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Venison to beef and deviance from truth: biotelemetry for detecting seasonal wolf prey selection in Alberta

by

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For all the people, past and present, who have assisted me in achieving my goals.

ABSTRACT

An abrupt interface between mountains and prairies in southwestern Alberta means wilderness areas and carnivore populations overlap cattle grazing lands. Consequently, there is concern about the effects of large carnivores, especially wolves, on livestock. I used GPS clusters and scat samples to determine year-round wolf diets in this region. Both methods indicated a significant seasonal shift in wolf diets from wild prey during the non-grazing season to cattle in the grazing season. The GPS cluster method effectively identified wolf kills but this method relies on telemetry with high accuracy and precision. In southwestern Alberta, Argos satellite radicollars have been used extensively by wildlife managers. I compare how differences in precision between GPS and Argos technologies affect the estimation of habitat-selection models. Differences in accuracy and precision can lead to erroneous conclusions about animal selection of habitat.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

BACKGROUND

Wolves *(Canis lupus)* have long been a species of concern in Alberta. During the 1950s and 60s the threat of rabies sparked aggressive control methods including aerial gunning and use of toxicants to reduce wolf populations across Alberta (Gunson 1992). The provincial wolf population fell from more than 5,000 to only 500-1,000 by 1960 (Gunson 1992). In southern Alberta wolves were extirpated but began to reappear in the 1970s (Gunson 1992). Since then, wolf populations have rebounded. As wolf populations have increased so has concern about their effects on the wild prey base and domestic livestock both within the province and throughout western North America. Consequently, renewed cullings have reduced wolf populations in an attempt to protect both threatened ungulate herds (e.g., Valkenburg et al. 2004, Robichaud 2009) and cattle (Bjorge and Gunson 1985, Musiani et al. 2005). In southwestern Alberta, where cattle ranching is the predominant land-use, it is livestock that are most at risk.

Southwestern Alberta is characterized by a sharp interface between mountains and prairies. With only a narrow strip of foothill montane habitat, wolves and wild ungulates are crowded into close proximity, and further overlap cattle-grazing lands. This region is a unique landscape that is important for maintaining connectivity between northern and southern populations of a variety of wildlife species. Yet this narrow buffer zone between wildlife and humans means conflict between wolves and livestock is higher here than elsewhere in the province.

For at least 5 decades southwestern Alberta was free of wolves so cattle were grazed without concern of wolf depredation. As wolf populations have increased so have conflicts with livestock. In 1974 Alberta Agriculture and Alberta Fish and Wildlife initiated a cooperative program for predator compensation to resolve conflicts between wildlife and livestock producers (Bergman and Mack 2005). Since 1997 this program has been administered by the Alberta Conservation Association and is now called the Wildlife Predator Compensation Program (Pybus 2005). Livestock producers are paid 100% of the market value for confirmed kills and 50% of the market value for confirmed probable kills (Bergman and Mack 2005).

Because investigation by a Fish and Wildlife officer is required for confirmation of predator depredation, one of the greatest concerns of producers in southwestern Alberta is missing livestock (Bergman and Mack 2005). During the summer grazing season, roughly mid-May through mid-October, livestock are grazed seasonally on public forest allotments. When producers remove cattle in October they often are missing a few animals. Producers in this region have long suspected the "missing" animals were being depredated by wolves. Despite this concern, there was no diet information for wolves in this region. Wolf diets may vary substantially from one geographic region to another and comparison with diets elsewhere in the province might not be sufficient. At the request of the Fish and Wildlife Division of Alberta Sustainable Resource Development, I began a wolf research project in 2008 in southwestern Alberta (Fig. 1.1) with the primary objective of assessing year-round wolf diets in a heavily ranched landscape.

Assessing wolf diets during summer, however, is challenging due to the abundance of smaller prey such as deer fawns (*Odocoileus sp.*) and elk calves (*Cervus elaphus*), which are rapidly consumed (Ballard et al. 1997, Peterson and Ciucci 2003), and the lack of snow for tracking. Consequently, summer diets typically have been analyzed using scat analysis (e.g., Potvin and Jolicoeur 1987; Merkle et al. 2009). Scat analysis, however, only provides information on what the wolves ate, not necessarily what they killed. I needed a new method that would allow me to investigate kill sites during summer as this was the time period of greatest concern of depredation. Anderson and Lindzey (2003) pioneered the use of the GPS cluster method to identify kill sites. This method has been successfully used with both cougars and wolves (Anderson and Lindzey 2003, Sand et al. 2005, Webb et al. 2008, Knopff et al. 2009). In Chapter 2, I describe how I used this method along with scat analysis to describe wolf diets across seasons.

The GPS cluster method relies on GPS radiocollars that are able to be downloaded on demand and have high spatial accuracy and precision. However, prior to my research, Alberta Fish and Wildlife in southwestern Alberta relied almost exclusively on Argos satellite radiocollars to gather information on wolf packs in the region. The Argos system uses transmitters to send a signal to a satellite, which then sends the signal back to a receiving center on the ground where it is processed and the position of the transmitter is calculated and forwarded to the researcher (Argos 2008). Argos radiocollars have been favoured by wildlife managers in the region because they can receive daily updates without having to physically relocate the animal, thereby saving field time and travel money. Further, they can use these daily updates to provide a general idea of a given pack's location to producers in the region that have been experiencing depredations in an effort to help prevent future losses.

However, in Argos telemetry the fix rate is not user-defined and is subject to the positioning of overhead satellites. Additionally, measurement error (difference between reported and actual location) is greater with Argos technology. Precision of GPS radiocollars is generally estimated to be 22m or less (Bradshaw et al. 2007), but Argos radiocollars have precision estimates of 1.5km or less (Argos 2008). Because of these disadvantages, Argos radiocollars are not suitable for identifying clusters of activity and locating kill sites. Yet, they remain a frequently used tool in wildlife research. Measurement error, however, is rarely examined and locations obtained from radiocollars (GPS and Argos) are often taken as truth regardless of the spatial precision and accuracy associated with the device. In chapter 3, I evaluate the effect of measurement error on a commonly used habitat selection model, the resource selection function (Manly et al. 2002), and discuss differences between the 2 telemetry systems in relation to landscape heterogeneity.

My thesis is organized as 2 independent manuscripts prepared for submission to peer reviewed wildlife management journals. I intend to submit Chapter 2 to the *Journal of Wildlife Management* and Chapter 3 to the *Wildlife*

Society Bulletin. I conclude with a general summary of my work and management recommendations.

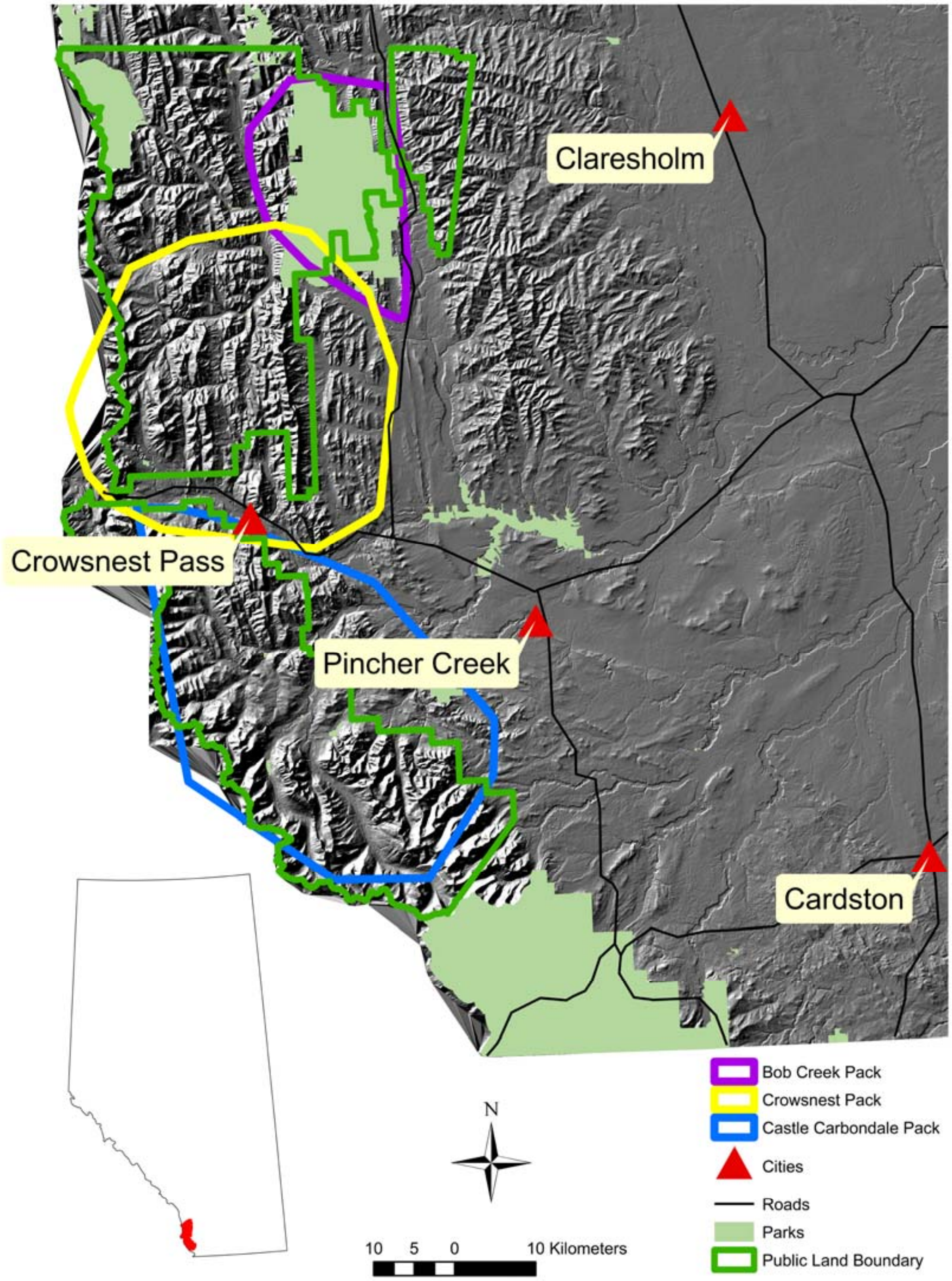

Figure 1.1. The study area and minimum convex polygons (MCP) for the 3 wolf packs studied for this research in southwestern Alberta. MCPs were estimated from GPS radiocollars (Bob Creek *n* =1, Crowsnest *n* =1, and Castle-Carbondale *n* =2)

