30 m between them, following a leader who usually remained the same for the hunt duration. Packs used the same in-line formation and traveled at a fast walk for most of their time in summer hunts, although individuals also spread out as they searched for fawns. Some searched for fawns in dense vegetation, while others looked from vantage points. Coyotes followed low ground by traveling along gullies or otherwise used barriers that restricted their visibility when they traveled toward areas where they hunted deer.

In winter, packs that hunted deer had 4.4 ± 1.3 coyotes (mean \pm SD, $n = 44$ hunts) and typically traveled in a loop or went one way, at times returning near their previous starting point on a later hunt. During one hunt, coyotes traveled 2.5 ± 1.3 km in 54 ± 23 min ($n = 15$ complete hunts) while they searched for deer (distance and time spent chasing deer are excluded). In summer 1995, 4.7 ± 1.3 adult coyotes were observed in 16 group hunts, traveling 1.7 ± 1.0 km in $29 \pm$

18 min ($n = 6$ complete hunts) while searching for fawns, with additional travel from a den to the fawning area or while they attacked deer.

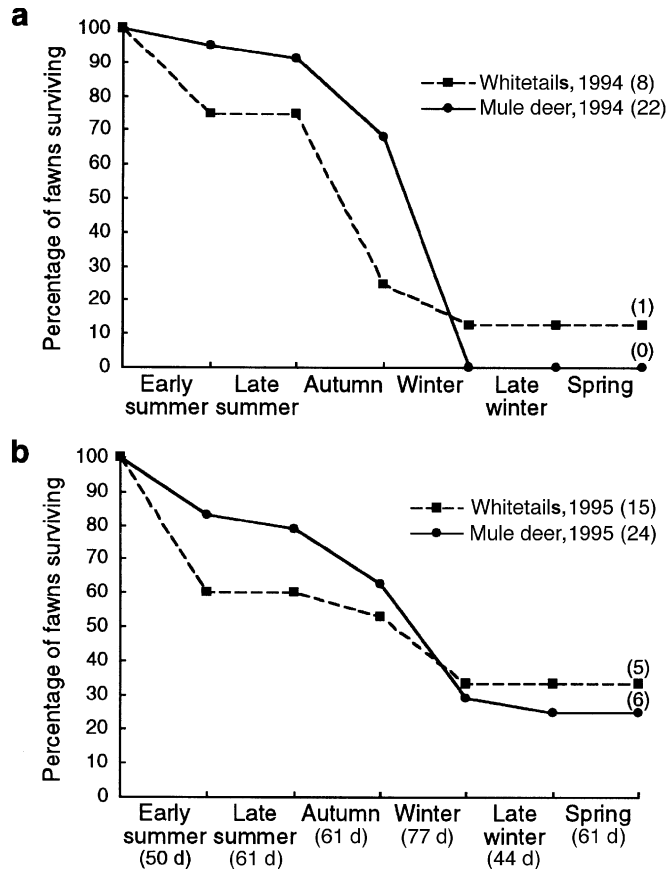
Prior to a hunt, coyotes usually engaged in a social rally, as has been described for other social predators, which included group howls and socializing. Some howls were made over an hour before a hunt and appeared to attract other individuals to the group. At other times, howls were made immediately before coyotes set out to hunt. Adult coyotes met at dens on summer evenings before embarking on hunts. Parents, both male and female, participated in hunts, but pups of the year were left at the den when coyotes hunted deer in summer.

Causes of mortality of whitetail and mule deer fawns

Coyote predation appeared to be the main proximate cause of mortality for tagged mule deer in both years and for tagged whitetails in 1995 (Table 3). Coyote predation appeared to cause 86–100% of 21 disappearances of mule deer born in 1994 and 89–94% of 18 disappearances of mule deer born in 1995 (Table 3, excluding fawns that shifted their range). Predation appeared to result in 22–67% of nine disappearances of whitetails born in 1994 and 70–100% of 10 disappearances of whitetails born in 1995.

Although only three cases of predation of tagged fawns were witnessed, there was overwhelming circumstantial evidence that most died from coyote predation. These fawns disappeared at times when coyotes were seen hunting and killing deer and not at times when range shifts were observed. These fawns were resighted regularly until they disappeared and showed no obvious signs of poor health, weight loss, or unusual behaviour. In many cases, I continued to see their mothers, twins, or common associates, and in all cases I found several groups of conspecifics in areas previously occupied by the fawn. The two mule deer categorized as “unknown cause of death” exhibited slightly unusual behaviour before they disappeared. One appeared to have been orphaned about 3 weeks before he disappeared at 3 months of age. Another 5-month-old juvenile was alternately observed with, and then absent from, her family group during the month prior to her disappearance. Although neither of these fawns showed signs of poor health, the dif-

Fig. 3. Percentages of tagged fawns alive at end of each season. (a) Fawns born in 1994. (b) Fawns born in 1995. Numbers at the right-hand end of curves show the number of fawns that survived to 1 year of age. Fawns known or suspected to have left the study area (one mule deer and three whitetails in 1994) were excluded for all seasons. In the text, these fawns were only excluded as of the season when they disappeared.



ference in behaviour could possibly reflect, or have led to, a deterioration in their condition and their dying from something other than coyote predation. On the other hand, these differences in behaviour could also have made these fawns more susceptible to coyote predation.

