SUMMER WOLF DIET IN NORTHWESTERN MONTANA

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Wolf (*Canis lupus*) diet can be estimated from undigested remains of prey in scats or through stable isotope analysis (SIA) of wolf hair when distinct $\delta^{13}C$ and $\delta^{15}N$ values of potential diet sources are known. Our objectives were to compare diet analysis methods, to estimate intra-population diet variability, and to determine proportions of prey consumed by wolves. We collected scats of 4 wolf packs in northwestern Montana from June to August 2008, and guard hairs of 45 wolves from 12 packs, May to August 2009. We calculated percent biomass consumed of deer (*Odocoileus* spp.), elk (*Cervus canadensis*), moose (*Alces alces*), and other items from scats, and used Pearson's chi-squared tests of proportions to measure differences among packs. We used hierarchical Bayesian stable isotope mixing models to determine diet and scales of diet variation from $\delta^{13}C$ and $\delta^{15}N$ values of wolves and prey. We used bootstrapped scat data, and Markov Chain Monte Carlo simulation data from stable isotopes to estimate confidence intervals of difference between results from each technique for 4 packs with matched samples. Diet results were not consistent between techniques. Deer was the most common prey item based on scats, and moose the most common based on SIA. Wolf diet was significantly different among packs based on scats, and differences among packs explained most variability in diet based on stable isotopes. We sampled 3 times as many packs for less than half the cost with SIA compared to scat analysis. Experimental data on wolf hair growth period and wolf-specific $\delta^{13}C$ and $\delta^{15}N$ fractionation values would provide important information for recommending the better technique.

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INTRODUCTION

Since 1986, when reproduction was documented for gray wolves (*Canis lupus*) within Glacier National Park, Montana (Ream et al. 1989), researchers have studied the life history characteristics of this recolonizing predator. Examination of wolf diet can provide information about how wolves use common and rare prey, and how this use varies over space and time. Diets of wolves and other large carnivores have traditionally been estimated from kills (Burkholder 1959, Boyd et al. 1994, Ballard et al. 1997, Kunkel et al.1999) and scats (Putman 1984, Leopold and Krausman 1986, Merkle 2009), or through a combination of these methods (Potvin and Jolicoeur 1988, Huggard 1993, Arjo et al. 2002). Stable isotope analysis (SIA) is an increasingly common technique that may provide more comprehensive information about wolf diet than scat (Szepanski et al. 1999). Until now, no researchers have used spatially and temporally matched samples to determine if these techniques provide similar results. Such a study could provide insight on this and help develop the utility of SIA.

The common goal of describing diet is attained through these contrasting approaches that incorporate different sets of assumptions. The relative proportions of prey species a wolf pack consumes can be inferred from undigested remains in scats collected from a home range (Spaulding et al. 1997). Methods that provide unbiased estimates of consumption have been refined to compensate for small prey size (Mech 1970, Floyd 1978, Weaver 1993), but sampling error is still likely because scats may be deposited anywhere within the large home ranges typical of wolves (e.g., in Montana, $\bar{x}$ = 320 km^2 Sime et al. 2010), making it difficult to collect a representative sample (Reynolds and Aebischer 1991). Another limitation is that a wolf scat generally

represents a single meal (Floyd et al. 1978), and any sample of scats represents only a collection of single meals of an unknown number of wolves. Stable isotope analysis measures changes that occur in isotope ratios as tissues are consumed, metabolized, and reorganized at each trophic level to determine the relative proportions of each food source in the diet of a consumer (Peterson and Fry 1987). A comprehensive diet record can be determined through SIA because isotopic compositions of consumer tissues reflect those of their prey, and all nutrients assimilated into tissues during growth can be measured, a (DeNiro and Epstein 1978, 1981; Szepanski et al. 1999). Depending on the turnover rates of the sample tissue, SIA can be used to describe diet over the short or long term (Peterson and Fry 1987). For example, blood contains isotopic values of food sources metabolized over the preceding 10-14 days (Hilderbrand et al. 1996), hair reflects diet over a period of months (Darimont and Reimchen 2002), and bone tissue stores a lifetime's diet history (Tieszen et al. 1983). Another advantage for SIA over scat analysis is the scale at which wolf diet variability can be described. Because scat samples are usually attributed, at the finest scale, to packs, variation in diet has been analyzed at this or coarser scales. Because hair samples can be attributed to individuals, SIA is a more powerful tool for estimating intra-population diet variability (Urton and Hobson 2005, Darimont et al. 2008, Semmens et al. 2009). Fine scale analysis may also provide insight on the summer diet of wolves, which is relatively unstudied (Peterson and Ciucci 2003).

Implicit in the advantages for SIA are 3 assumptions that do not apply to scat analysis. First, SIA requires a priori knowledge of available prey, and only the contribution of prey selected as potential diet sources for wolves can be measured. Second, the specific contribution of each dietary source can only be determined if sources

are isotopically distinct (Ben-David et al. 1997). The third assumption is that isotope values change predictably as they move from 1 trophic level to the next. The relative retention of the heavier isotope (i.e., enrichment or depletion) as prey tissues are metabolized and assimilated into consumer tissues is termed trophic fractionation. When SIA is used to determine diet, appropriate fractionation values are applied to stable isotope values of prey before comparison with the isotopic composition of a consumer's tissues. Experimental data are absent for most species, and the convention in SIA is to use fractionation values of the closest taxonomic relative to the consumer of interest. The most commonly used fractionation values in wolf diet studies were estimated from controlled feeding studies on red foxes (*Vulpes vulpes*) (Roth and Hobson 2000).

Scat and SIA approaches to determining diets are different, but they both essentially measure biomass of prey consumed by wolves; scat using the undigested remains of prey to infer what was digested, and SIA using a more direct translation of tissue structure. Only 1 other wolf diet study has compared matched scat and SIA data, and it was designed to assess seasonal contributions of Pacific salmon (*Onchorynchus* spp.) to diet (Darimont et al. 2008). Further studies across a range of multi-prey ecosystems will improve understanding of the methods' relative value.

Since diet of recolonizing wolves in the Northern Rockies was first examined, the northwestern Montana wolf population increased from ≥23 in 1995 (Pletscher et al. 1997) to >300 in 2009 (Sime et al. 2010). New data on what wolves consume, and the scales at which diet variation occurs will be useful to managers in 2 ways. First, they will be able to provide current information to the public. Second, such data may assist managers in setting hunting seasons for ungulates and wolves (J. S. Williams, Montana Fish, Wildlife

& Parks [MFWP], personal communication). The wolf was removed from the Endangered Species list in 2009, and regulated hunting of the species is used as a management tool in the Northern Rockies. If diet studies demonstrate rare species are consumed more than expected from availability in certain areas, harvest limits could be adjusted.