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CHAPTER 2: FROM VENISON TO BEEF: SEASONAL CHANGES IN WOLF DIET COMPOSITION IN SOUTHWESTERN ALBERTA

INTRODUCTION

Livestock depredation 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, Chavez and Gese 2005, Merkle et al. 2009). Wolf diets have been assessed using scat analysis (Putman 1984) or, more recently, visits to clusters of Global Positioning System (GPS) telemetry relocations (Anderson and Lindzey 2003). The majority of studies on wolf kill sites have been during winter when prey remains are easier to find, but do not account for seasonal variation in diet (Sand et al. 2008). However, the primary period of concern regarding livestock loss is during summer when cattle are allowed to graze freely on public land, often with little to no monitoring (Bjorge and Gunson 1983, Gunson 1983, Fritts et al. 1992). Assessing wolf diets during summer, however, has been challenging because small prey such as deer fawns (*Odocoileus sp.*) and elk calves (*Cervus elaphus*), are rapidly consumed (Ballard et al. 1997, Peterson and Ciucci 2003), and the lack of snow for tracking. Consequently, summer diets have been analyzed using scat analysis (e.g., Potvin and Jolicoeur 1987; Merkle et al. 2009), but this only provides information on what the wolves ate, not necessarily what they killed. In North America, most predator-compensation programs require physical evidence indicating the animal was killed by wolves before a livestock producer can receive compensation (Fischer 1982, Bergman and Mack 2007). The GPS cluster method can identify prey remains that can be used as evidence in the case of a cattle depredation, but this method may be biased towards large-bodied prey and may not accurately reflect total diet composition (Sand et al. 2005, Zimmermann et al. 2007).

In Alberta, depredation is a province-wide problem, but southwestern Alberta has the highest number of depredations accounting for 37% of all paid claims on a mere 3% of Alberta's land base (Alberta Conservation Association, unpublished data). Southwestern Alberta is a ranching landscape and depredation is a year-round problem for producers in this area. This region is characterized by an abrupt change in topography where the mountains meet the prairies. As such, there is a limited buffer zone, wildlife habitats overlap grazing lands, and potential for conflict between predators and livestock is higher here than in the rest of the province.

Wolves are the biggest source of livestock depredation in Alberta. Wolf depredation of cattle accounted for 74% of all monies paid through the provincial predator compensation program from 2000 through 2010 (Table 2.1). The number of claims and money paid for such claims has increased over the past decade. In 2000-2001 the total amount paid through Alberta's predator compensation program was $68,128.14 but by 2009-2010 payments had increased to $144,374.35 (Table 2.1).

Despite increasing conflicts between wolves and cattle in southwestern Alberta, no study has assessed wolf diets in this region. Because of the growing concern of livestock depredation and the lack of information in this region of high conflict, my objectives were to: 1) document the importance of cattle in southwestern Alberta wolf diets during both grazing and non-grazing seasons; 2) evaluate southwestern Alberta wolf diets year-round using both GPS cluster visits and scat analysis; and 3) examine differences in results between the 2 methods.

STUDY AREA

I studied wolf diets in a 3,300-km^2 area in southwestern Alberta on the east slopes of the Rocky Mountains. The study area was bounded by the north boundary of Bob Creek Wildland Park to the north, Highway 2 to the east, Waterton Lakes National Park to the south, and the British Columbia border to the west. The study area was a mix of private land (30%) and Crown land (70%) under the jurisdiction of the Alberta provincial government.

Southwestern Alberta is characterized by a sharp interface between the mountains and the prairies with limited forested foothills. The primary vegetation types in the study area were conifer forest (52%), deciduous forests (7%), and grasslands (15%). In 2003, the Lost Creek fire burned approximately 200 km^2 in the southern portion of the study area (6%). Conifer forests consisted of primarily Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Deciduous species were mainly aspen (*Populus tremuloides*) and cottonwood (*P. trichocarpa*). Heavy winds, warm, dry summers, and cold winters characterized the climate. Chinook winds were common in winter months causing rapid temperature increases lasting from several hours to a few days.

Oil and gas development, forest harvesting, and recreational activities occurred throughout the study area. The predominant land-use, however, was cattle ranching. Cattle were grazed seasonally on public forest land from as early as April to mid October and cattle were kept primarily on private lands during winter months. The majority of seasonally grazed cattle were cow-calf pairs and yearlings, but bulls and dry cows were also present. Widespread linear features provided access and included roads, trails, and seismic lines.

Other large carnivores in the area included grizzly bears (*Ursus arctos*) and cougars (*Puma concolor*). Large bodied prey for wolves included white tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and cattle (*Bos taurus*). Smaller prey items available included hare (*Lepus americanus*), ground squirrels (*Spermophilus* spp.), beaver (*Castor canadensis*), and a variety of small mammals.

METHODS

I captured 4 wolves from 3 packs using padded-jaw leg-hold traps or helicopter netgunning (University of Alberta Animal Care Protocol #565712). I physically restrained wolves and collared them with upload-capable Lotek 7000SU GPS radiocollars set to a one hour duty cycle (Lotek Engineering, Newmarket, Ontario, Canada). I monitored wolves from June 20, 2008 through October 14, 2009. Individual wolves wore GPS radiocollars for a range of 118 to 351 consecutive days ($\bar{x}$ =215, SE=51.86).

GPS Clusters

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

I searched clusters in cardinal directions following Knopff et al. (2009). For clusters with a radius of ≤50m I walked transect lines along the cardinal directions out to the cluster radius, turned to the right, walked 20m, and then zigzagged back to the cluster center. For clusters with a radius ≥50m I implemented the above technique out to 50m and then searched concentric circles 5-10m apart depending on the thickness of the vegetation out to the cluster radius.

I assigned a kill status to the site if I found prey remains that closely matched the time period during which the wolves were there and there was evidence that the animal had been killed by wolves (e.g.. rumen intact, carcass disarticulated, hide not eaten, spread over several metres, tracks, signs of struggle, scat, etc.) (Elbroch 2003, Peterson and Ciucci 2003, Webb et al. 2008). I carefully examined remains to identify prey species, sex, and age, as well as any abnormalities. Wild ungulates were aged in the field as young of the year, yearling, or adult based on tooth eruption patterns. Cattle were aged with confirmation by the producer. Sites were classified as scavenge events if there was clear evidence that the animal was not killed by wolves (i.e., other predator kill, a rancher's boneyard (livestock carcass dump), hunter kill, road kill). Sites were classified as bed sites if there was no evidence of a kill or scavenging and clear evidence of a bed (i.e. dugout areas with wolf hair). Similarly dens and rendezvous sites were easily identified by abundant GPS locations and evidence of pups. If there was no clear evidence of the above activities (kill, scavenge, bed, den, or rendezvous), the site was not given a specific classification.

I compared prey composition from GPS clusters between seasons using a chi-square test. I used the frequency of prey detections, body mass of prey, and expected prey utilization to estimate relative biomass of each prey species in wolf diets. Using estimates of consumable biomass in the literature (Głowaciflksi and Profus 1997, Hayes et al. 2000, Jedrzejewski et al. 2002, Sand et al. 2008), I assumed that wolves consumed 65% of the live mass of large-bodied prey (>100kg), 75% for medium-bodied prey (20-100kg), and 90% for small-bodied prey (<20kg). I used average live weights of Alberta ungulates adjusted for age (adult, yearling, or young of year) and season (grazing or non-grazing) (Schladweiler and Stevens 1973, Reneckelr and Samuel 1991, Stelfox 1993, Cook 2002, Hudson and Haigh 2002, Schwartz 2007). If the age of the prey found was not known, I used an average of all 3 ages classes for the given season. Livestock weights were estimated by a local grazing co-op (Mike Roberts, manager of the Waldron Ranch, personal communication). Biomass of each species is expressed as a percent of total estimated biomass consumed. Scavenge events were excluded from prey biomass calculations.

Scat

I collected scat samples opportunistically along roads and trails, at GPS cluster sites, and at den and rendezvous areas. To avoid accidental collection of non-wolf scats, I only collected scats that were ≥30mm in diameter (Weaver and Fritts 1979). Scats ≤30mm were collected only if they were in the vicinity of a known den or rendezvous area or if they were accompanied by fresh wolf tracks and no evidence of coyotes (Arjo et al. 2002; Merkle et al. 2009). Scats were collected in plastic ziplock bags, labeled with date, GPS locations, and suspected pack and were frozen for later analysis. Prior to analysis, scat samples were autoclaved, washed in a sieve and dried (Reynolds and Aebischer 1991, University of Alberta Biohazard Approval). I identified mammal hairs in the scat to species by microscopic examination of the medulla and cuticular scale patterns (Moore et al. 1974, Kennedy and Carbyn 1981). White-tailed deer and mule deer were pooled due to the difficulty in distinguishing between species (Moore et al. 1974). Similarly, marten (*Martes americana*), fisher (*Martes pennanti*) and weasels (*Mustela erminea*) were pooled as mustelids; Richardson's ground squirrels (*Spermophilus richardsonii*) and Columbian ground squirrels (*Spermophilus columbianus*) were pooled as squirrels; and mice, voles, and shrews were pooled as small rodents.