Human hunting was a major source of mortality for tagged whitetails, but not mule deer, in 1994 (Table 3). This resulted in at least 33% of the annual mortality of tagged whitetails in 1994 and possibly another 33%, since three other fawns were spotted prior to 2 weekends of hunting but not afterwards (Table 3; one was listed as "coyote or hunt," two as "dead or shifted range"). Whereas all of the 8 tagged whitetails that survived until November moved outside the ranch for at least part of the day, which exposed them to the hunt, only 2 of 19 mule deer appeared to do this (S. Lingle, unpublished data). Fewer tagged fawns ranged outside the ranch in 1995, so few were shot by hunters.

An investigation of fresh carcasses similarly indicated that most mortality inside the study area and most consumption of deer by coyotes resulted from coyote predation. Between October and the end of February in the 2 years, 23 fresh carcasses were found and 22 of these appeared to have been

killed by coyotes. I saw nine of these animals being captured, and the other carcasses had visible wounds or signs of struggle nearby. The last carcass was that of the male whitetail that was wounded by a human hunter. I found two fresh carcasses of adult female mule deer outside the study area that had no signs of having been injured by coyotes. Coyotes did not begin eating one of these carcasses for 3 weeks and had not started to eat the other after 3 months.

Eighteen carcasses of fawns were found during the two summers after observing six predations, seeing coyotes eating, searching near a den, or searching for fawns to tag. Fourteen of these were associated with coyotes, and the remaining 4 had been partially consumed by a large animal, which was probably a coyote, given the extent of damage (e.g., broken spine, limbs broken, head separated from backbone). Nonetheless, the cause of death was less obvious in summer than in winter. Carcasses were generally not as fresh, they were small and quickly consumed, and tall grass and an absence of snow meant that it was harder to find signs of events which had occurred before the death. Only one carcass found in summer, that of an adult female mule deer, appeared to be unrelated to coyote predation and was not consumed for at least 3 months.

Mortality rates

Data on seasonal and annual mortality rates of whitetail and mule deer fawns were obtained from three sources: sightings of tagged fawns, censuses, and examination of fresh carcasses. Results obtained using each method are presented as follows and then compared in the Discussion to see whether they are consistent, because each method has limitations.

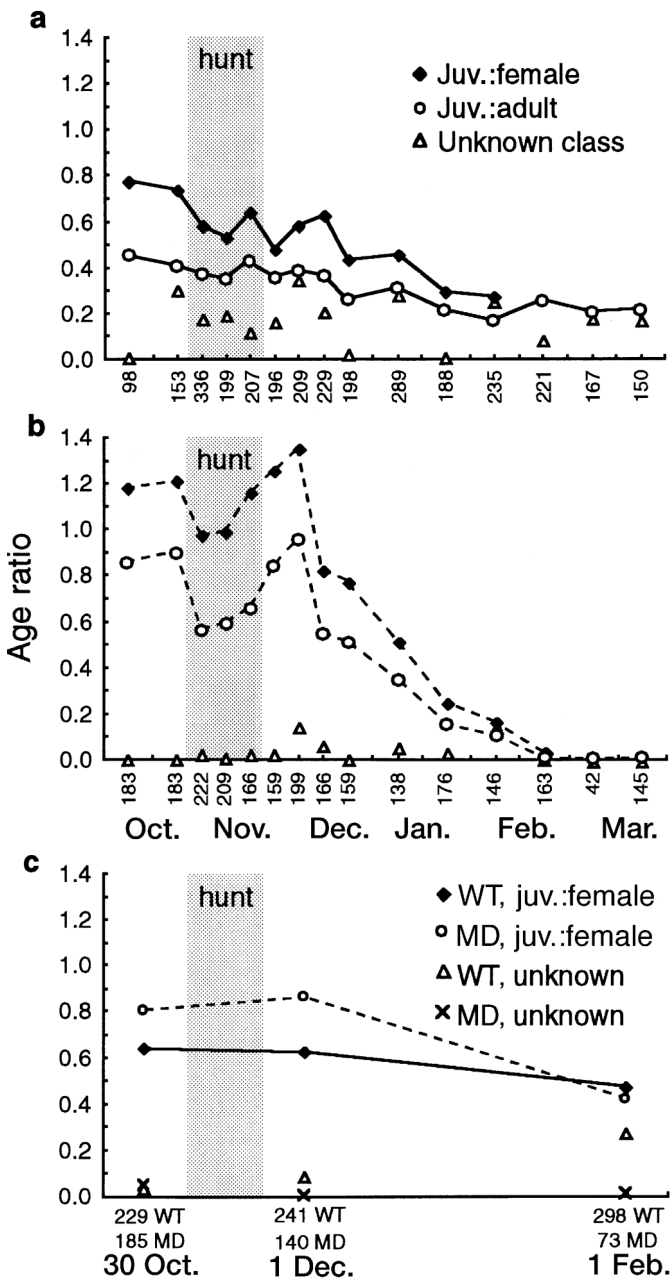
Seasonal and annual mortality rates based on sightings of tagged fawns

The small sample of tagged fawns did not justify statistical comparison of mortality rates among all six seasons. Basic trends were examined visually (Fig. 3), and mortality rates of whitetail and mule deer fawns were compared for seasons in which coyote predation was a major source of mortality. In particular, I compared the mortality rate of the youngest fawns in early summer with that of fawns in their first winter. Except when specified otherwise (i.e., mortality in autumn due to human hunters), the primary cause of whitetail and mule deer mortality seemed to be coyote predation.