We used wolf scat and stable isotope data from packs in northwestern Montana to address 4 questions. First, do scat analysis and stable isotope analysis methods provide similar results? Because scat and stable isotope analysis report proportions of prey biomass consumed, we expected the use of matched samples for both methods to yield similar results. Accordingly, we predicted that there would be no significant differences in prey biomass consumed estimated for each pack from scat and stable isotope data. Second, what is the summer diet of wolves in northwestern Montana? We used remains of prey in scats, and stable isotope values of prey and wolves to describe diet. Third, at what scale is most of the variation in wolf diet explained? Variation between packs was reported from kills in northwestern Montana (Kunkel et al. 2004) and elsewhere from summer scats (Van Ballenberghe 1975, Tremblay et al. 2001), and stable isotope data have been used to determine summer diet variability between individuals (Urton and Hobson 2005). Therefore, we predicted that diet would vary among packs based on scat data, and that pack and individual variability would explain most of the variation in diet among all wolves based on stable isotope data. Fourth, can the same results be achieved with greater efficiency for one of the methods? Both methods of diet analysis require financial expense, field effort, and laboratory-based analysis. Because of the effort

involved in scat collection and analysis, we predicted that SIA would require fewer resources to obtain dietary information.

STUDY AREA

The study area encompassed approximately 10,000 km^2 of northwestern Montana, including portions of Kootenai National Forest, Flathead National Forest, and Glacier National Park. Forests were dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.), western larch (*Larix occidentalis*), and ponderosa pine (*Pinus ponderosa*). Other conifers were western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and subalpine fir (*Abies lasiocarpa*). Common species in riparian areas were black cottonwood (*Populus trichocarpa*), willow (*Salix* spp.), and alder (*Alnus* spp.). Elevations ranged from 568 - 2,663 m, in a rugged mountainous landscape, interspersed with heavily forested valleys (Pfister et al. 1977). Potential wolf prey in the study area included bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginanus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and small mammals. Other predators were mountain lion (*Puma concolor*), black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), red fox, and wolverine (*Gulo gulo*).

There were 3 major rivers in the study area: the Kootenai, the Clark Fork, and the North Fork Flathead. The landscape was characterized by rugged mountainous terrain in the Cabinet Mountains Wilderness, the Bitterroot Range, Purcell Mountains, and Salish Mountains to the west, and the Whitefish Range to the east. The climate is moderated by the Pacific Ocean, and is characterized by warm dry summers and cool wet winters

(Caprio and Nielson 1992). Land use included commercial timber harvest, mineral and energy development, federal grazing allotments, hunting, recreational fishing, and off-road vehicle use.

METHODS

Wolves molt annually beginning in late spring (Mech 1974), with new hair growth continuing until late autumn (Young and Goldman 1944). Fully grown guard hairs, thus, contain individual summer diet records from the year of growth (Darimont and Reimchen 2002) that can be compared to summer scat samples from that year. We collected scats from 4 packs. Because hair samples reflect diet of individual wolves, we collected ≥2 hair samples/pack from the same 4 packs, and 8 other packs within the study. We assumed that common prey (i.e., white-tailed deer, mule deer, elk, and moose) would comprise the majority of diet, and that beaver (*Castor canadensis*) and snowshoe hare (*Lepus americanus*) could contribute ≥5% of the diet (Boyd et al. 1994, Kunkel et al. 1999, Arjo et al. 2002, Urton and Hobson 2005). Accordingly, we selected these 6 species as wolf diet sources for SIA.

We collected scats from home sites (i.e., dens and rendezvous sites) and opportunistically from roads within the home ranges of the Bearfite, Candy Mountain, Pulpit Mountain, and Twilight wolf packs between June and August 2008. We only collected scats ≥32 mm in diameter to minimize confusion between coyote and wolf scats (Arjo et al. 2002, Reed et al. 2006). We collected all adult canid scats <250 m from the center of home sites. We assumed all scats <15 mm diameter to be pup scats and did not collect them. We placed individual scats in brown paper bags labeled with date, pack, and location.

We sterilized scats in a 533LS Getinge/Castle steam sterilizer (Getinge/Castle, Rochester, NY, USA), hand-separated them, and used macro and microscopic characteristics of hair and bone to identify contents to species (Putman 1984, Leopold and Krausman 1986, Spaulding et al. 1997). We recorded frequency of occurrence (FO) of each prey species in scats for each pack, and calculated biomass consumed of each species/scat using the regression equation,

$$y = 0.439 + 0.008x,$$

where y was the mass (kg) of prey consumed/scat and x was the average adult mass of the prey species (Floyd et al. 1978, Weaver 1993). In the program R (R version 2.10.0, http://www.r-project.org/) we generated 5,000 bootstrapped samples to estimate mean and variance of prey biomass consumed by each pack using FO weighted by biomass from the regression equation. We tested for differences in diet between packs using Pearson's chi-squared tests of proportions on FO counts weighted by total FO (i.e., all prey occurrences for a given pack) and mean proportion prey biomass consumed from bootstrapped samples (SPSS Inc., Chicago, IL, USA).

We collected ≥100 whole hairs/sample from harvested white-tailed deer, mule deer, elk, and moose at 4 hunter check stations within the study area in November and December 2008. We collected hairs from snowshoe hare carcasses found during summer field work, and beaver hairs from animals trapped in damage control operations in September 2009. We collected guard hairs of wolves from individual day beds (i.e., circular substrate depressions ≤1 m^2) at home sites and kills from May to August 2009, assuming shed hairs to be 2008 growth. Because beds may include hairs from multiple wolves (Stenglein 2009), we only collected guard hairs from beds >1 m^2 if there were

sufficient hairs in a single clump for a complete sample (i.e., ≥30 hairs, Darimont et al. 2007). We also collected hair samples from wolves captured for population monitoring, and wolves from known packs killed in depredation control actions or on roads. All samples were placed in 118 mL Whirl-Pak® bags (Nasco, Fort Atkinson, WI, USA) labeled with date, pack, and location. Because coyotes were common in our study area, we sent subsamples of wolf scats and hairs to the University of California, Los Angeles for DNA analysis to verify species identification.

We sonicated hair samples in glass vials of deionized water using a Branson Tabletop Ultrasonic Cleaner, Model 3510 (Branson Ultrasonic Corporation, Danbury, CT, USA) to remove coarse debris from hairs, and dried samples for 24 hrs. We rinsed samples under a ventilation hood in a 2:1 chloroform/methanol solution to remove fine debris and oils (Darimont et al. 2007). Dried hairs were ground to powder in a Wig-L-Bug® DS-80 amalgamator (Crescent Dental Co., Chicago, IL, USA). We placed 1 mg of ground hair into 5×7 mm pre-combusted tin cups, and sent samples in 96-well plates to the University of California, Davis, Stable Isotope Facility for continuous-flow mass spectrometry analysis.

Samples were analyzed for stable isotopes of C and N using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope mass spectrometer (Sercon Ltd., Cheshire, UK). During mass spectrometry, samples are combusted , resuling in separation of CO_2 and N_2, which are then measured to calculate isotope ratios (Fry 2006). Isotope values are expressed in delta notation (δ) as:

$$\delta X = ([R_{sample}/R_{standard}] - 1)\ 1000,$$

where X is ^{13}C or ^{15}N, and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standards used in stable isotope analysis are PeeDee Belemnite limestone for carbon, and atmospheric N_2 for nitrogen (DeNiro and Epstein 1978, 1981).