I calculated the frequency of prey items occurring in the scats and express these data as a percentage that represents the occurrence of each prey item relative to the total number of prey items (Ciucci et al. 1996). I believe this measure to be more meaningful than expressing the number of prey occurrences relative to the total number of scats because it better accounts for the fact that there is often more than one prey item per scat (Ackerman et al. 1984, Spaulding 1996, Spaulding et al. 1997). 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 2 prey items. I also estimated relative biomass consumed because frequency data tend to overestimate small prey items and underestimate large prey items (Mech 1970, Floyd et al. 1978) and I believe estimated biomass to be a better representation of wolf diets.

I estimated relative biomass consumed 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). For each prey species, I multiplied y by the number of scats containing that species to estimate the biomass consumed. I derived the percent biomass by expressing the estimated consumed biomass of each species relative to the total biomass consumed. Live prey weights were the same as those used for the GPS cluster biomass calculations but also included smaller-bodied prey (Pattie and Fisher 1999). I adjusted these weights to reflect the distribution of age classes I found at kill sites in each season so that my biomass estimates would not be skewed toward adult weights if only young of the year were consumed. When possible, scats were grouped according to season (grazing vs. non-grazing). In the case that it was not possible to know with certainty which season (e.g., scats collected at dens and rendezvous sites visited after wolves had left), no seasonal status was assigned and these samples were used only for total diet assessment.

I compared frequency of prey items in wolf diets across seasons and techniques using chi-square analysis. For analysis prey items < 10kg were pooled due to small sample sizes.

RESULTS

I collected a total of 20,768 GPS telemetry relocations; fix success was high, 94.13%, thus no bias correction was necessary (Frair et al. 2004). I visited 698 GPS cluster sites (mean number of clusters/wolf = 174.5, SE = 39.94). I found 181 kill sites, 32 scavenge sites, and 299 bed sites. The remaining GPS cluster sites were dens, rendezvous sites, or areas where wolf activity could not be determined. With 1 exception, I found only 1 prey item per kill site. Ungulates and cattle made up 100% of prey items found by the GPS cluster technique and composition of these sites varied seasonally (Fig. 2.1). Wolves preyed predominately on wild ungulates during the non-grazing season and on cattle during the grazing season ($\chi^2_5 = 34.05$, $P < 0.001$). Cattle comprised 73.9% of the estimated biomass consumed during the grazing season and 30.6% during the non-grazing season (Fig. 2.2). While deer occurred more frequently than other wild ungulates, because of their small size, they represented a small amount of estimated biomass consumed in both seasons (Fig. 2.2). Scavenging was more prevalent during the non-grazing season, and 85% of these scavenging events were visits to ranchers' boneyards/rendering piles.

The age of animals found at GPS cluster sites differed significantly across seasons ($\chi^2_3 = 22.24$, $P < 0.001$) and between wild ungulates and cattle ($\chi^2_3 = 33.52$, $P < 0.001$) (Fig. 2.3). I observed that 19.2% more young of the year were killed during the grazing season than during the non-grazing season. Calves and yearling cattle were taken in approximately equal numbers (calves = 20, yearlings = 21), representing 82% of all cattle depredated; adult cattle were rarely killed by wolves.

I examined 319 scats and identified 675 prey items (mean prey items/ scat = 2.12, SE = 0.05). Wild ungulates and livestock accounted for 72.3% of all prey occurrences, but 91.4% of the estimated relative biomass consumed (Table 2.2). Data from scats also reflected a change in diet across seasons (Tables 2.3 & 2.4). The frequency of prey items and subsequently the estimated relative biomass consumed shifted from wild prey during the non-grazing season (Table 2.3) to cattle in the grazing season ($\chi^2_6 = 47.76$, P <0.001) (Table 2.4). Cattle and elk represented the majority of biomass consumed by wolves, with elk being highest during the non-grazing season at 42.6% and cattle the highest during the grazing season at 58.9% (Table 2.3 and Table 2.4). When all scats were considered, deer represented the highest percent occurrence of prey items at 25.8% whereas cattle accounted for the highest estimated relative biomass consumed at 38.7% (Table 2.2).

Ranking of large-bodied prey (cattle, deer, elk, and moose) was not different across methods during the grazing season ($\chi^2_3 = 3.57$, $0.5> P > 0.25$), but was different across methods during the non-grazing season ($\chi^2_3 = 9.49$, P <0.05). During the non-grazing season deer was the primary prey found at kill sites, and elk was the primary prey found in scat.

DISCUSSION

Most studies of wolf diets in North America indicate that wild ungulates are the primary prey of wolves (Peterson and Ciucci 2003). In my study area cattle, were a larger component of the diet than in previous studies, especially during the livestock-grazing season. During the course of monitoring I identified 50 cattle at wolf-kill sites from 3 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 wolves across 242 packs in 2009 down from 214 confirmed losses across 217 packs in 2008 (Sime and Bangs 2010), or < 1 head of cattle per pack.

My study is the first to my knowledge to use the GPS-cluster method to assess wolf diets in a ranching landscape. This method allowed me to locate cattle that would otherwise be classified as "missing" when the producer removed cattle from the grazing allotment at the end of the grazing season. 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 confirmed "probable" kills (Bergman and Mack 2007). The program, however, no longer pays for missing animals (Gunson 1992). Thus, missing animals are a main concern of livestock producers because they cannot be used to obtain compensation payments (Bergman and Mack 2007). Missing livestock are recognized to be a problem elsewhere as well (Bangs et al 1998, Oakleaf et al 2003). Nyhus et al. (2005) estimated that in Wyoming for every confirmed livestock loss due to grizzly bears there was the equivalent of another ⅔ of an animal that was never found. Because wolves tend to scatter bones and other remains from a kill, the fraction of livestock losses that are never found might be even higher, especially in areas with thick vegetation.

Data from wolf depredations on cattle in the United States indicates that wolves kill calves more frequently than other age classes, in contrast to Alberta where yearlings are the most frequently depredated age group (Stone et al. 2008). However, I found no difference in wolf depredations between livestock yearlings and calves. Cow-calf pairs and yearlings were the dominate age classes grazed in the study area and whether wolves depredated calves or yearling livestock was simply a reflection of what was grazed in a given allotment. Mature cows and bulls are less vulnerable and rarely killed by wolves.

Both the scat data and the GPS cluster data indicate a strong seasonal shift in prey composition in wolf diets. As expected, the GPS clusters reflected a bias towards large-bodied prey whereas the scat analysis detected a number of smaller prey items. Small prey (≤10 kg) occurred in wolf scat frequently but these accounted for <8% of the total estimated biomass consumed.

One of the main concerns of the GPS cluster method is its inability to detect small prey such as neonate ungulates that can be consumed very rapidly (Sand et al. 2008, Webb et al. 2008). My results, however, suggest that I am not missing a large number of young of the year ungulates because there was no significant difference in prey occurrence between kill sites and scat analysis during the grazing season. Had I missed ungulate neonates in my GPS cluster searches, I would have expected to see a higher proportion of deer and elk in the scat as compared to the GPS cluster kill sites.

However, scat analysis does not provide details about wolf predation. I observed several instances of scavenging especially during the non-grazing season when 19% of the GPS cluster sites at which prey were found were scavenging sites. Almost all scavenge events were on dead livestock which increased the percent occurrence and estimated percent biomass of cattle in scat during the non-grazing season. Researchers should use caution if transforming estimated biomass consumed into estimated number of individuals consumed if scavenging is suspected.

Of the scavenge events I detected, 85% were visits to rancher's boneyards. These piles of dead livestock are a growing problem in southwestern Alberta. Since the first detection of bovine spongiform encephalopathy (BSE, mad cow disease) in Canadian cattle in 2003 and subsequent changes in regulations by the Canadian Food Inspection Agency, producers must now obtain a permit on each occasion prior to transporting any dead livestock and local landfills must be equipped and permitted to accept dead livestock (Canadian Food Inspection Agency 2007). However, many landfills do not meet those requirements. Alternatively, producers may hire a rendering truck to dispose of livestock carcasses, but the cost of rendering trucks has greatly increased because rendering companies must now update their equipment to comply with the new regulations, and are no longer allowed to use rendered parts in feed. In southwestern Alberta this cost has doubled between 2008 and 2009 (Morehouse and Boyce 2009).

Consequently, boneyards are becoming more prevalent because they are a convenient alternative to transporting dead livestock. Boneyards are legal in Alberta provided they meet the regulations outlined by the provincial government (Province of Alberta 2009).

Boneyards represented an important food source for wolves during winter, and they often made repeated visits to these locations. These areas are attractants for bears as well as wolves (Wilson et al. 2005, Wilson et al. 2006). Boneyards are allowed on private and leased land provided they are at least 400m from livestock facilities and residences (Province of Alberta 2009). From the perspective of a large carnivore 400m is a short distance, and repeated visitation of these sites potentially brings them within close contact of other stock-growing activities (e.g. calving), which could result in further conflict (e.g. depredation). Naturally, if large carnivores are visiting these locations regularly it is not unreasonable to believe they would develop a taste for beef. Bear-proof metal storage bins have been suggested as an alternative to boneyards and as a way to reduce conflicts and prevent carnivores from becoming accustomed to feeding on livestock. Partnerships are developing in both Canada and the United States to assist producers in securing funding for metal storage bins (e.g. Blackfoot Challenge and Drywood Yarrow Watershed Group). These programs have been successful and are currently expanding (Northrup 2010)

Both GPS cluster and scat methods indicate a strong seasonal shift in wolf diets. However, it is not clear if wolf prey selection changes seasonally. Alternatively, wolf selection of prey might remain constant and the influx of cattle during the grazing season is resulting in an increase of cattle in their diet. Further work is needed to tease apart the mechanisms driving prey selection in this landscape.