Summer: Compared with their mortality rates in other seasons, whitetail fawns had moderately high mortality rates in early summer, when they were less than 8 weeks old, with 18% of 11 dying in early summer 1994 and 35% of 17 in 1995 (Fig. 3). Mule deer had relatively low mortality rates in early summer, with 4% of 23 dying in 1994 and 17% of 24 in 1995. The difference between the species approached significance (both years combined, $G = 3.65$, $df = 1$, $P = 0.06$). Mortality rates seemed to be low for whitetails, as well as for mule deer in late summer; however, additional data are needed to compare mortality rates in early and late summer more precisely (Fig. 3).

Autumn: In 1994, the highest mortality rate for tagged whitetail fawns occurred in autumn. Five to seven of nine tagged whitetail fawns died in autumn, and between three

Fig. 4. Changes in the age structure of whitetail (WT) and mule deer (MD) populations from autumn to late winter, as indicated by the juvenile:female and juvenile:adult ratios obtained during censuses. (a) Whitetails in 1994. (b) Mule deer in 1994. (c) Both species in 1995. The number of deer counted within the study area in each census is shown on the x axis. The apparent sharp decline in mule deer numbers on certain dates (b, 42 in March; c, 73 on 1 February) was only due to daily variations in range use. Additional deer spotted immediately outside the study area were censused on those days, resulting in a population size similar to that on other dates with an age structure similar to that of the sample found within the study area. A few concurrent events during the hunt may have contributed to vacillations in the age ratios, including the immigration of deer to the study area following the onset of hunting and greater adult mortality at this time.



and six of these were killed by humans during 12 days of hunting in November. In contrast with 1994, no tagged whitetails were shot in 1995 and only one of nine died from probable coyote predation in autumn. For tagged mule deer, 25% of 20 fawns died in autumn 1994 and 21% of 19 in 1995, suggesting an increase in mortality from late summer. All but one of these deaths were attributed to coyote predation.

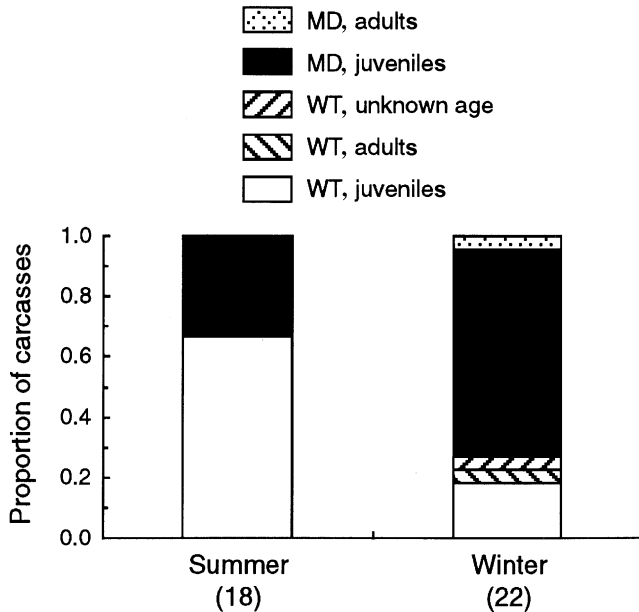
Winter through spring: Only one tagged whitetail fawn survived beyond autumn in 1994, so mortality rates for subsequent seasons of that year could not be calculated for tagged fawns of that species. The following year, the mortality rate for tagged whitetails was moderately high in winter and similar to that seen in early summer (37% of 8 fawns in winter vs. 35% of 17 in early summer; Fisher's exact test, $P > 0.99$). In contrast, mule deer fawns had particularly high mortality rates in both winters (Fig. 3). All 15 tagged mule deer fawns died in winter 1994, 53% of 15 died in 1995, and 86–100% of these deaths were due to coyote predation. The proportion of mule deer dying in winter was significantly higher than that in early summer for both years (1994, $G = 41.69$, $df = 1$, $P < 0.0001$; 1995, $G = 5.51$, $df = 1$, $P = 0.02$). The mortality rate following winter appeared low for both species. Among the five tagged whitetails and seven tagged mule deer fawns that survived to mid-February 1996, only one mule deer fawn died before the following June (Fig. 3).

Annual mortality: None of the 22 tagged mule deer fawns and only 1 of 10 tagged whitetail fawns born in 1994 survived to 1 year of age (excluding fawns that shifted range). The survival rate was better for fawns born in 1995, with 25% of 24 mule deer and 33% of 15 whitetails surviving to 1 year. This was a significant improvement for mule deer but not for whitetails, although this may be due to the small sample of tagged whitetails (mule deer, $G = 7.95$, $df = 1$, $P = 0.005$; whitetails, $G = 0.93$, $df = 1$, $P = 0.33$). The nearly absolute mortality of mule deer fawns in the winter of 1994 accounted for the difference in their annual mortality rates (0 of 15 survived the winter of 1994 versus 7 of 15 in 1995, $G = 11.03$, $df = 1$, $P = 0.0009$).

