From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape

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Wild ungulates are the primary prey for wolves in North America, but livestock predation is a concern in areas where wolves and livestock overlap. Using clusters of global positioning system telemetry relocations and scat analysis, we investigated wolf diets year-round in southwestern Alberta, where seasonal cattle grazing is the predominant land use and wolf–cattle conflicts have increased in recent years. Both methods indicated a seasonal shift in wolf diets, from wild prey during the non-grazing season to cattle in the grazing season. Wolves scavenged more frequently during the non-grazing season than during the grazing season; 85% of all scavenging events occurred at ranchers' boneyards (where livestock carcasses are dumped), where wolves fed on dead livestock. Cattle represent a higher proportion of wolf diets than previously thought; we recommend the sanitary disposal of dead livestock to prevent wolves from becoming accustomed to feeding on livestock, and the development of management plans aimed at reducing predation on cattle if humans and wolves are to coexist on landscapes that are dominated by livestock ranching.

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Large carnivores have important influences on ecosystem structure and function (Ripple and Beschta 2004), but conflicts with agriculture often limit management options. Predation on livestock is a concern wherever wolves (*Canis lupus*) and livestock overlap, yet research across North America indicates that wild ungulates, not livestock, are the main prey in wolf diets (Bjorge and Gunson 1983; Fritts *et al.* 1992; Peterson and Ciucci 2003). Understanding wolf diets is particularly important in agricultural landscapes, where the response to livestock predation may be to remove entire wolf packs.

The primary period of concern regarding livestock loss is summer and early fall, when cattle (*Bos taurus*) graze freely on public land, often in high densities, with little to no monitoring (Bjorge and Gunson 1983; Gunson 1983; Fritts *et al.* 1992). Grazing season timing coincides with the wolf pup-rearing season (Figure 1); the nutritional demands of wolves are considerable during this period, due to the need to satisfy growing pups. This potentially heightens the risk of predation on cattle throughout the grazing season (Fritts *et al.* 2003). The change in the abundance of cattle within the wolf-pack territories – from an absence during the non-grazing season to high densities during the grazing season – may result in prey switching (Murdoch 1969) and a greater proportion of cattle in the diet of wolves.

Wolf diets are typically assessed by scat analysis or, more recently, field searches of clusters of global positioning system (GPS) telemetry relocations (Sand *et al.* 2005; Webb *et al.* 2008). The majority of studies on wolf kill sites have been undertaken in winter, when prey remains are easier to find, but such analyses do not account for seasonal variation in diet (Sand *et al.* 2008). Assessing wolf diets during the summer is more challenging, because small prey, such as deer (*Odocoileus* spp) fawns and elk (*Cervus elaphus*) calves, are rapidly consumed (Peterson and Ciucci 2003), and the lack of snow makes tracking wolves more difficult. Consequently, summer diets have been studied through scat analysis, although this only reveals what the wolves ate and not necessarily what they killed. In North America, most predator-compensation programs require physical evidence to indicate that the animal was killed by wolves before a livestock producer can receive compensation (Bergman and Mack 2007). The GPS-cluster method can identify prey remains for evidence of predation on cattle (Figure 2), but this method can be biased toward large-bodied prey and might not accurately reflect total wolf diet composition (Sand *et al.* 2005).

In Alberta, Canada, the highest levels of predation on cattle occurred in the southwestern corner of the province, an area that represents only 3% of Alberta's land area but accounts for 37% of all paid claims (Alberta Conservation Association unpublished data). Southwestern Alberta is a heavily ranched landscape, characterized by an abrupt change in topography where the Rocky Mountains meet the prairies; here, predation is a year-round problem for cattle producers, as wildlife habitats overlap grazing lands, so that the potential for conflict between predators and cattle is higher than elsewhere in the province.

Predation on cattle in Alberta is largely attributable to wolves, accounting for 74% of all monies paid through

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the provincial predator-compensation program between 2000 and 2010 (Table 1). Moreover, the number of claims and the amount of money paid through such claims have risen over the past decade (Table 1). Despite increasing conflicts between wolves and cattle in southwestern Alberta, no study has assessed year-round wolf diets in this region. We used GPS-cluster visits and scat analysis to test the hypothesis that an increase in cattle abundance in the grazing season results in a seasonal increase in the proportion of cattle in wolf diets.