MANAGEMENT IMPLICATIONS

Wherever wolves and livestock overlap there is likely to be conflict, and southwestern Alberta is no exception. A variety of solutions have been attempted, with varying degrees of success, to help mitigate conflicts between wolves and livestock including fladry, electric fencing, range riders, guard dogs, and even electric shock collars (Shivik 2006). My work, however, highlights a management issue that has not received as much attention in reducing wolf-livestock conflicts: dead livestock. Boneyards are an attractant for multiple large carnivores and provide a situation in which they may become accustomed to feeding on livestock. Repeated use of these boneyards by carnivores may result in other conflicts such as depredation of livestock or pets. Metal carcass storage bins might be a simple solution to reducing this particular attractant.

Further, depredation of livestock during summer is an issue deserving further research. The livestock located by the GPS cluster method were animals that would otherwise be missing. On occasion, producers received compensation for these animals. This is compensation that they otherwise would not have received. Local concern is growing over how missing cattle will be handled under the compensation program in light of the information provided by my study. Some producers believe Alberta's predator compensation program should be reevaluated to incorporate my findings and pay producers for a portion of their missing animals.

I caution that my results are from an area of intense overlap between wolf distribution and livestock grazing, and livestock depredation is much less of a problem in other areas of the province (e.g. Webb et al. 2008). I recommend further use of the GPS cluster method to identify wolf diets in ranching landscapes, particularly in areas where missing animals are a concern among producers.

Table 2.1. Compensation payments paid to livestock producers through Alberta's predator compensation program from 2000 through 2010

Year	Total compensation paid ($)[a]	Compensation paid due to wolf injury or depredation of cattle ($)[b]
2000-2001	68,128.14	45,320.92
2001-2002	78,030.99	48,376.26
2002-2003	60,561.34	40,273.80
2003-2004	91,784.48	66,813.96
2004-2005	49,178.61	35,555.38
2005-2006	95,588.02	78,491.12
2006-2007	91,576.96	68,281.02
2007-2008	118,858.39	86,813.69
2008-2009	145,924.90	123,857.00
2009-2010	144,374.35	110,046.14
Total	944,006.18	703,829.29

[a] Includes payments for injury and death to all domestic livestock (cattle, sheep, horses, lamas, and goats) due to black bears, grizzly bears, wolves, cougars, and eagles

[b] Includes only payments for injury and death to cattle due to wolves

Table 2.2. Frequency of prey items and estimated relative biomass of prey detected in wolf scats (*n*=319) from 3 wolf packs in southwestern Alberta from June 2008 through October 2009

Prey[a]	Mass of prey (kg)[b]	kg/scat[c]	Number of scats[d]	Frequency of prey items (%)[e]	Relative Biomass	
					(kg)[f]	(%)[g]
Moose	220.41	2.20	23	3.43	50.65	4.95
Deer	57.83	0.90	184	27.42	165.90	16.22
Elk	199.49	2.03	158	23.55	321.52	31.44
Cow	358.13	3.30	120	17.88	396.48	38.77
Beaver	22.50	0.62	4	0.60	2.48	0.24
Hare	1.50	0.45	13	1.94	5.86	0.57
Ground Squirrel	0.36	0.44	45	6.71	19.88	1.94
Small Rodent	0.04	0.44	70	10.43	30.75	3.01
Mustelid	1.07	0.45	26	3.87	11.64	1.14
Horse	454.50	4.08	2	0.30	8.15	0.80
Skunk	3.05	0.46	4	0.60	1.85	0.18
Muskrat	1.50	0.45	3	0.45	1.35	0.13
Bobcat	11.05	0.53	3	0.45	1.58	0.15
Porcupine	10.00	0.52	6	0.89	3.11	0.30
Racoon	7.00	0.50	1	0.15	0.50	0.05
Badger	7.00	0.50	2	0.30	0.99	0.10
Unknown			7	1.04		
Total			671	100.00	1022.71	100.00

[a] excludes 4 bird feathers and a piece of snake skin
[b] Average lives weight of Alberta ungulates (Schladweiler and Stevens 1973, Reneckelr and Samuel 1991, Stelfox 1993, Pattie and Fisher 1999, Cook 2002, Hudson and Haigh 2002, Schwartz 2007) adjusted to reflect seasonal variation and age class composition as found at wolf GPS kill sites
[c] Calculated by equation $y = 0.439 + 0.008x$ (Weaver 1993)
[d] indicates the number of scats in which each prey item was found, total represents total prey items
[e] occurrence of each prey item relative to the total number of prey items
[f] relative biomass (kg) is equal to the kg/scat multiplied by the number of scats containing that prey item
[g] relative biomass (%) is equal to the relative biomass (kg) consumed divided by the total relative biomass consumed (kg)

Table 2.3. Frequency of prey items and estimated relative biomass of prey detected in wolf scats (n=124) from 3 wolf packs in southwestern Alberta during the non-grazing season 2008-2009

Prey[a]	Mass of prey (kg)[b]	kg/scat[c]	Number of scats[d]	Frequency of prey items (%)[e]	Relative Biomass (kg)[f]	Relative Biomass (%)[g]
Moose	307.19	2.90	7	2.70	20.28	4.69
Deer	69.49	0.99	76	29.34	75.61	17.47
Elk	224.38	2.23	82	31.66	183.19	42.33
Cow	403.43	3.67	35	13.51	128.33	29.65
Beaver	22.50	0.62	0	0.00	0.00	0.00
Hare	1.50	0.45	5	1.93	2.26	0.52
Ground Squirrel	0.36	0.44	20	7.72	8.84	2.04
Small Rodent	0.04	0.44	24	9.27	10.54	2.44
Mustelid	1.07	0.45	3	1.16	1.34	0.31
Horse	454.50	4.08	0	0.00	0.00	0.00
Skunk	3.05	0.46	1	0.39	0.46	0.11
Muskrat	1.50	0.45	2	0.77	0.90	0.21
Bobcat	11.05	0.53	0	0.00	0.00	0.00
Porcupine	10.00	0.52	1	0.39	0.52	0.12
Racoon	7.00	0.50	0	0.00	0.00	0.00
Badger	7.00	0.50	1	0.39	0.50	0.11
Unknown			2	0.77		
Total			259	100.00	432.76	100.00

[a] excludes 4 bird feathers

[b] Average lives weight of Alberta ungulates (Schladweiler and Stevens 1973, Reneckelr and Samuel 1991, Stelfox 1993, Pattie and Fisher 1999, Cook 2002, Hudson and Haigh 2002, Schwartz 2007) adjusted to reflect seasonal variation and age class composition as found at wolf GPS kill sites

[c] Calculated by equation $y = 0.439 + 0.008x$ (Weaver 1993)

[d] indicates the number of scats in which each prey item was found, total represents total prey items

[e] occurrence of each prey item relative to the total number of prey items

[f] relative biomass (kg) is equal to the kg/scat multiplied by the number of scats containing that prey item

[g] relative biomass (%) is equal to the relative biomass (kg) consumed divided by the total relative biomass consumed (kg)

Table 2.4. Frequency of prey items and estimated relative biomass of prey detected in wolf scats (*n*=101) from 3 wolf packs in southwestern Alberta during the 2008 and 2009 grazing seasons

Prey	Mass of prey (kg)[a]	kg/scat[b]	Number of scats[c]	Frequency of prey items (%)[d]	Relative Biomass	
					(kg)[e]	(%)[f]
Moose	134.86	1.52	6	2.86	9.11	2.91
Deer	46.18	0.81	38	18.10	30.72	9.80
Elk	175.67	1.84	28	13.33	51.64	16.48
Cow	312.83	2.94	63	30.00	185.32	59.14
Beaver	22.50	0.62	3	1.43	1.86	0.59
Hare	1.50	0.45	3	1.43	1.35	0.43
Ground Squirrel	0.36	0.44	22	10.48	9.72	3.10
Small Rodent	0.04	0.44	26	12.38	11.42	3.64
Mustelid	1.07	0.45	15	7.14	6.71	2.14
Horse	454.50	4.08	1	0.48	4.08	1.30
Skunk	3.05	0.46	1	0.48	0.46	0.15
Muskrat	1.50	0.45	1	0.48	0.45	0.14
Bobcat	11.05	0.53	1	0.48	0.53	0.17
Porcupine	10.00	0.52	0	0.00	0.00	0.00
Racoon	7.00	0.50	0	0.00	0.00	0.00
Badger	7.00	0.50	0	0.00	0.00	0.00
Uknown			2	0.95		
Total			210	100.00	313.377	100.00

[a] Average lives weight of Alberta ungulates (Schladweiler and Stevens 1973, Reneckelr and Samuel 1991, Stelfox 1993, Pattie and Fisher 1999, Cook 2002, Hudson and Haigh 2002, Schwartz 2007) adjusted to reflect seasonal variation and age class composition as found at wolf GPS kill sites

[b] Calculated by equation $y = 0.439 + 0.008x$ (Weaver 1993)

[c] indicates the number of scats in which each prey item was found, total represents total prey items

[d] occurrence of each prey item relative to the total number of prey items

[e] relative biomass (kg) is equal to the kg/scat multiplied by the number of scats containing that prey item

[f] relative biomass (%) is equal to the relative biomass (kg) consumed divided by the total relative biomass consumed (kg)