Seasonal and annual mortality patterns based on census data

Census data revealed changes in the age structure of the population that were consistent with those expected from the mortality patterns of tagged animals (Fig. 4). There were fewer juveniles in the whitetail than in the mule deer population by the end of summer 1994 and also at the end of autumn following the hunt (Figs. 4a and 4b; juvenile:adult ratio, 10 October, $G = 5.96$, $df = 1$, $P = 0.01$; 28 November, $G = 13.07$, $df = 1$, $P = 0.0003$). The juvenile:female ratio also tended to be lower for whitetails than for mule deer (10 October, $G = 2.5$, $df = 1$, $P = 0.12$; 28 November, $G = 10.3$, $df = 1$, $P = 0.001$). Over winter, the proportion of juveniles in the population declined for both species but much more steeply for mule deer (Figs. 4a and 4b). The juvenile:female ratio for mule deer dropped from 1.35 on 4 December to 0.02 on February 28, i.e., only 3 months later, with the juvenile:adult ratio similarly declining from 0.95 to 0.01. By this time, the juvenile:adult ratio was significantly lower for mule deer than for whitetails (28 February, $G = 37.51$, $df =$

Fig. 5. Species (MD, mule deer; WT, whitetail) and age (juvenile, adult, unknown) of carcasses found in summer and winter. Winter carcasses only include those that appeared to result from coyote predation. All coyote-associated carcasses found in summer are included (i.e., those from observed predations, observed being consumed by coyotes, found near a den, or with major wounds or consumption patterns typical of coyotes), even though the cause of death was less obvious during this season. Numbers in parentheses are sample sizes.



1, $P < 0.0001$). The failure to classify some individuals by age does not appear to be related to trends in age ratios (Fig. 4). The low juvenile:adult ratio for mule deer was consistent with field observations. From exhaustive searches of the study area between March and May, I knew that only one mule deer fawn with a range that straddled the study area had survived the winter of 1994. The census results for 1994 suggest that recruitment of fawns into the adult population was significantly higher for whitetails than for mule deer that year.

The direction of seasonal changes in juvenile:female ratios was the same in 1995 as in 1994 (Fig. 4c). The juvenile:female ratio was 0.64 for whitetails and 0.80 for mule deer following summer. Ratios then declined from 0.63 following the hunt to 0.47 over winter for whitetails, but from 0.86 to 0.44 for mule deer. The magnitude of these changes was muted compared with those in 1994, and the juvenile:female ratios did not differ significantly between the species at any season (before the hunt, October 30, $G = 0.99$, $df = 1$, $P = 0.32$; after the hunt, 1 December, $G = 1.62$, $df = 1$, $P = 0.20$; late winter, 1 February, $G = 0.13$, $df = 1$, $P = 0.72$). Nonetheless, it is important to note that the juvenile:female ratio for mule deer decreased by 0.44 over winter, while that for whitetails only declined by 0.16; statistical tests compare the juvenile:female ratios on a particular date rather than the rate of change. Fawn:doe ratios for whitetails and mule deer probably differed more by the end of winter than is shown (Fig. 4c.) The last census was conducted on 1 February 1996. Observations of coyotes and tagged fawns

indicated that fawns continued to be killed at a high rate through mid-February.

Seasonal and age-related variation in mortality rates based on carcass data

Species and age of carcasses: Whitetail carcasses were more likely to be found in summer and mule deer carcasses in winter (Fig. 5; including data for both years, $G = 6.24$, $df = 1$, $P = 0.01$). All carcasses found in summer that were associated with coyote predation were fawns. Juvenile white-tails showed a tendency to be more vulnerable than adults in the winter of 1995, which was probably not significant because of the small sample of carcasses (two-tailed binomial test: expected proportion of fawn carcasses = 0.32; $n = 5$, observed fawn carcasses = 4, $P = 0.07$). Based on carcass data, mule deer juveniles were significantly more vulnerable than adults in the winter of 1995 (binomial test: expected proportion of fawn carcasses = 0.34; $n = 9$, observed fawn carcasses = 8, $P = 0.002$).

Does the seasonal shift in numbers of whitetail and mule deer carcasses reflect their abundance? The seasonal difference in the numbers of whitetail and mule deer carcasses cannot be explained by the relative abundance of each species. Mule deer fawns appear to have been slightly more common than whitetail fawns in both summers, when more whitetail carcasses were found. During summer censuses, 1 of 4.95 mule deer fawns and 1 of 6.26 whitetail fawns that were sighted were tagged. With 24 tagged mule deer and 17 tagged whitetails, this gives a ratio of 1.12 mule deer:whitetail fawns. Mule deer seem to have been relatively more abundant than whitetails in 1994 than in 1995. Female mule deer were sighted 1.2 times more often than female whitetail in five censuses from the summer of 1995, but 1.7 times more often in seven censuses from the summer of 1994. (The ratio of female mule deer to female whitetails does not reflect differences between the absolute abundance of female whitetails and mule deer in summer because female whitetails were particularly well concealed at this time (S. Lingle, unpublished data).