We calculated mean and SD from individual $\delta^{13}C$ and $\delta^{15}N$ values of all prey species, and used non-parametric Mann-Whitney U tests to determine if species were isotopically distinct at the 0.05 significance level. We used a hierarchical Bayesian stable isotope mixing model approach recently developed and tested on similar data to estimate intra-population variation and determine proportional contributions of prey to wolf diet (Moore and Semmens 2008, Semmens et al. 2009). This technique represents an important advance in the use of stable isotope data for diet studies because it can account for variability in prey species isotope values and trophic fractionation, and it can limit the uncertainty inherent in having many potential diet sources. Variability in source isotope values occurs spatially and temporally, even within species (Urton and Hobson 2005), but no formal method of accounting for this uncertainty was possible with earlier mixing model techniques such as IsoSource (Philips and Gregg 2003). The Bayesian approach explicitly incorporates source isotope uncertainty by factoring in mean and variance parameters for each source and isotope (e.g., mean and variance of $\delta^{15}N$ for elk). Constant mean fractionation values are assumed (i.e., the same mean fractionation values are applied to all potential diet source isotope values), but unlike earlier mixing models, this approach allows fractionation variance to be included in the analysis. This may provide a useful degree of flexibility when fractionation values for the species of interest are unavailable (e.g., those for wolves).

Another advantage of a Bayesian analysis is that prior information can be used to incorporate uncertainty inherent in having multiple diet sources. Deterministic solutions to a mixture (i.e., consumer isotope values) are not possible when the number of isotopes (n) used for diet analysis exceeds the number of sources by $>n+1$, and uncertainty in the contribution of each source increases as more sources are included (Philips and Gregg 2003). The use of prior information (e.g., prior knowledge of wolf diet) can help to resolve such uncertainties, and refine estimates. To calculate informative priors, we used summer wolf scat data from a 4-year study in the eastern portion of our study area (Arjo et al. 2002). We converted frequency of occurrence of deer, elk, moose, and beaver reported in scats for each year to biomass consumed (Weaver 1993). In R, we calculated a Dirichlet prior distribution of alpha values for models with informative priors from these data. We used trophic fractionation (Roth and Hobson 2000) and variance values (J. D. Roth, University of Manitoba, personal communication) from the only known experimental feeding study of wild canids.

Using R code adapted from Semmens et al. (2009), we estimated 8 hierarchically structured models to determine the scale at which most wolf diet variability occurred within our study area. To explore the sensitivity of the choice of prior, all models were estimated with informative and non-informative priors. All models were estimated with and without residual error terms to incorporate variability in individual isotope values unrelated to diet. Two models assumed a single invariant diet for all wolves and incorporated random effects at the group level (i.e., packs had a shared global mean diet, and varied around that). Two models assumed a shared mean diet for all packs and incorporated random effects at the individual level, with diet allowed to vary among

individuals but not packs. Two fixed effects models allowed packs to have independent mean diets and no variation among individuals. Two fixed effects models allowed independent pack means and variation among individuals (i.e., random effects).

To compare results of analysis techniques, we used R to estimate confidence intervals of difference between the CIs from bootstrapped scat data and CIs estimated in the Markov Chain Monte Carlo simulations from the best Bayesian model for the 4 packs with matched samples. We determined the level of similarity between techniques by identifying whether or not CIs of difference contained 0, and report statistical significance at the 0.05, 0.01, and 0.001 levels for 32 comparisons (i.e., 4 for each pack's scat data compared to SIA data from Bayesian models with informative and non-informative priors).

We ranked the 4 most common prey species in diet for each pack from scat analysis, and SIA results from the best model with informative and non-informative priors, giving scores of 4 – 1 in descending order. We summed ranks for each species and analysis method across the 4 packs with matched samples, and divided each species total by the total number of ranks to determine a rank sum percent and facilitate a graphical comparison of rank order of importance of prey to diet.

Finally, to examine the comparative efficiency and cost of obtaining diet estimates from both methods, we summed field and laboratory hours, laboratory, equipment, and vehicle costs, and compared the amount of data collected each season (i.e., how many pack diets were described). We calculated the ratios of packs covered/field hour, and cost/pack to determine the relative economy of each method.

RESULTS

We collected 222 scats from home sites (n = 112), and roads and trails (n = 110) between 14 June and 31 August, 2008. We examined contents of 204 scats, identified contents as deer, elk, or moose, and combined all other animal remains in a single group (i.e., other). We collected 45 wolf hair samples from 12 packs ($\bar{x}$ = 3.8 samples/pack, range = 2 - 9), at home sites (n = 37), kills (n = 2), captures (n = 3), and from dead wolves (n = 3). We collected hair samples from 3 snowshoe hares. We collected 194 hair samples from white-tailed deer (n = 76), mule deer (n = 59), elk (n = 47), moose (n = 9), and beaver (n = 3). We sent all wolf, moose, snowshoe hare, beaver, and a subset of white-tailed deer (n = 31), mule deer (n = 30), and elk (n = 26) hair samples for stable isotope analysis. There were no coyote scats or hairs in the tested subsamples according to DNA tests.

From scats, deer (42%) contributed the largest proportion of biomass to wolf diet, followed by elk (36%), and moose (18%). The remaining 4% of biomass consumed consisted of Columbian ground squirrel (*Spermophilus columbianus*) and unidentified mammals (Table 1). Diet varied between packs (Fig. 1). Bearfite was different from Candy Mountain (χ^2 = 21.142, P < 0.001) and Pulpit Mountain (χ^2 = 18.61, P < 0.001), but not Twilight (χ^2 = 1.233, P = 0.54). Candy Mountain was different from Twilight (χ^2 = 30.685, P < 0.001), but not Pulpit Mountain (χ^2 = 4.073, P = 0.13). Pulpit Mountain was different from Bearfite (χ^2 = 18.61, P < 0.001) and Twilight (χ^2 = 22.801, P < 0.001).

We report means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ for wolves and diet sources from our samples, and literature values (Roth et al. 2007) for Columbian ground squirrel (Table 2). Because white-tailed deer and mule deer were combined in our scat

analysis and in the scat data used to inform our Bayesian models, and because they were not completely separated in the stable isotope mixing space (Fig. 2), we combined them into 1 group (i.e., deer; Fig.3). We removed snowshoe hare and Columbian ground squirrel from the analysis because they were not isotopically distinct from moose and beaver, respectively. Because beaver and other potential rodent (i.e., Columbian ground squirrel, deer mouse [*Peromyscus maniculatus*]) and lagomorph (i.e., mountain cottontail [*Sylvilagus nuttalii*]) diet sources would share the same region of the stable isotope mixing space (Roth et al. 2007), we combined these prey into 1 group (i.e., other) and used our beaver stable isotope values to represent it. All remaining wolf diet sources were isotopically distinct for ≥1 isotope value (Table 3). Mean isotope values for wolf packs were centered on the ungulate prey species in the mixing space (Fig. 3).