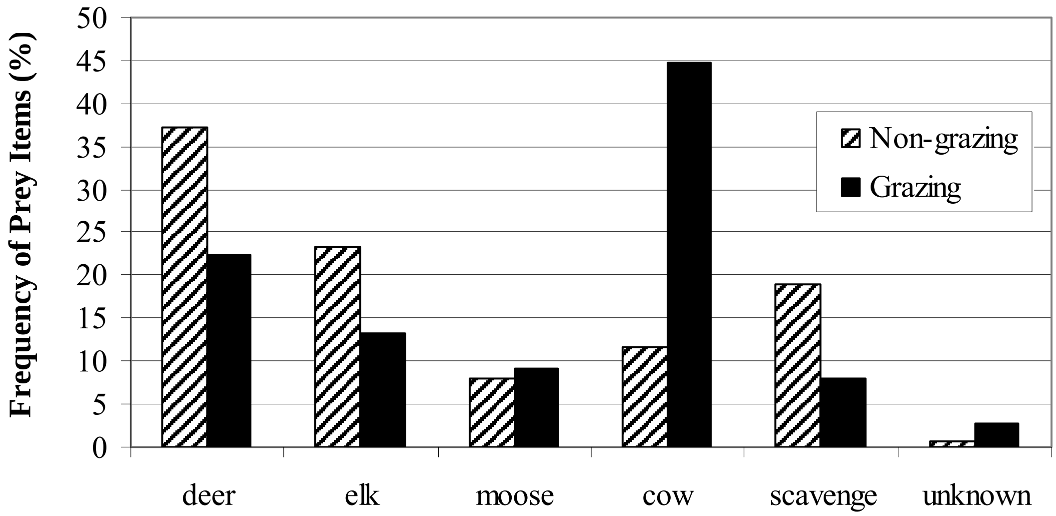

Figure 2.1. Frequency of prey items found at GPS cluster sites identified by radiocollared wolves expressed as a percentage of the total prey items found during the non-grazing (n = 137) and grazing (n = 76) seasons in southwestern Alberta 2008 - 2009.

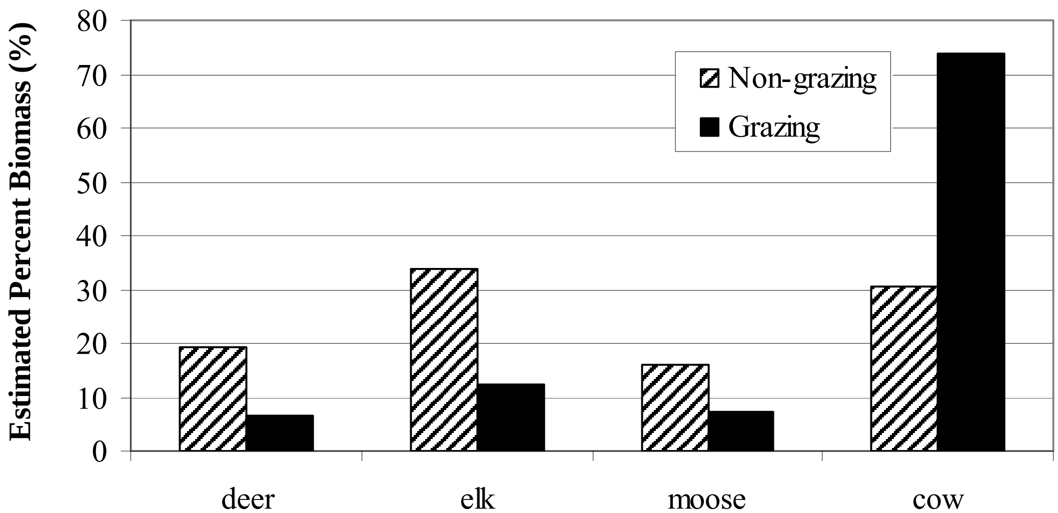

Figure 2.2. Estimated percent biomass of prey items consumed by wolves as found from GPS cluster sites during the non-grazing (n = 110) and grazing (n = 68) seasons in southwestern Alberta 2008 - 2009. Scavenge events are not included. Average live weights of Alberta ungulates adjusted for age and season were used (Schladweiler and Stevens 1973, Reneckelr and Samuel 1991, Stelfox, 1993, Cook 2002, Hudson and Haigh 2002, Schwartz 2007)

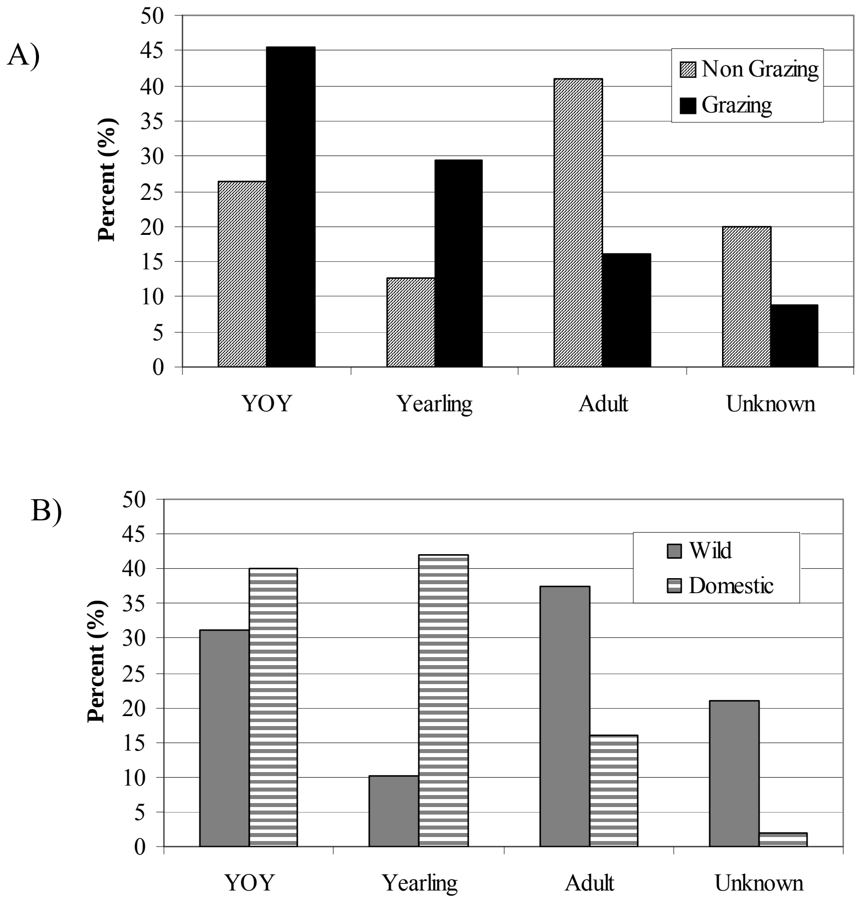

Figure 2.3. A) Age class of prey found at GPS cluster sites during the non-grazing (*n*=110) and grazing (*n*=68) seasons; and B) age class of wild (*n*=50) and domestic (*n*=128) prey items found from GPS cluster sites in southwestern Alberta June 2008 through October 2009. Scavenge events are excluded from calculations.

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CHAPTER 3: DEVIANCE FROM TRUTH: EFFECTS OF BIOTELEMETRY ACCURACY AND PRECISION ON A HABITAT SELECTION MODEL

INTRODUCTION

Recent developments in radiotelemetry permit remote compilation and transmission of relocation data, facilitating our ability to collect extensive datasets on wide-ranging and elusive species. Relocations are much easier to obtain than with VHF radiocollars, saving staff and travel resources. Two common technologies that are being used in radiocollars are Global Positioning System (GPS) telemetry and Argos satellite technologies. However, these 2 methods differ substantially in spatial and temporal accuracy and precision as well as design (Rodgers 2001).

GPS radiocollars have spatial precision estimated to be within 22 m (Bradshaw et al. 2007). In GPS radiocollars, location data are collected at user-defined fix rates and either stored on board or remotely downloaded by the user. In contrast, the Argos system uses transmitters to send a location signal to a satellite, which then sends the signal back to a receiving center on the ground where it is processed and the position of the transmitter is calculated and forwarded to the researcher (Argos 2008). One advantage of the Argos system is that the researcher can receive updates without physically relocating the animal. However, the fix rate is not user defined and is subject to the positioning of overhead satellites.

As with any remotely collected data measurement error is a problem in both GPS and Argos technologies that can affect both precision and accuracy. I define accuracy of a location estimator as being consistent with the actual location; deviance from the true location is reported as bias (White et al. 1982). If accuracy is high, the average of relocations is near to the true value. I define precision as the repeatability of the measurement, typically measured as the standard error of the mean (White et al. 1982). If accuracy is poor (bias), results will not represent the true parameters in question (i.e., model estimates will be incorrect). If precision is poor, there will be more variance in the results (i.e., the standard errors of the estimator will be larger).

Measurement error is much greater with Argos technology. Argos assigns a quality index, or location class (LC) to each location based on the estimated error. Error is assumed to be isotropic and is represented by a single number called the radius of error (Argos 2008). The radius of error is equal to 1 standard deviation of the estimated location error with a confidence limit in the 68th percentile (Argos 2008). The location class assigned by Argos is based on this radius of error, and is an estimate of precision (Argos 2008). Argos defines 7 levels of precision that currently have the following error estimates: LC3 error < 250m, LC2 error of 250m<500m, LC1 error of 500<1500m, LC0 error is >1,500m, and LC A, LC B, and LC Z do not include error estimates (Argos 2008). Thus, for LC3 68% (1 SD) of the locations should fall within 250m of the true location. Some researchers group location classes LC1-LC3 together and specify the precision as <LC1 (Rodger 2001). Argos, however, refers to these

location classes as an estimates of "location accuracy," which I believe has perpetuated confusion between the concepts of accuracy and precision for telemetry relocations.