Study area

We studied wolf diets in a 3300-km^2 area in southwestern Alberta, on the eastern slopes of the Rocky Mountains west of Pincher Creek (Figure 3). We focused on this area because wolf–cattle conflicts are highest here, and because it is a narrow region of public land that represents an important corridor between a large population of wolves in northern Canada (Gunson 1992) and the US, where wolf recovery has been ongoing since 1986 (Ream *et al.* 1989; Bangs and Fritts 1996).

Our study area was a mix of public Crown land, under the jurisdiction of the Alberta provincial government (70%), and private land (30%). Oil and gas development, forest harvesting, and recreational activities occur throughout the study area, but the predominant land use is cattle ranching. Cattle are grazed seasonally on public forest land from as early as April to mid-October (grazing season) and kept primarily on private lands the remainder of the year (non-grazing season). The majority of seasonally grazed cattle consist of cow–calf pairs and yearlings, but also includes bulls and dry cows (ie cows without calves). Widespread linear features, such as roads, trails, and seismic lines, provide access for land users.

Large-bodied prey for wolves in this area include white-tailed deer (*O virginianus*), mule deer (*O hemionus*), elk, moose (*Alces alces*), and cattle; smaller prey species include snowshoe hares (*Lepus americanus*), ground squirrels (*Urocitellus* spp), beaver (*Castor canadensis*), and other small mammals and birds.

Table 1. Compensation payments (in Canadian dollars) paid to livestock producers through Alberta's predator compensation program, 2000–2010

Year	Total compensation paid (CAN$)[a]	Compensation paid due to wolf predation on, or injury to, cattle (CAN$)[b]
2000–2001	68 128	45 321
2001–2002	78 031	48 376
2002–2003	60 561	40 274
2003–2004	91 784	66 814
2004–2005	49 179	35 555
2005–2006	95 588	78 491
2006–2007	91 577	68 281
2007–2008	118 858	86 814
2008–2009	145 925	123 857
2009–2010	144 374	110 046
Total	944 006	703 829

Notes: [a] Includes payments for death or injury to all domestic livestock (cattle, bison, sheep, swine, and goats) due to black bears, grizzly bears, wolves, cougars, and eagles. [b] Includes only payments for death and injury to cattle due to wolves.

Figure 1. *Female wolf with cubs. Grazing season is also wolf pup-rearing season, leading to wolf–cattle conflicts.*

Methods

We captured four wolves from three packs using padded-jaw leg-hold traps or helicopter netgunning (University of Alberta Animal Care Protocol #565712). We collared the captured wolves with upload-capable Lotek 7000SU GPS radiocollars set to a one-hour duty cycle (Lotek Engineering, Newmarket, Canada). We monitored these individuals from 20 June 2008 through 14 October 2009. Individual wolves wore GPS radiocollars for 118–351 consecutive days ($\bar{x}$ = 215, SE = 51.86).

GPS clusters

We downloaded GPS telemetry data from the ground every 7–10 days during the grazing season and every 2–3 weeks during the non-grazing season. Location data were plotted in ArcMap 9.2 (ESRI, Redlands, CA), and clusters were identified as any location where the wolf spent ≥ 3 hours and GPS locations were within 100 m of each other. We visited GPS-cluster sites 1–47 days ($\bar{x}$ = 12.76, SE = 0.27) after the wolves were first detected there; however, den sites were visited several weeks later.