The model that included pack variation alone with no residual error term received the strongest data support for models with informative and non-informative priors. No other models using non-informative priors were supported by data, but 3 other models using informative priors were supported. There was strong support for the model that assumed a single invariant diet for all wolves and included a residual error term. There was moderate support for the model that assumed a single invariant diet with no residual error term, and the model that included pack and individual variation with no residual error term (Table 4). We report wolf diet at the pack level (i.e., posterior density estimates from the model with the most data support) because most of the diet variation in our study area was explained by differences among packs. Moose was the most common prey item in diet for 11 packs (i.e., all except Ksanka) from models with both types of priors (Figs. 4 and 5). For the same 11 packs, deer was the second most

common prey item from the model with informative priors (Fig. 4), and elk the second most common prey item from the model with non-informative priors (Fig. 5). Apart from results for the Ksanka pack from the model with non-informative priors, other prey comprised the lowest proportion of all pack diets from models with both types of priors.

For packs with matched samples, 5 and 6 proportions of prey biomass consumed were different in comparisons of scat data to SIA data from the best Bayesian model using informative and non-informative priors, respectively. All but 1 proportions of moose consumed (i.e., Twilight informative priors model) were different, 3 deer proportions were different, and 1 elk proportion was different across all comparisons. None of the proportions of other prey consumed was different (Table 5 a and b).

Non-parametric tests ranked deer and elk as the most common prey item from scats, followed by moose and other prey items. Moose was ranked first by SIA from models with both types of priors, deer and elk were second from models with informative and non-informative priors, respectively, and other prey the least common for both (Fig. 6).

Field effort (i.e., hours/technique) for each diet analysis technique was similar, but we estimated diet for more packs through stable isotope analysis. Stable isotope field and laboratory costs were higher than those for scat analysis, but the cost/pack for scat analysis was greater than twice the cost for stable isotope analysis (Table 6).

DISCUSSION

The conclusion that wolf diet in northwestern Montana varies by pack was supported by the results from both analysis techniques, however, scat and stable isotope data did not provide consistent results on proportions of prey biomass consumed by the 4

packs for which we obtained matched samples. The clearest discrepancies were in the proportions of moose reported in diet. In our comparison of scat to SIA data from models with both types of priors, only the proportion of moose in diet for the Twilight pack from the model with informative priors agreed with the matched scat sample data. Moose was the most common item in diet from SIA data, but was the third most common in diet from scat data. No moose was detected in Pulpit Mountain scats, and only 1 Candy Mountain scat contained moose, but SIA with informative priors reported mean moose biomass consumed by these packs as 39% and 40%, respectively. The Pulpit Mountain scat sample size (n = 24) was relatively low, and 22 of these scats were collected from home sites. If moose were killed by Pulpit Mountain wolves away from home sites it is possible that scats containing moose would have been missed. The high proportion of deer in Pulpit Mountain scats may also reflect a more common occurrence of deer near the home sites. Such explanations would not, however, account for the similar discrepancy in results for the Candy Mountain pack. The scat sample size (n = 78) was the largest of any pack and we collected approximately 50% of scats from each location (i.e., home sites, or roads and trails).

We present 3 possible explanations for the discrepancies between the results of each technique. First, the problems with scat analysis described in the literature (Floyd et al. 1978, Reynolds and Aebischer 1991, Trites and Joy 2005) may have been particularly influential in our analysis. For ≥50% of the 2008 field season (i.e., the year of scat collection) only 1 worker was able to conduct field work, and scats were only collected between June and August. This limited our opportunities to make repeated collections within each home range, which may have reduced the scat sample size and our ability to

describe diet for June to August. Regardless of scat sample size, scats collected during this period may not represent diet during May, September and October (i.e., the other months of diet record contained by stable isotopes in hairs) because wolves may vary their prey use throughout the 6 month period of diet represented by hairs (Fritts and Mech 1980, Fuller et al. 1989, Darimont and Reimchen 2002).

The other explanations concern 2 of the important assumptions in SIA for wolf diet: hair growth period and fractionation. As with other studies, we cited a 1944 reference on hair growth for wolves that is not supported by experimental data (Young and Goldman 1944). We know of no data that dispute this reference, and its validity was supported by the results of Darimont and Reimchen (2002), however, we suggest experimentally derived data on hair growth in wolves would be an asset to future diet studies using SIA.

We used fractionation values from the most closely related taxon to wolves for which experimental data were available (i.e., red fox). Other researchers using these values to place potential wolf prey in the appropriate area of the stable isotope mixing space have described plausible diet results (Darimont and Reimchen 2002, Urton and Hobson 2005, Darimont et al. 2009, Adams et al. 2010), but these values may not be an adequate approximation for our study area. In particular, the amount of moose consumed by wolves reported from stable isotope data is unlikely to be accurate because moose comprise <6% of ungulate biomass available to wolves (calculated from, http://fwp.mt.gov/hunting/planahunt/), and wolves consume less moose than our results would suggest in areas with similar prey bases (Boyd et al. 1994, Huggard 1993, Kunkel et al. 1999, Urton and Hobson 2005). The researchers who reported the red fox fractionation values

we used rightly asserted their results to represent important baseline data for SIA of carnivore diet, but they also noted that the commercial feed used in the study may have led to higher nitrogen fractionation values than might be seen in the wild (Roth and Hobson 2000). In our study, a lower nitrogen fractionation value would have moved moose further away from all packs in the mixing space and would likely have resulted in a lower proportion of moose reported in diet. Our results may, thus, have described diet more accurately with fractionation values experimentally derived for wolves, and we suggest this work would be an important contribution to SIA of wolf diet.

Once wolf-specific fractionation values are available, diet studies using SIA could provide more useful information to managers on the level and variation of use of large ungulate prey by wolves within their regions. For example, our results suggest that wolves consume moose more than would be expected based on availability across the study area, but with more appropriate fractionation values, our analysis may have shown that fewer packs derive most of their nutrition from moose. In northwestern Montana, where the moose is a relatively rare but popular game species, managers could use a combination of accurate SIA data on wolf diet and monitoring data on moose to inform decisions on adjusting moose harvest quotas to maintain populations.

Beyond these 2 general areas of concern, it is important to clarify how the removal of some diet sources from the analysis may have affected our results. Although no evidence of beaver was found in scats, we used our beaver isotope values to represent other rodents and 1 lagomorph because all species in this group shared a peripheral region of the stable isotope mixing space, and scat data suggested ≥95% of biomass consumed consisted of large ungulates. We also removed snowshoe hare from the

analysis because it occupied a similar position in the mixing space to moose. It is reasonable to assume that snowshoe hare contributed some of the proportion of wolf diet reported as moose, but unlike with the relative contributions of each species lumped into the "other" category, snowshoe hare's contribution to a moose/hare group is unlikely to have been substantial. Wolves do eat snowshoe hares, but they generally comprise <5% of biomass consumed (Fritts and Mech 1980, Peterson et al. 1984, Ballard et al. 1987, Arjo et al. 2002).

When prior knowledge of potential prey is available, the Bayesian approach to analysis of stable isotope data is a robust statistical tool for study of wide-ranging, elusive predators such as wolves. In our study, the same best model was chosen with informative and non-informative priors, which adds strength to the conclusion that diet varies among packs. Our results suggest that prior information of wolf diet from a previous study in the eastern portion of our study area helped to refine estimates of wolf diet because the CIs of prey consumption for all packs were narrower than those from the model with non-informative priors. It is also possible, however, that the prior information we calculated from scat data in Arjo et al. (2002) contributed to the unexpectedly high proportion of moose reported from SIA because moose was the second most important prey source in that study.