Past research has sought to examine differences in measurement error both across different landscape conditions and collar brands (Moen et al. 1997, D'Eon et al. 2002, Di Orio et al. 2003, D'Eon and Delparte 2005, Cargnelutti et al. 2007). A few studies have examined the effect of measurement error on estimates of habitat selection (White and Garrott 1986, Frair et al. 2004, Sager-Fradkin et al. 2007), and fewer studies have examined how measurement error affects the estimation of movement metrics (Jerde and Visscher 2005, Bradshaw et al. 2007). However, I am not aware of any study that directly addresses the effect of radiocollar technology (GPS vs. Argos) and associated measurement error on the estimation and selection of habitat models.

Species habitat relationships can be modeled using a number of methods, but each relies on collecting locations of animal use. Resource selection functions (RSFs) can be used to statistically identify habitats that animals select relative to those available (Manly et al. 2002, Johnson et al. 2006). Furthermore, they can be used to create maps that identify areas on the landscape that predict a higher relative probability of selection by the species in question (Erickson et al. 1998). In modeling species habitat relationships, researchers often make the assumption that radiocollar locations represent the true location of an animal and associated habitat regardless of the measurement error associated with their chosen radiotelemetry technology. However, variation in accuracy and precision in remotely collected data can influence conclusions drawn from habitat models (McKelvey and Noon 2001), and this problem might be exacerbated in heterogeneous landscapes.

Large mammals with extensive movements are expected to perceive the landscape at a large scale (Boyce 2006), so under some circumstances (e.g. in homogenous landscapes, or coarse scale selection studies) measurement error might be of little consequence. I studied wolves in southwestern Alberta where pack territories averaged 988 km^2. Argos radiocollars have been used by wildlife biologists in the area to monitor broad-scale movements and to alert ranchers to the presence of wolves on their property. To obtain finer resolution data and compare the 2 technologies, I attached GPS radiocollars on wolves in the same pack with Argos radiocollared wolves.

My objectives were to: 1) compare RSF models estimated with GPS and Argos radiocollar data to test the null hypothesis that telemetry with different spatial precision will result in the same conclusions about animal selection of habitats, 2) test the null hypothesis that GPS and Argos radiotelemetry relocations are independent of landscape heterogeneity, and 3) test the null hypothesis that differences in vegetation types associated with GPS vs. Argos telemetry relocations are independent of landscape heterogeneity.

STUDY AREA

I used data collected from Argos and GPS radiocollared wolves in a 3,300-km^2 area in southwestern Alberta on the east slopes of the Rocky Mountains to investigate differences in habitat-selection models. The study area was bounded by the northern boundary of Bob Creek Wildland Park to the north, Highway 2 to the east, Waterton Lakes National Park to the south, and the British Columbia border to the west. The study area was a mix of private land (30%) and Crown land (70%) under the jurisdiction of the Alberta provincial government.

Southwestern Alberta is characterized by a sharp interface between the mountains and the prairies with limited forested foothills. The predominant vegetation types in the study area were conifer forest (52%), deciduous forests (7%), and grasslands (15%). In 2003, the Lost Creek fire burned approximately 200 km^2 in the southern portion of the study area (6%). Conifer forests consisted of primarily Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Deciduous species were mainly aspen (*Populus tremuloides*) and cottonwood (*P. trichocarpa*). Heavy winds, warm, dry summers, and cold winters characterized the climate. Chinook winds were common in winter months causing rapid temperature increases lasting from several hours to a few days. Oil and gas development, forest harvesting, and recreational activities occurred throughout the study area. Cattle ranching, however, was the primary land use in this region.

METHODS

I captured 6 wolves from 3 packs (Bob Creek, Crowsnest, and Castle-Carbondale) using padded-jaw leghold traps or helicopter netgunning (University of Alberta Animal Care Protocol #565712). I physically restrained wolves and collared them with either upload-capable Lotek 7000SU GPS radiocollars set to a one hour duty cycle or Lotek Argos radiocollars such that there was one type of each collar technology in all packs (Lotek Engineering, Newmarket, Ontario, Canada). I monitored wolves from June 20, 2008 through October 14, 2009. Individual wolves wore GPS radiocollars for a range of 118 to 351 consecutive days ($\bar{x}$ = 215, SE = 51.86) and Argos radiocollars for a range of 34 to 118 consecutive days ($\bar{x}$ = 72.67, SE = 24.48). Pack size ranged from 2 to 5 adults.

Argos data were edited so that only those locations with estimated spatial accuracy <1.5 km resolution were included (LC 1, 2 or 3). To control for differences in fix rate, the GPS radiocollar data were reduced to temporally match the Argos location set as closely as possible, such that there were the same number of data points in each set (*n* = 374) over December 18, 2008 through April 15, 2009. Wolves typically travel as a cohesive pack during the non-breeding season (Mech 1970) so a collared wolf during this time period should be representative of the entire pack's habitat-use patterns (Fuller 1989). I defined radiocollar relocations to be used locations. I estimated minimum convex polygons (MCPs) as a measure of the home range for each pack using radiocollar data (Hawth's Analysis Tools for ArcGIS, www.spatialecology.com). Available locations were sampled in a GIS within each pack MCP at an intensity of 1 point per 5 km^2 (average per pack $\bar{x}$ =2,940, SE=913.3).

I generated spatial layers in ArcMap 9.2 (Economic and Social Research Institute, Redlands, CA) related to land cover, terrain, and human disturbance. Alberta Vegetation Inventory (AVI) data as a polygon layer were available for the entire study area from the Alberta provincial government. I reclassified this layer into 11 habitat classes (Python Software Foundation, Wolfeboro Falls, NH, www.python.org). Additional spatial layers included linear features, a digital elevation model, and a terrain ruggedness index. I intersected my used and available data with all spatial layers using Hawth's Tools.

To determine whether GPS vs. Argos telemetry would result in different conclusions of wolf habitat selection, I estimated RSFs for each pack for each collar type following a used (1) vs. available (0) design with the following exponential form:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots + \beta_k x_k)$$

where $w(\mathbf{x})$ represents the relative probability of selection and β_is are selection coefficients associated with the i-th covariate, x_i, estimated using logistic regression (Manly et al. 2002, Johnson et al. 2006). For analysis, available locations remained constant for estimation of models using GPS and Argos data to ensure that any differences detected were a result of the use points rather than the available locations. Predictor variables (Table 3.1) were screened for collinearity using Pearson's correlations with a cutoff limit of $|r| \geq 0.6$. If the correlation coefficient between variables exceeded this limit then only 1 of the correlated variables was included in a model. I generated 27 candidate models and used Akaike's Information Criterion (AIC) to identify the most parsimonious model for each collar type in each pack (Burnham and Anderson 2002).

I examined differences in predictor variables between GPS and Argos top models identified using information-theoretic methods. Using the top GPS and Argos models I created a series of RSF maps in ArcMap that highlighted the areas of highest probability of use by wolves in their respective pack territories.

Additionally, top models based on GPS telemetry data were compared to the equivalent Argos model in each pack to examine differences between predictor-variable coefficients. I calculated the coefficient of variation (CV) for the β coefficient associated with each covariate in equivalent GPS and Argos models to compare relative variation.

To identify landscape associations that were likely to result in differences between GPS and Argos RSF models, I used matched-case logistic regression to contrast landscapes between each GPS and matched Argos use point. I created 1.5 km buffers around each GPS and Argos location and used Patch Analyst (Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario) to calculate spatial heterogeneity metrics. I chose 1.5 km for my buffer distance because it is the highest level of error associated with Argos LC 1. Because I was interested in how differences between telemetry technologies may be related to landscape heterogeneity, I chose total edge (TE), interspersion juxtaposition index (IJI), area weighted mean patch fractal dimension (AWMPFD), and modified Simpson's diversity index (MSIDI) to represent edge, patch adjacency, patch complexity, and patch diversity respectively. If differences between Argos and GPS locations were independent of spatial heterogeneity I would expect there to be no significant difference between the chosen landscape metrics in the GPS and matched Argos buffers.

Finally, I was interested in how GPS and Argos radiocollars might differ in response to increasing landscape heterogeneity. To do so I needed to establish a response variable to quantify such differences. If the landscape is homogenous, differences in precision between GPS and Argos radiocollars should not result in differences in vegetation type identified as used by the wolf. Because the majority of variables included in my RSF models were categorical measures of vegetation (Table 3.1), I chose to examine the probability of the vegetation type being the same between GPS and Argos used locations as a function of landscape heterogeneity. I created a binary variable "same" to identify whether (0) or not (1) the matched GPS and Argos telemetry locations were in the same vegetation type. I used logistic regression to assess the probability that the vegetation type differed between GPS and Argos radiocollars as a function of the landscape heterogeneity metrics (TE, IJI, AWMPFD, MSIDI). If differences in vegetation type were independent of spatial heterogeneity, I would expect there to be no relationship between the landscape metrics and the probability of the vegetation types being the same. All statistical analyses were conducted in STATA 10 (StataCorp LP, College Station, Texas).

RESULTS

The top model selected using information-theoretic methods was different across GPS and Argos technologies in all packs (Table 3.2). For example, top models for the Castle-Carbondale wolf pack only shared one predictor variable, elevation. Additionally, the top models for both the Bob Creek and Crowsnest packs had predictor variables that exhibited a sign change. The RSF model based on GPS telemetry data suggests that wolves in the Bob Creek pack were relatively less likely to use rugged terrain, while the model estimated using Argos data suggested the opposite. Likewise, the top GPS-based model for the Crowsnest pack suggests greater selection of areas further from roads whereas the top Argos model suggested greater selection of areas closer to roads.