Figure 2. *Cattle remains following predation by wolves.*

We searched clusters in cardinal directions, following methods detailed by Knopff *et al.* (2009). We assigned a "kill" status to the site if we found prey remains that closely matched the time period during which wolves were present and there was evidence that the animal had been killed by wolves (Peterson and Ciucci 2003; Webb *et al.* 2008). We examined prey remains to identify species, sex, age, and any abnormalities. Wild ungulates were aged in the field as young-of-the-year (< 1 year), yearling (>1 year but < 2 years), or adult (> 2 years) based on tooth-eruption patterns. Cattle ages were confirmed by the producer. Sites were classified as scavenge events if there was clear evidence the animal had not been killed by wolves (eg other predator kills, boneyards [where carcasses are dumped], hunter kills, and road kills).

We compared prey composition from GPS clusters between seasons using a chi-square test. We used frequency of prey detections, body mass of prey, and expected prey consumption to estimate relative biomass of each prey species in wolf diets. Using published estimates of consumable biomass (Głowaciflksi and Profus 1997; Hayes *et al.* 2000; Jedrzejewski *et al.* 2002; Sand *et al.* 2008), we assumed wolves consumed 65% of the live mass of large-bodied prey (> 100 kg), 75% of medium-bodied prey (20–100 kg), and 90% of small-bodied prey (< 20 kg). We calculated average live weights of Alberta ungulates adjusted for age and season. If the age of found prey was unknown, we used an average of all three age classes for the given season. Livestock weights were estimated by a local grazing co-op (M Roberts pers comm). Biomass of each species is expressed as a percentage of total estimated biomass consumed. Scavenging events were excluded from prey biomass calculations.

Scat

We collected scat samples opportunistically along roads, on trails, at GPS-cluster sites, and at den and resting sites known as rendezvous areas. Scats were collected, stored, and analyzed through established methods (see WebPanel 1 for details). We calculated the frequency of prey items occurring in scats and expressed these data as a percentage that represents the occurrence of each prey item relative to the total number of prey items. An "item" is defined as the occurrence of a particular prey species in the scat sample; if, for example, both deer and ground squirrel were detected in a scat sample, that sample would be said to have two prey items. We also estimated relative biomass consumed by wolves using Weaver's (1993) regression equation ($y = 0.439 + 0.008x$), which describes the mass of prey (kg) (y) consumed per collectable scat as a function of body mass of prey (kg) (x). We derived percent biomass by expressing the estimated consumed biomass of each species relative to the total biomass consumed. We adjusted prey weights to reflect the distribution of age classes found at kill sites in each season. When possible, scats were grouped by season. If it was not possible to know which season the scat was from (eg scats collected at dens and rendezvous sites visited after wolves had departed), no seasonal status was assigned and samples were used only for total diet assessment. We compared frequency of prey items in wolf scats across seasons using a chi-square test. For analysis, prey items < 10 kg were pooled due to small sample sizes. We also compared frequency of prey items across methods (GPS clusters versus scat samples) using a chi-square test.

Results

We visited 698 GPS-cluster sites (mean number of clusters/wolf = 174.5, SE = 39.94). We found 181 kill sites and 32 scavenge sites. With one exception, we found only a single prey item per kill site. Wild ungulates and cattle made up 100% of prey items found by the GPS-cluster technique, and composition of these sites varied seasonally (Figure 4, a and b). We examined 319 scats and identified 675 prey items (mean prey items/scat = 2.12, SE = 0.05). Wild ungulates and cattle accounted for 72.3% of all prey occurrences in scat, but 91.4% of the estimated relative biomass consumed (WebFigure 1).

Both methods indicated a seasonal prey shift, from wild ungulates during the non-grazing season to cattle in the grazing season (kill sites: $\chi^2_5 = 34.05$, $P < 0.001$; scats: $\chi^2_6 = 47.76$, $P < 0.001$). Cattle comprised 73.9% of the estimated biomass consumed during the grazing season (Figure 4d). GPS-cluster visits indicate scavenging was more prevalent during the non-grazing season, with 85% of these scavenging events consisting of wolf visits to ranchers' boneyards. Patterns were consistent across wolf packs.

Frequency ranking of large-bodied prey (eg cattle, deer, elk, and moose) was the same across methods in the grazing season (χ^2_3 = 3.57, 0.5 > P > 0.25), but differed across methods in the non-grazing season (χ^2_3= 9.49, P < 0.05). In the non-grazing season, deer were found most frequently at kill sites, and evidence of elk consumption was found most frequently in scat.