Whitetails were more common in winter, when more mule deer carcasses were found (11.3 whitetails/km² and 8 mule deer/km² in 1994; 13.5 whitetails/km² and 5.3 mule deer/km² in 1995). Even though there were more mule deer fawns at the start of winter 1994 (2.7 whitetail fawns/km² and 3.6 mule deer fawns/km² in December), coyotes continued to hunt mule deer fawns disproportionately after their numbers fell far below those of whitetails. In the winter of 1994 overall, more whitetail than mule deer fawns were present in the study area (2.5 fawns/km² and 1.8 mule deer fawns/km²). Whitetail fawns were more common than mule deer fawns during all of the winter of 1995 (4.3 whitetail fawns/km² and 1.9 mule deer fawns/km²).

Discussion

Do coyotes capture the deer they eat, and if so, how?

Coyotes formed groups that embarked on regular and extended outings during which their main goal appeared to be to hunt deer. Group hunts of deer were observed in the summer, as well as in both autumn and winter. The coyotes'

behaviour during these hunts was similar in form to that described for wolves and other social canids, e.g., they socialized and howled before hunts and traveled in line while searching for prey (Estes and Goddard 1967; Mech 1970), even if the distance covered by coyotes was considerably shorter. Even though the behavioural patterns used to hunt deer were described in this paper rather than analyzed quantitatively, the description is based on 81 continuous group hunts observed in 1995, which followed additional observations of predation attempts during the previous 2 years. Several isolated examples of coyotes trying to capture deer and other ungulates have been reported previously (young fawns, MacConnell-Yount and Smith 1978; Hamlin and Schweitzer 1979; Truett 1979; Wenger 1981; older ungulates in winter, Bowen 1981; Bowyer 1987; Gese and Grothe 1995), tactics coyotes use to search for hiding pronghorn (*Antilocapra americana*) fawns have been described (Byers 1997), and researchers have identified the role of different pack members in initiating predation attempts on elk and deer (Gese and Grothe 1995). Until now there has been no evidence as to whether coyotes' attempts to capture ungulates were opportunistic events or part of continuous and regular hunts.

At this site, coyotes killed the vast majority of deer that they consumed. The seasons in which coyotes were observed hunting deer most frequently coincided with the amount of deer in their scats and with increased mortality of deer. Hunts of deer, deer mortality, and the amount of deer found in coyote scats increased once the last ground squirrels hibernated in mid-November and became less common once ground squirrels started to emerge in mid-February. There is no cause of death, other than predation, that can explain the close relationship between coyotes' use of ground squirrels and the mortality patterns of deer. If deer died from malnutrition (winter kill), mortality rates should have increased from winter into late winter, if not into spring, rather than mirror the availability of ground squirrels. Vegetation remained dormant throughout late winter (mid-February through March), and so would not have led to an improvement in the condition of deer in that season. Inspection of carcasses provided additional evidence that coyotes killed the vast majority of deer that they consumed (22 of 23 carcasses found in autumn and winter). Furthermore, deer that were known to have died from other causes were left untouched for weeks or months. Coyotes were the only non-human predator present that could have captured deer. No golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaeetus leucocephalus*), foxes (*Vulpes vulpes*), or bobcats (*Lynx rufus*) were present in the study area in early summer, when they could have posed a threat to young fawns, and no larger predators were present at any time of the year.

Adult coyotes formed packs that hunted deer in summer, when other food was abundant. This was curious, because hunting deer did not appear to be the most efficient way to obtain food at that time: ground squirrels were abundant and several adult cow carcasses were ignored even though they were close to dens and were encountered on a daily basis. These carcasses were only consumed when food became restricted in October and November after the majority of ground squirrels had hibernated.

The fawn mortality rate due to predation was especially high during the winter of 1994, which was mild with little

snow; fawn survival improved the following year despite a cold winter and more snow. There was generally no snow on the ground in the winter of 1994 and little in that of 1995 (usually <10 cm). These results indicate that coyotes can be a significant source of mortality for relatively large ungulates even in the absence of severe winters, deep or crusted snow, or animals that are obviously in poor condition.

The use of deer versus alternative prey species by coyotes

The seasonal schedule of deer hunting appeared to be directly related to the availability of ground squirrels, as discussed above. A similar inverse correlation between the consumption of ground squirrels and ungulates by coyotes was previously reported by Bowen (1981). The availability of alternative prey has also been shown to affect the extent to which coyotes hunt deer in summer elsewhere (Hamlin et al. 1984). In warmer climates, where small rodents are available year-round, deer appears to be a minor component of this predator's diet (Andrews and Boggess 1978; Bowyer 1987).

The daily schedule of deer hunting also appeared to be related to the activity of ground squirrels. Coyotes hunted deer early and late in the day in summer and autumn, when ground squirrels were available diurnally. In winter, the daytime peak of deer hunting appeared to occur at midday. (Observations were not made at night.) Alternatively, temperature could have affected the scheduling of deer hunts in a similar way: fewer hunts during the heat of day in summer and more in the warmth of the midday sun in winter, as Mech (1970) suggested in order to explain a similar seasonal pattern of hunting by wolves. Availability of ground squirrels still seems more likely than temperature to explain the rapid waning of crepuscular hunts in late November and their rapid onset in late February, because temperatures did not similarly change on these dates.