When the top RSF model based on GPS data was compared to the same model based on Argos data the CVs for all β coefficients were higher in the Argos data (Table 3.3). The only exception for this pattern is the elevation predictor variable in the Castle-Carbondale pack. Additionally, for the Castle-Carbondale pack, 3 of the 4 predictor variables exhibited a sign change (Table 3.3). However, confidence intervals overlapped zero for all of the β coefficients for the model based on Argos collar data in the Castle-Carbondale pack.

The RSF maps visually illustrate the difference between the top GPS and Argos models (Fig. 3.1). The predicted areas of highest selection are different across technologies. For Bob Creek the Argos model suggests a smaller portion of the landscape is likely to be selected by wolves, whereas the Crowsnest map created with the Argos model suggests that more of the landscape has a high relative probability of selection. The most striking difference is seen in the Castle-Carbondale pack where the areas of highest probability of selection in the Argos model are visually opposite of those in the GPS model.

Of the 4 spatial heterogeneity metrics compared between GPS and Argos 1.5km buffers using matched-case logistic regression, only TE was significant ($\beta = 0.03$, SE = 0.01, $P = 0.02$; β and SE are presented at 1,000 times their value for TE). However, both TE ($\beta = 0.03$, SE = 0.01, $P = 0.004$) and MSIDI ($\beta = 1.01$, SE = 0.32, $P = 0.002$) were significant predictors of the probability of the vegetation type differing between GPS and Argos use locations. As edge and patch diversity increased the probability of the vegetation type being the same decreased.

DISCUSSION

I reject the null hypothesis that data from GPS vs. Argos radiocollars result in similar conclusions about selection of habitats by wolves. Researchers often ignore measurement error associated with radiocollar data, but my results show that this might lead to erroneous conclusions about animal selection of habitat.

Indeed, the differences in precision between GPS and Argos satellite radiocollars did not result in the same conclusions of wolf habitat selection. I expected poor precision to result in the more noise in the estimates of beta but not a difference in the top model selected. Not only do Argos satellite radiocollars have poor precision, but they also have poor accuracy. This deviance from truth, or bias, has altered my conclusions of wolf selection of habitat. For example, had I deployed only GPS radiocollars in the Crowsnest pack I would have concluded that areas at lower elevations, shrublands, further from roads, and closer to streams have a higher probability of selection by wolves. In contrast, had I deployed only an Argos radiocollar, my conclusions would have been that wolves in the Crowsnest pack are more likely to select areas that are less rugged, closer to roads, and at lower elevations.

The observed bias might be a result of differences in selection between the radiocollared wolves, landscape characteristics, or measurement error itself. My radiocollars for comparisons were on different animals, and if there was differential selection between individuals this might have created the bias.

However, my radiocollar data are from winter when wolves typically travel as a cohesive unit (Peterson et al. 1984, Fuller 1989, Mech and Boitani 2003) and pack cohesion tends to be strongest (Peterson et al. 1984). Additionally, pack cohesion tends to be stronger in smaller packs (Peterson et al. 1984) and pack size during my study was 2-5 individuals. Certainly much research on wolves makes the assumption that pack movements can be represented by one individual in the winter months (Ciucci et al. 1997), and sometimes only one animal per pack is collared with GPS or Argos telemetry (e.g. Fritts and Mech 1981, Sand et al. 2005, Houle et al. 2010). For the above reasons, I do not believe that collaring different individuals within each wolf pack has substantially influenced my results.

Alternatively, the observed bias could be a result of landscape characteristics. Although there are a number of studies examining habitat bias for GPS radiocollars (e.g., D'Eon et al. 2002, Frair et al. 2004, Sager-Fradkin et al. 2007, Hansen and Riggs 2008), the literature on habitat bias for Argos data is sparse. Argos radiocollar location accuracy, however, is influenced by altitude, landscape features, electromagnetic interference, and satellite visibility (Keating et al. 1991, Soutullo et al. 2007, Argos 2008). Sampling frequency (number of daily satellite passes) increases with latitude (Argos 2008) and the ability of the radiocollar to communicate with overhead satellites might be influenced by topography, terrain ruggedness, and forest cover (Keating et al. 1991, Will Harrrison, CLS America, personal communication).

While landscape characteristics may be a potential source of bias, I believe the most parsimonious explanation to be that measurement error itself directly caused the bias. For every predictor covariate in the Argos models, the coefficient of variation was higher and the betas were closer to zero. The only exception to this pattern was the coefficient for elevation in the Castle-Carbondale pack. Yet, in both the GPS and Argos models for this pack the confidence intervals for elevation overlapped 0. Location computations from Argos are particularly sensitive to changes in altitude (Argos 2008), which might explain the inconsistency in the pattern for this variable. Because Argos relocations are burdened with high measurement error (poor precision), the logistic regression betas become closer to zero thereby shifting the slope of the curve (Zar 1999). Poor precision in the Argos relocations resulted in poor accuracy. Thus, measurement error alone can cause a deviance from truth, or bias.

Measurement error in wildlife habitat studies is rarely reported, and even less frequently incorporated into the conclusions drawn from the research (McKelvey and Noon 2001). The potential for erroneous conclusions due to measurement error is heightened in highly heterogeneous landscapes. My results show that landscape heterogeneity reduces the probability that GPS and Argos technologies will identify selection for the same vegetation. There is an abrupt transition between the prairies and the mountains in southwestern Alberta and the landscape is made up of patches of diverse habitats, with no one type accounting for greater than 27%. In fragmented or patchy landscapes different habitat types often are adjacent increasing the potential for misclassification of animal use of a given vegetation type (Visscher 2006). Because GPS and Argos radiocollars are dependent on communicating with overhead satellites to estimate a location, the ability to obtain a fix might be biased towards open habitat types (e.g., grasslands). If the landscape is homogenous, the accuracy should be uniform and the relocations from the radiocollar unbiased. In a heterogeneous landscape relocations might not be indicative of true use by the animal, but rather the ability of the radiocollar to communicate with overhead satellites in a particular habitat type.

As I have demonstrated, differences in telemetry accuracy and precision are exacerbated in heterogeneous landscapes. However, the issue of scale must also be considered. Scale can be defined by grain and extent, where grain is the size of the smallest sampling unit or resolution, and extent is the size of the area studied. Ideally the grain and extent of spatial layers should match the data or processes of interest (Stine and Hunsaker 2001). Argos data will likely be most informative if they are used to answer a question that matches the spatial precision and accuracy of the technology. For example, had I reclassified my landscape into broader habitat generalizations (e.g. binned continuous variables into discrete categories, classified vegetation as "conifer" rather than "open conifer" and "closed conifer") or used a larger grain size, I might have seen less pronounced differences in results. Landscapes can be assessed using various spatial mapping programs, but it is important to consider the precision of all components. Clearly biotelemetry with poor precision, e.g., Argos, should not be used for a fine-scale analysis. Likewise, if the precision and accuracy of landcover layers are poor, the effects of measurement error might be compounded (McKelvey and Noon 2001).

MANAGEMENT IMPLICATIONS

My results highlight the influence of measurement error on habitat selection models. Naturally effects of erroneous conclusions will be most serious when researchers use these habitat models to make recommendations on management and policy (e.g., Thomas et al. 2005, Alberta Sustainable Resource Development 2008). I caution researchers to carefully assess the spatial heterogeneity of habitats in their study area, the behaviour of the species in question, the appropriate scale for analyses, and the nature of the research question itself before deciding which technology best suits their needs and how to incorporate the associated measurement error into results. Technology is continually changing and several companies now offer GPS Argos radiocollars (e.g. Lotek, Telonics), marrying the precision of GPS with the global-scale monitoring and satellite transmission available with Argos technology.

Table 3.1. Predictor variables used for estimating RSFs for 3 wolf packs in southwestern Alberta using GPS and Argos radiocollars

Variable Code	Description	Type	Range
elevat	Elevation of location (m)	Continuous	1220-2656
closedc	>80% coniferous and >50% canopy closure	Categorical	Yes or No
openc	>80% coniferous and <50% canopy closure	Categorical	Yes or No
decid	>80% broadleaf and <20% coniferous	Categorical	Yes or No
mixed	21-79% coniferous forest	Categorical	Yes or No
crops	Perennial and annual cropland	Categorical	Yes or No
cut	Forestry cuts 0-5 years old	Categorical	Yes or No
grass	Natural grasslands	Categorical	Yes or No
graze	Livestock grazing areas	Categorical	Yes or No
regen	Forestry cuts >5 and <15 years old	Categorical	Yes or No
shrub	Shrubland	Categorical	Yes or No
burn	Burned areas	Categorical	Yes or No
rugg	Terrain ruggedness index[a]	Continuous	0-92.606
rdist	Distance to nearest drivable road or trail (quad or truck) (m)	Continuous	0.088-3236.711
stream	Distance to nearest stream (m)	Continuous	0-1677.051

[a]Nielsen et al. 2004

Table 3.2. Comparison of top-ranking RSF models as identified using AIC. Models were estimated from GPS (n=3) and Argos (n=3) radiocollared wolves from 3 packs in southwestern Alberta.