Discussion

Most studies of wolf diets in North America indicate that wolves primarily prey on wild ungulates (Peterson and Ciucci 2003). In our study area, however, cattle made up a larger component of wolf diet than has been reported in previous studies, especially during the livestock-grazing season; this supports our hypothesis that an increase in cattle abundance would lead to an increase in predation on cattle by wolves. During the course of our study, we identified the remains of 50 cattle at wolf kill sites from three packs, or roughly 17 cattle killed per pack per year. In contrast, the Northern Rocky Mountain Distinct Population Segment (Idaho, Montana, Wyoming, eastern one-third of Washington and Oregon, and a small part of north-central Utah) reported 192 confirmed cattle losses to 242 wolf packs in 2009 – down from 214 confirmed cattle losses to 217 wolf packs in 2008 (Sime and Bangs 2010) – or less than one head of cattle per pack.

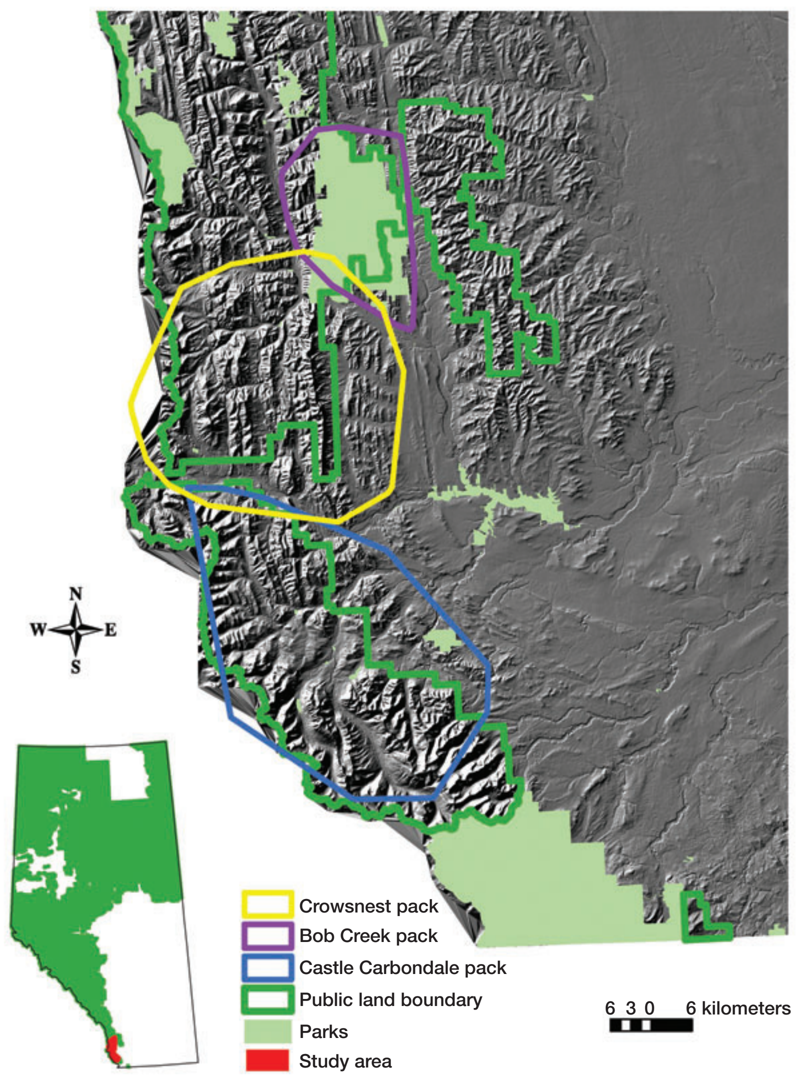

***Figure 3**. The study area (inset) and minimum convex polygons for the three wolf packs (Crowsnest, Bob Creek, and Castle Carbondale) studied in southwestern Alberta, Canada.*