Despite the differences in results from each technique, the conclusion that summer wolf diet varies among packs is supported. Summer diet of wolves has previously been examined at the regional, pack, and individual levels, and combinations of these scales. Most studies examined wolf diet through scat analysis in relatively homogeneous landscapes (Fritts and Mech 1981, Peterson et al. 1984, Huggard 1993).

More recent studies have used stable isotopes to examine diet variation across heterogeneous landscapes where prey availability may vary seasonally (e.g., where wolves have differential access to spawning Pacific salmon; Darimont and Reimchen 2002, Darimont et al. 2009, Adams et al. 2010). We conducted the first study of wolf diet using both techniques in a relatively homogeneous landscape where prey availability is relatively constant (i.e., the same prey are available to wolves throughout the year), and our results emphasize the pack as a unit of interest for wolf diet, and the importance of considering social structure of wolves in management decisions (Hebblewhite and Merrill 2008).

Few summer diet studies have been conducted in ecosystems with a diversity of potential prey similar to our study area. In Banff National Park, Alberta, Canada, where 6 wild ungulate species were available to wolves, 2 wolf pack diets were comprised of ≥70% elk (Huggard 1993). One study in the eastern portion of our study area, reported winter diet from kills to vary between packs with different amounts of deer and elk being consumed (Kunkel et al. 2004), and the only summer diet study in our area did not report pack diets (Arjo et al. 2002). We focused on an area of northwestern Montana where we assumed deer comprised most of the biomass available to wolves (i.e., >75%: calculated from, fwp.mt.gov/hunting/planahunt/), but elk and moose were also present and expected to comprise some proportion of wolf diet. Our results from scat and stable isotope analysis confirmed that deer, elk and moose comprise the bulk of diet, but also suggest that information on what wolves eat could be strongly affected by which packs and how many of them are selected for study, and which diet analysis technique is used.

The most obvious benefit of SIA compared to scat analysis is that more wolf packs can be covered for a given set of resources (i.e., ≥3 times as many packs for SIA). Indeed, we would have needed to conduct field work during 3 extra months (i.e., May, September, October, 2008) to collect scats for every month of hair growth. There were several occasions during field work for hair collection where we collected multiple hair samples in a single day, each of which represented continuous 6 month records of diet for an individual wolf. Thus, when reliable locations are available for wolf home sites it is possible to collect sufficient hair samples to estimate the diet of several packs in a few days.

Regardless of each technique's relative economy, managers may be unlikely to budget for the intensive field studies we have described. In Montana, however, 3 existing sources of wolf hair could be exploited for negligible extra field hours or costs. Hairs could be collected by MFWP wolf management specialists during annual capture and radio-collaring of wolves for population monitoring (n = 17 in 2009), from wolves killed or radio-collared in control actions by United States Department of Agriculture Wildlife Services agents (n = 158 in 2009), and from wolves harvested by hunters during the regulated hunting season (n = 72 in 2009) (Sime et al. 2010). Because hair samples for SIA require no special storage, and take up little space compared to scats, managers could store hairs indefinitely and conduct SIA at any time. We reported 200 hours of SIA laboratory work for our study, but ≥50% of this time was spent on preparing prey species hairs, and this will not need to be repeated for northwestern Montana. Laboratory time must be budgeted, but some stable isotope facilities (e.g., the University of California, Davis Stable Isotope Facility, Davis, CA, USA) offer specimen preparation services.

Managers interested in obtaining isotope data would still have to devote time to sample labeling, data recording, and statistical analysis, but the exploratory work detailed here and in previous studies provides step-by-step instructions on how to use stable isotope mixing models to interpret diet data (Moore and Semmens 2008, Semmens et al. 2009).

MANAGEMENT IMPLICATIONS

Ours was the second study to use Bayesian mixing models to analyze these kinds of data for wolf diet, and we anticipate continued use of this approach as more wildlife managers in the US need baseline information on what ungulate prey wolves consume. Stable isotope analysis is a relatively low cost method for obtaining a general picture of what wolves eat in a given area, but a clearer picture will become possible when uncertainties over fractionation values and hair growth period have been overcome. When specific packs are of interest to managers, $\delta^{13}C$ and $\delta^{15}N$ values of potential prey can be distinguished, and multiple samples from a pack can be obtained, SIA certainly has the potential to provide managers with a more comprehensive record of how wolves use prey than scat analysis. This may be particularly important when trying to understand how much livestock a wolf pack consumes. Domestic cattle are isotopically distinct from wild ungulates (Stewart et al. 2003, Derbridge and Krausman unpublished data), and different levels of reliance on livestock could be determined depending on whether hair (i.e., a 6 month diet record) or bone (i.e., a lifetime diet record) is examined (Tieszen et al. 1983, Peterson and Fry 1987, Darimont and Reimchen 2002).

We reported a high proportion of moose in the diet of northwestern Montana wolves. The fractionation values we used for SIA may have inflated this proportion, but the Twilight and Bearfite packs consumed >25% moose according to results from both

scat and stable isotope data. In northwestern Montana, MFWP moose population estimates are very general, and if some wolf packs consume higher proportions of moose than expected, it may be important for managers to monitor the moose population more closely. Such recommendations would apply to any ungulate population vulnerable to wolf predation, and our results suggest that it would be very difficult to predict effects on a regional scale because wolf packs have different diets.

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Table 1. Diet estimated from scats of 4 northwestern Montana wolf packs between June and August 2008.

Prey	Mass (kg)	kg/scat[e]	FO[f]	Weighted FO[g]	% biomass[h]
Deer	60[a]	0.92	136	96.17	0.42
Elk	260[b]	2.52	47	81.72	0.36
Moose	318[c]	2.98	22	40.26	0.18
Other	14[d]	0.55	22	8.85	0.04
Total			227	227.00	1.00

[a] Assumed from Dusek et al. (1989).

[b] From Quimby and Johnson (1951).

[c] From Shladweiler and Stevens (1973).

[d] From Fuller et al. (1980).

[e] We calculated biomass consumed/scat from regression equations (Floyd et al. 1978, Weaver 1993).

[f] Frequency of occurrence of prey items from all scats.

[g] We calculated mean proportions of biomass consumed by each pack with bootstrapped data from FO of each prey item weighted by values from the regression equation. Weighted FO for each pack was the product of bootstrapped mean values for each species and total FO of all species. This column represents weighted FO totals for each species across all packs.

Table 2. Means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ values estimated from hairs for wolves and diet sources in northwestern Montana, 2008.

		$\delta^{13}C$		$\delta^{15}N$	
Species	***n***	$\bar{x}$	**SD**	$\bar{x}$	**SD**
Wolf	44	-22.91	0.32	5.29	0.67
White-tailed deer	31	-24.88	1.32	3.67	0.75
Mule deer	30	-25.14	0.66	2.55	1.71
Elk	26	-25.48	0.44	2.48	0.71
Moose	9	-25.57	0.44	0.56	0.61
Beaver	3	-24.44	0.22	6.24	1.09
Snowshoe hare	3	-26.66	0.84	0.10	0.66
Ground squirrel	16[a]	-25.30	0.56	5.90	2.24

[a] Columbian ground squirrel stable isotope values are from Roth et al. (2007).