Pack and Top Model	K	LL	AIC	ΔAIC	*w*
Bob Creek					
Null	1	-707.48	1416.95	107.71	0.00
GPS: elevat + closedc + crops + decid + grass + graze + mixed + rugg + stream	10	-644.62	1309.24	0.00	0.84
Argos: elevat + closedc + openc + crops + decid + grass + graze + mixed + shrug + rug + rdist + stream	13	-659.95	1345.90	0.00	0.85
Crowsnest					
Null	1	-475.20	953.50	35.74	0.00
GPS: elevat + shrub + rdist + stream	5	-453.88	917.77	0.00	0.34
Argos: elevat + rdist + rugg	4	-463.68	935.36	0.00	0.24
Castle-Carbondale					
Null	1	-284.96	571.91	4.79	0.02
GPS: elevat + shrub + grass+ closedc	5	-277.48	566.96	0.00	0.51
Argos: elevat + rugg	3	-280.56	567.11	0.00	0.21

Table 3.3. Coefficients, standard errors, coefficients of variation and AIC scores of the top ranking GPS RSF models for each wolf pack (Bob Creek *n*=213 used locations, Croswnest *n*=97 used locations, Castle-Carbondal *n*=64 used location) compared to the same Argos from each wolf pack in southwestern Alberta

Bob Creek							
GPS: AIC = 1309.2				Argos: AIC = 1345.9			
Variable Name	β	SE	CV	Variable Name	β	SE	CV
elevat[a]	-3.243	0.717	3.229	elevat	-2.990	0.680	3.317
closedc	-0.671	0.266	5.782	closedc	-0.512	0.254	7.227
crops	-1.007	0.388	5.624	crops	-0.390	0.378	14.149
decid	-0.954	0.265	4.058	decid	-0.186	0.234	18.371
grass	-0.579	0.211	5.323	grass	-0.397	0.220	8.086
graze	-0.751	0.249	4.838	graze	-0.360	0.252	10.214
mixed	-1.365	0.605	6.469	mixed	-0.261	0.419	23.461
rugg	-0.020	0.010	7.113	rugg	0.010	0.009	12.533
stream[a]	-1.915	0.800	6.097	stream	-1.092	0.753	10.062

Crowsnest							
GPS: AIC = 917.8				Argos: AIC = 935.4			
Variable Name	β	SE	CV	Variable Name	β	SE	CV
elevat	-3.430	0.624	1.792	elevat	-2.751	0.597	2.137
shrub	0.997	0.409	4.040	shrub	0.455	0.522	11.295
rdist[a]	0.498	0.185	3.662	rdist	0.436	0.186	4.206
stream	-1.736	0.783	4.443	stream	-0.729	0.708	9.560

Castle-Carbondale							
GPS: AIC = 565.0				Argos: AIC = 567.1			
Variable Name	β	SE	CV	Variable Name	β	SE	CV
elevat	-1.339	1.137	6.793	elevat	-1.432	1.105	6.173
shrub	1.053	0.627	4.765	shrub	-0.518	1.023	15.791
grass	1.053	0.323	2.454	grass	-0.247	0.414	13.389
closedc	0.442	0.319	5.781	closedc	-0.465	0.346	5.965

[a]Coefficients for elevat, stream, and rdist are reported at 1000 times their value

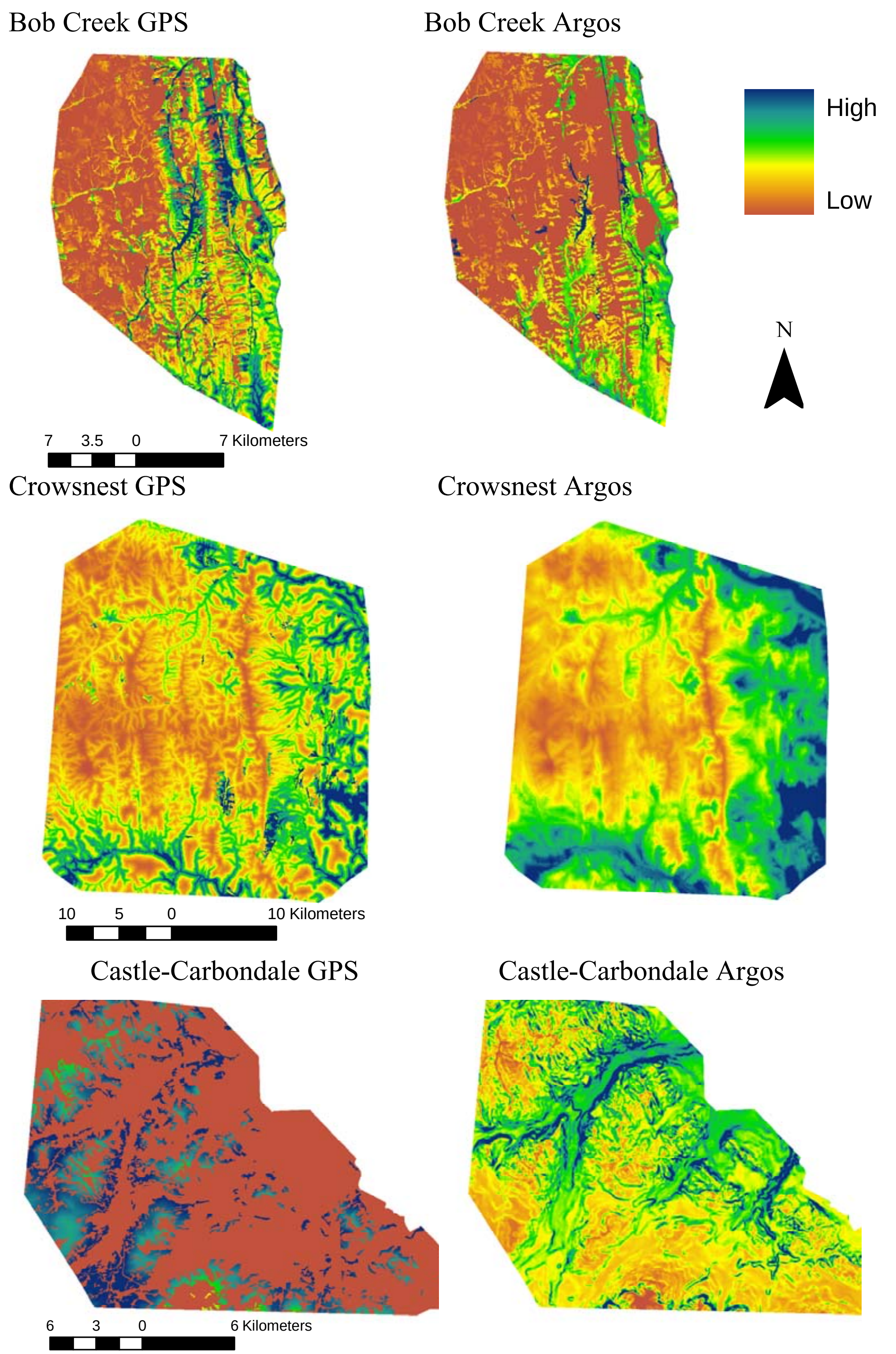

Figure 3.1. RSF maps for Bob Creek, Crowsnest, and Castle-Carbondale wolf packs in southwestern Alberta created using the top models identified by AIC estimated from GPS or Argos radiocollar data from wolves (GPS *n*=3, Argos *n*=3) collared December, 2008 through April, 2009. See Table 2 (this paper) for models used.

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CHAPTER 4: GENERAL CONCLUSIONS AND MANAGEMENT IMPLICATIONS

GENERAL CONCLUSIONS

My study area is an area of intense overlap between wolf distribution and livestock grazing. Depredation had long been a problem in this region and concern over wolf depredation of livestock was growing. Thus, I began this project with the objective of documenting year-round wolf diets in this region of heavy cattle use.

In Chapter 2, I presented two methods, GPS clusters and scat analysis, which I used to document wolf diets in this region. Both methods indicated a significant shift in wolf diets from wild prey during the non-grazing season to domestic livestock during the grazing season. Wherever wolves and livestock overlap there is likely to be some livestock depredation (e.g. Chavez and Gese 2005, Merkle et al. 2009). However, the magnitude of this depredation and the seasonal shift in diets was surprising. Producers in southwestern Alberta have long claimed that their missing cattle were being depredated by wolves, but until my research there had been no proof for that claim.

The GPS radiocollars deployed allowed me to locate kill sites and obtain detailed information on wolf pack locations and habitat use. However, prior to my project Alberta Fish and Wildlife relied almost exclusively on Argos satellite radiocollars. In Chapter 3, I investigated the effects of differences in spatial accuracy and precision between GPS and Argos radiocollars on the estimation of a commonly used habitat selection model: the resource selection function (RSF). Interestingly, the low precision of Argos relocations did not result in imprecise estimates of betas with greater standard errors. Instead I found a difference in the top model as selected by information-theoretic methods. The different models resulted in different conclusions about animal selection of habitat.

MANAGEMENT IMPLICATIONS

In Chapter 2, I highlighted a management issue that has not received much attention in reducing wolf-livestock conflicts: boneyards (livestock carcass piles). Boneyards have been identified as a growing problem as an attractant for bears (Wilson et al. 2005, Wilson et al. 2006), but they are also an attractant for wolves. Packs made repeated visits to these locations which put them in close proximity to other stock growing activities such as calving. Repeated use of these boneyards by carnivores may result in other conflicts. There has been success with bear-proof metal storage bins for carcasses as an alternative to boneyards (e.g. Blackfoot Challenge and Drywood Yarrow Watershed Group) and I recommend their further use.

Additionally, I recommend further use of the GPS cluster method to identify wolf diets in ranching landscapes, particularly in areas where missing animals are a concern among producers. Missing animals are not covered by Alberta's predator compensation program and thus represent a source of lost income to producers. Many ranchers in southwest Alberta are interested in developing creative solutions to reduce their losses, but would also like to see the compensation program revaluated in light of this project's findings.

The results of Chapter 3 illustrated some of the problems with radiotelemetry data. There is error associated with any remotely collected data, yet researchers often assume these data represent truth. Habitat suitability mapping is commonly used in wildlife management. I have highlighted some of the consequences in assuming that telemetry data are reliable. Because of poor accuracy and precision with Argo telemetry, I conclude that data from Argos satellite radiocollars are only suitable for coarse-scale analysis or broad generalizations of animal movements and habitat use. I recommend further use of GPS radiocollar technology to help tease apart the mechanisms driving wolf prey selection and habitat use in southwestern Alberta.

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