To our knowledge, our study is the first to use the GPS-cluster method to assess wolf diets in a ranching landscape. This method allowed us to locate cattle that would otherwise be classified as "missing" when livestock producers removed cattle from grazing allotments at the end of the grazing season. Local producers have long suspected that missing livestock could be attributed to wolf predation, but lacked evidence to support this claim. In Alberta, the predator-compensation program pays 100% of the market value for confirmed predator kills of livestock, and 50% of the market value for "probable" kills (Bergman and Mack 2007). The program, however, no longer pays for missing animals (Gunson 1992). Missing animals are therefore a primary concern of livestock producers, because they receive no compensation payments for them (Bergman and Mack 2007). Producers occasionally received compensation for animals found by our GPS-cluster method, compensation they otherwise would not have received. Missing livestock are recognized as a problem elsewhere as well (Bangs *et al.* 1998). Nyhus *et al.* (2005) estimated that, in Wyoming, for every confirmed livestock loss due to grizzly bears (*Ursus arctos horribilis*), there was the equivalent of another two-thirds of an animal that was never located. Because wolves tend to scatter bones and other remains at some distance from a kill site (Sand *et al.* 2008), the numbers of missing cattle may be even higher, especially in areas where locating remains is difficult (eg in thick vegetation).

As expected, GPS clusters reflected a bias toward large-bodied prey, whereas scat analysis detected smaller prey items. Evidence of small prey (≤ 10 kg) occurred in wolf scat frequently but accounted for < 8% of the total estimated biomass consumed. A key worry with the GPS-cluster method is its inability to detect small prey, such as neonate ungulates (Sand *et al.* 2008; Webb *et al.* 2008). Our results, however, suggest we did not miss many young-of-the-year ungulates because there was no significant dif-

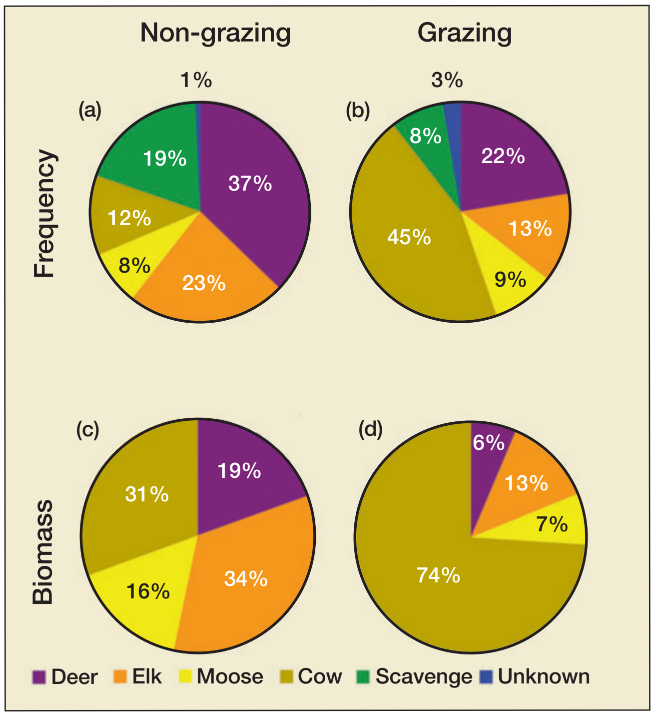

Figure 4. *Frequency and estimated relative biomass of prey items consumed by wolves, as found at GPS-cluster sites. Frequency (a, b) is expressed as a percentage of the total prey items found during the non-grazing (a:* n = *137) and grazing (b:* n = *76) seasons in southwestern Alberta (2008–2009). Percent biomass was calculated by average live weights of Alberta ungulates adjusted for age and season; non-grazing (c:* n = *110) and grazing (d:* n = *68). Scavenge events are not included in the estimated biomass.*

ference in prey occurrence between kill sites and scat analysis during the grazing season. Had we missed ungulate neonates in our GPS-cluster searches, we would have expected to see a higher proportion of deer and elk remains in scat when compared to the GPS-cluster kill sites.