Factors underlying the seasonal variation in mortality of whitetails and mule deer due to coyote predation

All three sources of data on mortality (sightings of tagged fawns, age-structure data from censuses, and inspection of carcasses) indicate that whitetail fawns experienced higher mortality rates than did mule deer fawns in early summer, when fawns were less than 8 weeks old, and that mule deer fawns experienced higher mortality rates than whitetail fawns did in the winter, when they were 5–9 months old. Each method has its limitations. The sample of tagged fawns was relatively small, and I monitored fawns by means of intensive field observations and searches without the aid of telemetry. Mortality rates cannot be obtained directly from census data, but in some circumstances, patterns can be inferred from changes in the age structure of a population. Despite these limitations, the consistency of results from the three data sets suggests that the trends they reveal are accurate.

Tagged whitetail fawns had similar mortality rates in early summer and winter (35 and 37%, respectively, in 1995). Tagged mule deer had low mortality rates in the early summer (4% in 1994 and 17% in 1995) and significantly higher rates in winter (100% in 1994 and 53% in 1995). Changes in the age structure of censused animals indicated that the

seasonal difference in fawn mortality applied to the general population. Although species differences in female productivity, adult movements, and adult mortality can also affect age ratios, these were unlikely to be important influences during either the summer or winter. First, a difference in female productivity, either from variation in twinning rates or in the number of breeding females, is unlikely to explain why the fawn:doe ratio was 0.43 lower for whitetails at the end of the summer of 1994. Whitetails have similar or higher productivity to mule deer in this region (Wishart 1986; Mackie et al. 1998). Mothers of fawns that were tagged during this study appeared to have similar twinning rates (Lingle 1998). Second, observation of hunts and examination of carcasses indicated that coyotes killed few adults and that few adults died in either summer or winter. Finally, movement of animals, as well as most adult mortality, occurred primarily during the autumn hunt (see sample sizes in Fig. 4 indicating an influx of animals at this time). The number of adults was stable over winter.

The seasonal shift in vulnerability of the two species was also confirmed by inspecting carcasses resulting from predation: whitetail carcasses were more likely to be found in summer and mule deer carcasses in winter. The cumulative effect of these seasonal trends was lower recruitment of mule deer than whitetail fawns following the winter of 1994, but similar recruitment of fawns to populations of both species following the winter of 1995 (based on age structure).

More uncertainty surrounded the cause of death for fawns that died in the 3 weeks following birth than later in summer or in winter, because insufficient sightings had been made to assess their condition. Abandonment, health problems, or accidents may have been responsible for a few deaths, but coyote predation seems the most likely cause of death for the majority of these fawns, for several reasons. The rate of disappearance in the first 3 weeks closely resembled the rate of death for each species during the next 4 weeks, which appeared to be due to predation. Furthermore, accidental deaths, e.g., catching a leg in a radio collar, road kill, and drowning, rarely constitute more than 1–3% of total mortality (Steigers and Flinders 1980; Hamlin et al. 1984; Wood et al. 1989; Nelson and Woolf 1987), and should have been less likely to occur because radio collars and roads were not present to add to the risk. Closer monitoring of fawns in the initial days or weeks following birth is needed to determine the role of coyote predation in mortality of this age group more precisely and to compare mortality rates in early summer with those in late summer.

I was also less confident about concluding that a fawn had died or identifying the cause of death if it had disappeared in autumn. This was the season when many animals shifted from summer to winter ranges, and humans hunted deer outside the ranch. Nevertheless, hunting by humans appeared to be a major source of mortality for tagged whitetail fawns in November 1994, undoubtedly because their frequent travel outside the ranch (unpublished data) exposed them to hunting. Few tagged mule deer moved outside the ranch in 1994 and few animals of either species ranged outside the ranch in November 1995.

The seasonal shift in vulnerability of whitetail and mule deer fawns to predation cannot be explained by factors such as predator or prey abundance or the availability of alterna-

tive prey (Hamlin et al. 1984; Potvin et al. 1988; Huggard 1993a; Forbes and Theberge 1996), extrinsic factors such as climate or snow depth (Paquet 1992; Huggard 1993b), or physical characteristics of the prey (Stander and Albon 1993; Caro 1994; Creel and Creel 1995), all of which are commonly used to explain variation in predation rates. In early summer, when whitetails were most vulnerable, fawns of the two species were present in similar numbers (with more mule deer if anything) and occupied the same habitats. In winter, when mule deer suffered increased mortality, whitetail fawns were more abundant (1.4 times in 1994, 2.3 times in 1995). The two species lived in similar conditions (same alternative prey, climate, and snow depth), were exposed to the same packs of coyotes, and are similar in size and overall morphology (Eslinger 1976; Wishart 1986). Differences in mortality rates were also not due to coyotes hunting in a specific habitat occupied by only one of the deer species. Whitetail and mule deer females and fawns coexisted on slopes in summer. In winter, whitetails suffered less predation even though they had more habitat overlap with coyotes during deer hunts (Lingle 1998).

The role of physical condition in the seasonal differences between whitetail and mule deer mortality rates needs examination. It seems unlikely that the relative condition of sympatric whitetails and mule deer would differ seasonally and so lead to a shift in mortality, however, this possibility cannot be ruled out. A similar seasonal shift in mortality was reported for whitetails and mule deer in Montana (Wood et al. 1989); however, coyote predation was not believed to be a significant source of mortality (A. Wood, personal communication). In Colorado, mule deer fawns had high mortality rates in winter, both in an area where fawns died from coyote predation and in an area where they died from malnutrition (White et al. 1987). Nonetheless, it seems reasonable that physical condition may have affected annual variation in susceptibility to predation (Unsworth et al. 1999), but less likely to result in interspecific variation in the timing of mortality.