Table 3. Mann-Whitney *U* test scores for tests of difference between $\delta^{13}C$ and $\delta^{15}N$ values of wolf diet sources from hairs collected in northwestern Montana in 2008 and 2009.

Prey		Deer	White-tailed deer	Mule deer	Elk	Moose	Beaver	Snowshoe hare	Ground squirrel[a]
Deer	$\delta^{13}C$		915.5	885	540 *	168	37	15 *	467
(*n* = 61)	$\delta^{15}N$		646.5 *	616 *	586	7 ***	6 **	0 **	137 ***
White-tailed deer	$\delta^{13}C$	915.5		435	275 *	86	24	8 *	229
(*n* = 31)	$\delta^{15}N$	646.5 *		166 ***	94 ***	0 ***	0 ***	0 **	75 ***
Mule deer	$\delta^{13}C$	885	435		265 *	82	13 *	7 *	238
(*n* = 30)	$\delta^{15}N$	616 *	166 ***		288	7 ***	6 *	0 **	62 ***
Elk	$\delta^{13}C$	540 *	275 *	265 *		93	1 **	8 *	135
(*n* = 26)	$\delta^{15}N$	586	94 ***	288		0 ***	0 **	0 **	33 ***
Moose	$\delta^{13}C$	168	86	82	93		1 *	5	37 *
(*n* = 9)	$\delta^{15}N$	7 ***	0 ***	7 ***	0 ***		0 *	6	0 ***
Beaver	$\delta^{13}C$	37	24	13 *	1 **	1 *		0 *	9
(*n* = 3)	$\delta^{15}N$	6 **	0 ***	6 *	0 **	0 *		0 *	18
Snowshoe hare	$\delta^{13}C$	15 *	8 *	7 *	8 *	5	0 *		3 *
(*n* = 3)	$\delta^{15}N$	0 **	0 **	0 **	0 **	6	0 *		0 **
Ground squirrel	$\delta^{13}C$	467	229	238	135	37 *	9	3 *	
(*n* = 16)	$\delta^{15}N$	137 ***	75 ***	62 ***	33 ***	0 ***	18	0 **	

[a] Columbian ground squirrel stable isotope values are from Roth et al. (2007).

*, **, *** are statistically different at the 0.05, 0.01, and 0.001 significance levels, respectively.

Table 4. Summary of 8 stable isotope mixing models explaining summer diet variation among 45 wolves and 12 packs in northwestern Montana, 2008.

	Informative priors[a]				Non-informative priors[b]			
Model[c]	**Pack**	**Individual**	**Residual**	**DIC[d]**	**Pack**	**Individual**	**Residual**	**DIC**
1	Y	N	N	130.0	Y	N	N	87.7
2	N	N	Y	130.6	Y	N	Y	96.7
3	N	N	N	131.4	Y	Y	N	108.6
4	Y	Y	N	131.6	N	N	Y	124.1
5	Y	Y	Y	136.4	Y	Y	Y	127.3
6	Y	N	Y	140.5	N	Y	N	130.8
7	N	Y	N	155.9	N	N	N	131.9
8	N	Y	Y	186.6	N	Y	Y	189.0

[a] We calculated prior information on summer wolf diet from scat data in Arjo et al. (2002).

[b] Models with non-informative prior information assumed diet source contributions were identical.

[c] Models could include variation among packs, individuals or residual error.

[d] The Deviance Information Criterion is used to evaluate data support. Smaller values indicate greater support for a model.

Table 5 (a and b). 95 % confidence intervals of difference between estimates of diet source contributions from scat and stable isotope data. We estimated stable isotope mixing models using informative (a) and non-informative (b) priors. We collected matched wolf scat and hair samples for 4 packs in northwestern Montana in 2008 and 2009.

a.

	95 % CI of difference between scat and SIA estimates			
Wolf pack	**Deer**	**Elk**	**Moose**	**Other**
Bearfite	-0.16, 0.21	0.04, 0.42 *	-0.47, -0.06 *	-0.04, 0.04
Candy Mountain	-0.01, 0.43	-0.07, 0.35	-0.55, -0.19 ***	-0.07, 0.06
Pulpit Mountain	0.22, 0.73 ***	-0.36, 0.19	-0.52, -0.25 ***	-0.09, 0.09
Twilight	-0.23, 0.14	-0.05, 0.36	-0.36, 0.08	-0.04, 0.07

b.

	95 % CI of difference between scat and SIA estimates			
Wolf pack	**Deer**	**Elk**	**Moose**	**Other**
Bearfite	-0.01, 0.36	-0.08, 0.46	-0.62, -0.16 **	-0.10, 0.03
Candy Mountain	0.10, 0.61 *	-0.27, 0.40	-0.72, -0.17 **	-0.15, 0.05
Pulpit Mountain	0.37, 0.90 ***	-0.54, 0.18	-0.62, -0.19 ***	-0.17, 0.06
Twilight	-0.07, 0.30	-0.13, 0.40	-0.51, -0.04 *	-0.10, 0.06

*, **, *** are statistically different at the 0.05, 0.01, and 0.001 significance levels, respectively.

Table 6. Comparing hours spent on collection of wolf hair samples and scats, number of packs covered by each technique, associated costs/pack, and costs associated with stable isotope and scat analysis of wolf diet in northwestern Montana, 2008.

	Analysis technique	
Items	**SIA**	**Scat**
Field hours	490	470
Wolf packs	12	4
Packs/field hour	0.024	0.009
Cost/pack ($US)[a]	560	1,160
	Analysis technique costs	
Stable isotope lab ($8/sample)	$ 1,680	$ 0
DNA lab ($30/sample)	180	390
Lab technician hours ($10/hr)	1,250	1,000
Lab equipment	250	160
Field equipment	50	100
Vehicle costs	3,330	3,000
Total	$ 6,740	$ 4,650

[a] Calculated by dividing the total cost for each technique by the number of packs covered. Hours and costs are rounded to the nearest 10.