Scat analysis does not provide details about wolf predation. We observed several instances of scavenging during the non-grazing season; scavenging sites made up 19% of GPS-cluster sites at which prey were found. Almost all scavenging events were on dead cattle, which increased the percent occurrence and estimated percent biomass of cattle remains in scat during the non-grazing season. The number of scavenging incidents in the grazing season was low and spread across prey species; there is therefore no reason to believe that cattle were over-represented in the scat analysis for this period.

Although both GPS-cluster data and scat analysis indicated a strong seasonal shift in wolf diets, the mechanism driving wolf prey selection remains unclear. It may be that prey selection remains constant, and the higher proportion of cattle in the wolves' diet is attributable to the increased numbers of cattle arriving in the area during the grazing season. Alternatively, the evidence of higher proportions of cattle in wolf diets could be explained by prey switching, whereby the wolves' selection of cattle as prey increases as the relative abundance of cattle increases (Murdoch 1969). Seasonal differences in prey vulnerability may also influence wolf prey selection (Lingle *et al.* 2008). We recommend further use of the GPS-cluster method because it provides information on what the wolves killed, not just what they consumed.

Wolf visits to ranchers' boneyards accounted for 85% of non-grazing-season scavenging events. These piles of dead livestock are a growing problem in southwestern Alberta, and have become even more prevalent since the detection of bovine spongiform encephalopathy (BSE, or "mad cow disease") in Canadian cattle in 2003. Prior to BSE, rendering trucks removed dead stock free of charge and used the carcasses in dog-food and cattle feed supplements. However, changes in regulations by the Canadian Food Inspection Agency (CFIA) now prohibit the inclusion of specified risk material (SRM, ie tissues capable of transmitting BSE) in livestock feed, pet food, and fertilizer (CFIA 2007). SRM must now be disposed of separately, through either burial or incineration. Rendering companies pass on the costs of dealing with these new regulations to producers; these costs are prohibitively expensive for local producers, causing many to pile up carcasses in boneyards instead. Natural disposal, in the form of wildlife scavenging from boneyards, is currently legal in Alberta and is one of five government-approved livestock-carcass disposal options (Province of Alberta 2009). All large carnivores in southwestern Alberta have been reported to scavenge from these boneyards. Ironically, the CFIA regulations designed to prevent the spread of the BSE-causing prions might actually be promoting further contamination; if the cattle carcasses in boneyards are contaminated with BSE, there is a risk that it may spread to the carnivores feeding on them (Williams and Miller 2003).

Boneyards represented an important food source for wolves during winter, and they often made repeated visits to these locations. This is especially problematic because boneyards are required to be a minimum of only 400 m from livestock facilities and residences (Province of Alberta 2009). This brings carnivores into close contact with other stock-growing activities (eg calving), which could result in further conflict between wildlife and ranchers. Bear-proof metal storage bins have been suggested as an alternative to boneyards, to reduce scavenging and prevent carnivores from becoming accustomed to feeding on livestock (Northrup 2010). Restricting access to attractants (eg carcasses, grain bins, garbage dumps, etc) is a powerful tool for both conservation and management of carnivores (eg Bino *et al.* 2010). Partnerships are being developed in Canada and the US, to assist producers in securing funding for metal storage bins (eg Blackfoot Challenge and Drywood Yarrow Conservation Partnership). These programs offer a sensible solution for preventing BSE spread (Northrup 2010).

We caution that our results are from an area of intense overlap between wolf territories and cattle grazing areas; predation on cattle is less prevalent in many other areas of western North America (eg Webb *et al.* 2008). We recommend further use of the GPS-cluster method to help identify wolf diets in ranching landscapes, particularly in areas where missing animals are a concern among cattle producers.

Wolves and other carnivores are important components of healthy ecosystems, but maintaining wolves on the landscape is largely dependent on societal values. Tolerance of carnivores diminishes as conflicts with livestock, pets, and people increase. Finding ways to reduce wolf–livestock conflicts is therefore fundamental to ensuring future coexistence between humans and wolves.

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