The most plausible explanation for the species difference in vulnerability is that the conspicuously different antipredator behaviour of whitetails and mule deer leads to the seasonal shift in their vulnerability to predation. Mule deer, but not whitetails, aggressively defend their young and other adults against coyotes in winter, whereas whitetails simply flee without direct assistance from conspecifics (Lingle 1998). If whitetail mothers fail to defend their fawns against coyotes as effectively as do mule deer in summer, whitetail fawns could be more vulnerable in their first 8 weeks of life, when they are too young to outrun coyotes. The development of flight speed should matter less to mule deer, which rely on social defenses rather than flight to evade coyotes, even in winter. The antipredator defenses used by these species in summer and the effectiveness of whitetail and mule deer defenses in both seasons need to be examined to test the hypothesis that interspecific variation in prey defenses leads to seasonal variation in their mortality rates.

Acknowledgements

I am grateful to the Thrall family and employees of the McIntyre Ranching Company for the opportunity to conduct

fieldwork at their ranch. I thank Ralph and Rae Ann Thrall, Leo and Loreen Beauchamp, Brooke Culley, Pat Schad, Duane Spitzer, Sam Stahl, and other employees of the McIntyre Ranching Company for logistical assistance during the fieldwork, and all the families at the ranch for their hospitality. Financial support was primarily provided by a Challenge Grant in Biodiversity, funded by the Alberta Conservation Association and administered by the University of Alberta. Gary Haas of Big Sky Laboratory in Florence, Mont., identified food items in coyote scats. I thank Cathy Bellerive, Michele Gruninger, Chris Kirchner, Garth Mowat, Sheila Rambousek, Paula Rodriguez, and Finbarr Wilson for assistance in the field or with data analysis or illustrations. I am also grateful for the help of several employees from Alberta Fish and Wildlife, including Ron Bjorge, Gary Erickson, Leo Gudmondson, Bob McClymont, Ron Sears, Garry Shmorong, and Bill Wishart. Tim Clutton-Brock, Franck Courchamp, Hans Kruuk, and two anonymous reviewers made useful comments on drafts of this paper.

References

- Adams, L.G., Singer, F.J., and Dale, B.W. 1995. Caribou calf mortality in Denali National Park, Alaska. *J. Wildl. Manage.* **59**: 584–594.
- Andrews, R.D., and Boggess, E.K. 1978. Ecology of coyotes in Iowa. In *Coyotes: biology, behavior and management*. Edited by M. Bekoff. Academic Press, New York. pp. 249–265.
- Anthony, R.G., and Smith, N.S. 1977. Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. *Ecol. Monogr.* **47**: 451–461.
- Ballard, W.B., Whitman, J.S., and Reed, D.J. 1991. Population dynamics of moose in southcentral Alaska. *Wildl. Monogr.* **114**: 1–49.
- Barrett, M.W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. *J. Wildl. Manage.* **48**: 542–550.
- Bekoff, M. 1978. Behavioral development in coyotes and eastern coyotes. In *coyotes: biology, behavior and management*. Edited by M. Bekoff. Academic Press, New York. pp. 249–265.
- Bekoff, M., and Wells, M.C. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use, and resource defense. *Z. Tierpsychol.* **60**: 281–305.
- Bekoff, M., and Wells, M.C. 1986. Social ecology and behavior of coyotes. *Adv. Study Behav.* **16**: 251–338.
- Bowen, W.D. 1981. Variation in coyote social organization: the influence of prey size. *Can. J. Zool.* **59**: 639–652.
- Bowyer, R.T. 1987. Coyote group size relative to predation on mule deer. *Mammalia*, **51**: 515–526.
- Byers, J.A. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago.
- Caro, T.M. 1994. Cheetahs of the Serengeti Plains. University of Chicago Press, Chicago.
- Carroll, B.K., and Brown, D.L. 1977. Factors affecting neonatal fawn survival in south-central Texas. *J. Wildl. Manage.* **41**: 63–69.
- Caughley, G. 1974. Interpretation of age ratios. *J. Wildl. Manage.* **38**: 557–562.
- Cook, R.S., White, M., Trainer, D.O., and Glazener, W.C. 1971. Mortality of young white-tailed deer fawns in south Texas. *J. Wildl. Manage.* **35**: 47–56.
- Creel, S., and Creel, N.M. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Anim. Behav.* **50**: 1325–1339.
- Eslinger, D.H. 1976. Form, function and biological role in the locomotory apparatus of the genus *Odocoileus* in Alberta (*Mammalia: Artiodactyla*). M.Sc. thesis, University of Calgary, Calgary, Alta.
- Estes, R.D., and Goddard, J. 1967. Prey selection and hunting behavior of the African wild dog. *J. Wildl. Manage.* **31**: 52–70.
- FitzGibbon, C.D. 1990. Anti-predator strategies of immature Thomson's gazelles: hiding and the prone response. *Anim. Behav.* **40**: 846–855.
- Forbes, G.J., and Theberge, J.B. 1996. Response by wolves to prey variation in central Ontario. *Can. J. Zool.* **74**: 1511–1520.
- Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O., and Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr. No. 120*. pp. 1–59.
- Gese, E.M., and Grothe, S. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *Am. Midl. Nat.* **133**: 36–43.
- Gunson, J.R., Jalkotzy, M., Carbyn, L.N., and Row, L. 1993. Predation. In *Hoofed mammals of Alberta*. Edited by J.B. Stelfox. Lone Pine, Edmonton, Alta. pp. 69–80.
- Hamlin, K.L., and Schweitzer, L.L. 1979. Cooperation by coyote pairs attacking mule deer fawns. *J. Mammal.* **60**: 849–850.
- Hamlin, K.L., Riley, S.J., Pyrah, D., Dood, A.R., and Mackie, R.J. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *J. Wildl. Manage.* **48**: 489–499.
- Hilton, H. 1978. Systematics and ecology of the eastern coyote. In *Coyotes: biology, behavior, and management*. Edited by M. Bekoff. Academic Press, New York. pp. 210–228.
- Huggard, D.J. 1993a. Prey selectivity of wolves in Banff National Park. I. Prey species. *Can. J. Zool.* **71**: 130–139.
- Huggard, D.J. 1993b. Effect of snow depth on predation and scavenging by gray wolves. *J. Wildl. Manage.* **57**: 382–388.
- Kunkel, K.E., and Mech, L.D. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Can. J. Zool.* **72**: 1557–1565.
- Lent, P.C. 1974. Mother–infant relationships in ungulates. IUCN (Int. Union Conserv. Nat. Resour.) Publ. New Ser. Vol. 1. pp. 14–55.
- Lingle, S. 1998. Antipredator behavior, coyote predation, and habitat segregation of white-tailed deer and mule deer. Ph.D. thesis, University of Cambridge, Cambridge.
- MacConnell-Yount, E., and Smith, C. 1978. Mule deer–coyote interactions in north-central Colorado. *J. Mammal.* **59**: 422–423.
- Mackie, R.J. Pac, D.F., Hamlin, K.L., and Dusek, G.L. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Montana Fish, Wildlife, and Parks, Helena.
- Mathews, N.E., and Porter, W.F. 1988. Black bear predation of white-tailed deer neonates in the central Adirondacks. *Can. J. Zool.* **66**: 1241–1242.
- Mech, L.D. 1970. The wolf: ecology and behavior of an endangered species. Natural History Press, Garden City, N.Y.
- Nelson, T.A., and Woolf, A. 1987. Mortality of white-tailed deer fawns in southern Illinois. *J. Wildl. Manage.* **51**: 326–329.
- Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *J. Mammal.* **73**: 337–343.