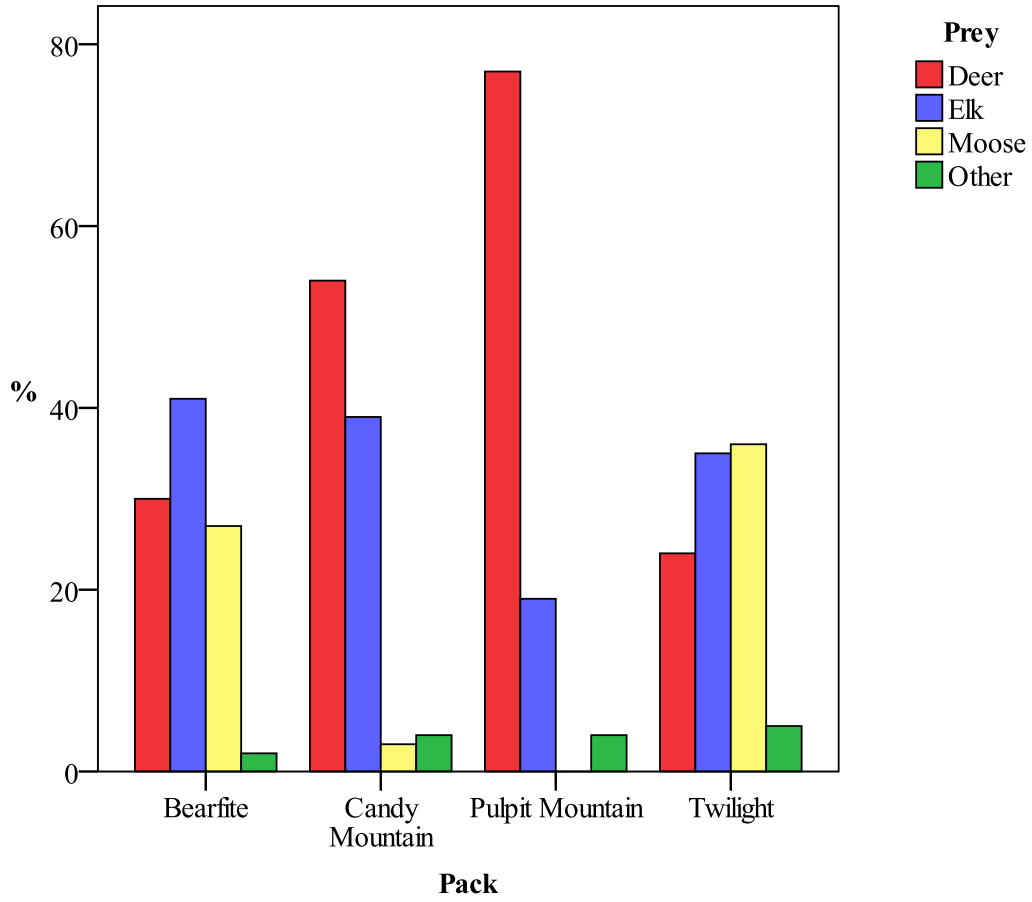

Figure 1. Percent biomass consumed (kg/pack) of each diet source estimated from scats of 4 wolf packs in northwestern Montana between June and August 2008. We weighted proportions by scat sample size for each pack. We used frequency of occurrence of species weighted by biomass consumed/scat for each pack and 5,000 bootstrapped samples to estimate means and variance. We used average adult mass of identified species from the literature, and used beaver as the representative diet source for the "Other" category.

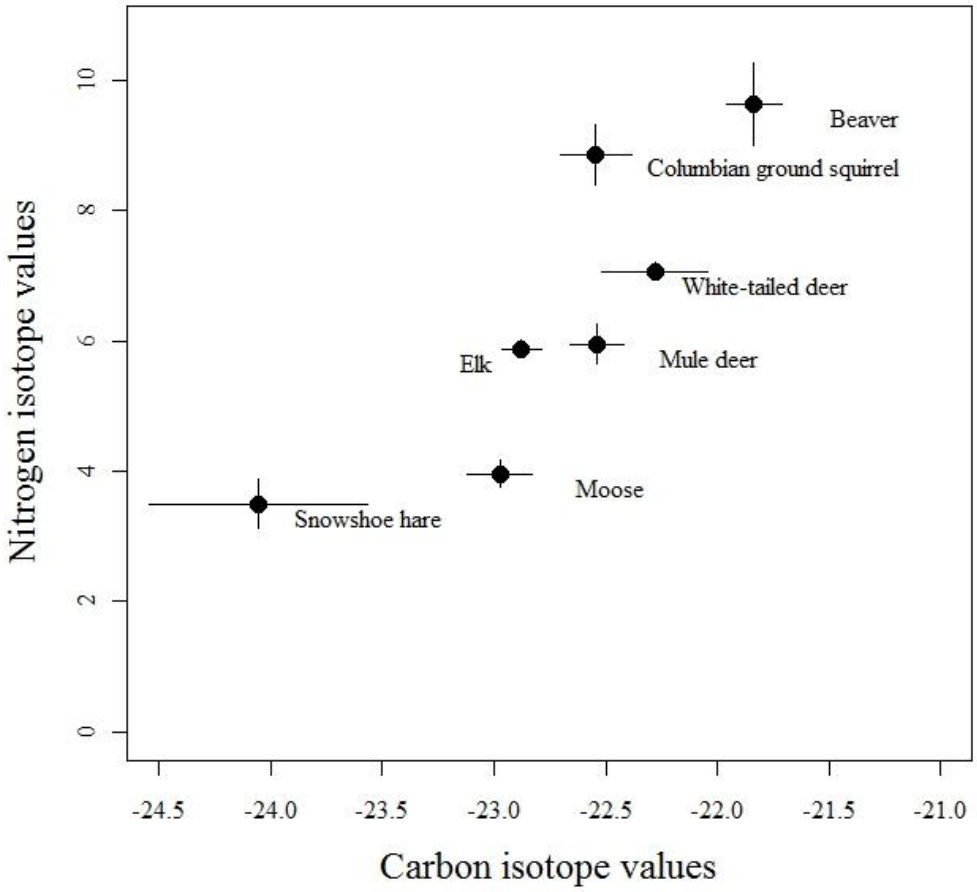

Figure 2. The mixing space with mean $\delta^{15}N$ and $\delta^{13}C$ values (± SE) of potential wolf prey in northwestern Montana, 2008. Columbian ground squirrel values are from Roth et al. (2007).

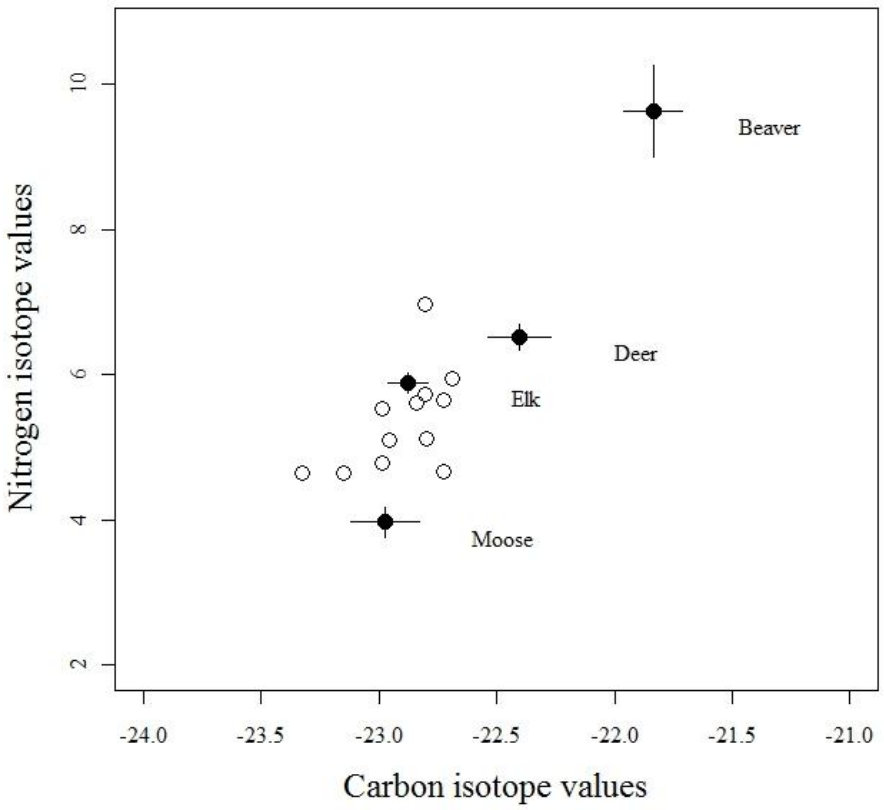

Figure 3. The mixing space with mean $\delta^{15}N$ and $\delta^{13}C$ values of potential wolf prey, and mean values for 12 wolf packs (open circles) in northwestern Montana, 2008. We combined white-tailed deer and mule deer, and removed snowshoe hare and Columbian ground squirrel.