- Potvin, F., Jolicoeur, H., and Huot, J. 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. *Can. J. Zool.* **66**: 1274–1279.
- Siegel, S., and Castellan, N.J., Jr. 1988. *Nonparametric statistics for the behavioral sciences*. 2nd ed. McGraw-Hill, New York.
- Singer, F.J., Harting, A., Symonds, K.K., Coughenour, M.B. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J. Wildl. Manage.* **61**: 12–25.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W.H. Freeman and Co., New York.
- Stander, P.E., and Albon, S.D. 1993. Hunting success of lions in a semi-arid environment. *Symp. Zool. Soc. Lond.* No. 65. pp. 127–143.
- Steigers, W.D., Jr., and Flinders, J.T. 1980. Mortality and movements of mule deer fawns in Washington. *J. Wildl. Manage.* **44**: 381–388.
- Stuart-Smith, A.K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M., and Ripplin, A.B. 1997. Woodland caribou relative to landscape patterns in Northeastern Alberta. *J. Wildl. Manage.* **61**: 622–633.
- Truett, J.C. 1979. Observations of coyote predation on mule deer fawns in Arizona. *J. Wildl. Manage.* **43**: 956–958.
- Unsworth, J.W., Pac. D.F., White, G.C., and Bartmann, R.M. 1999. Mule deer survival in Colorado, Idaho, and Montana. *J. Wildl. Manage.* **63**: 315–326.
- Wells, M.E., and Bekoff, M. 1982. Predation by wild coyotes: behavioral and ecological analyses. *J. Mammal.* **63**: 118–127.
- Wenger, C.R. 1981. Coyote-mule deer interaction observations in central Wyoming. *J. Wildl. Manage.* **45**: 770–772.
- White, G.C., and Garrott, R.A. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego.
- White, G.C., Garrott, R.A., Bartmann, R.M., Carpenter, L.H., and Alldredge, A.W. 1987. Survival of mule deer in northwest Colorado. *J. Wildl. Manage.* **51**: 852–859.
- Wiggers, E.P., and Beasom, S.L. 1986. Characterization of sympatric or adjacent habitats of 2 deer species in west Texas. *J. Wildl. Manage.* **50**: 129–134.
- Wishart, W.D. 1986. White-tailed deer and mule deer. *In* Alberta wildlife trophies. Alberta Fish and Game Association, Edmonton. pp. 134–143.
- Wood, A.K., Mackie, R.J., and Hamlin, K.L. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Montana Department of Fish, Wildlife, and Parks, Bozeman.