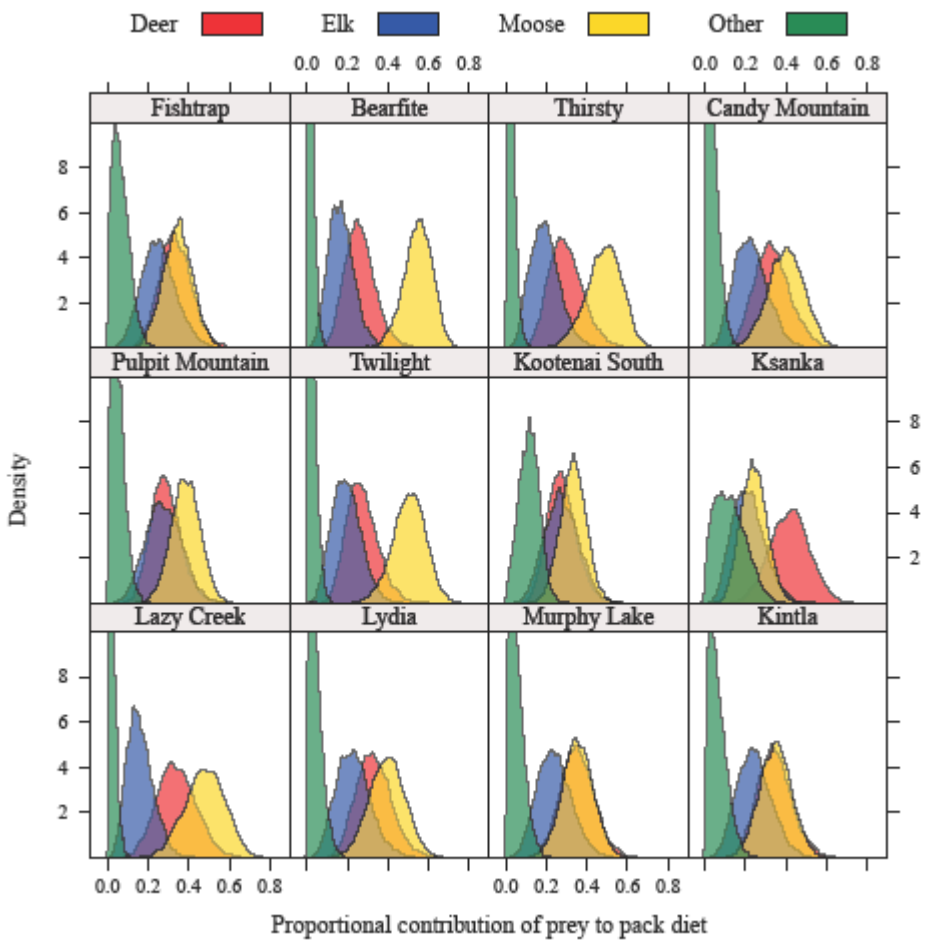

Figure 4. Posterior density estimates of diet source contributions to the summer diet of 12 wolf packs in northwestern Montana, 2008. Posterior densities are from a model estimated with variation among packs and informative priors.

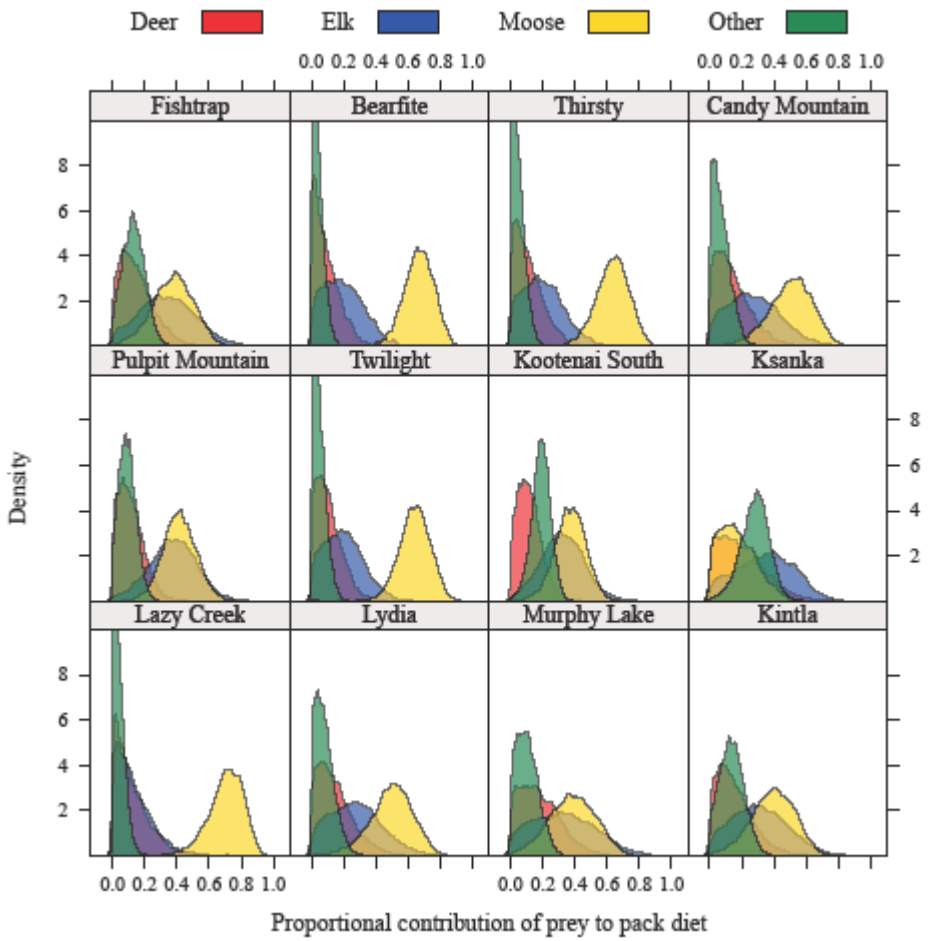

Figure 5. Posterior density estimates of diet source contributions to the summer diet of 12 wolf packs in northwestern Montana, 2008. Posterior densities are from a model estimated with variation among packs and non-informative priors (i.e., prior information in the Bayesian mixing model assumes all sources contribute equally to the mixture).

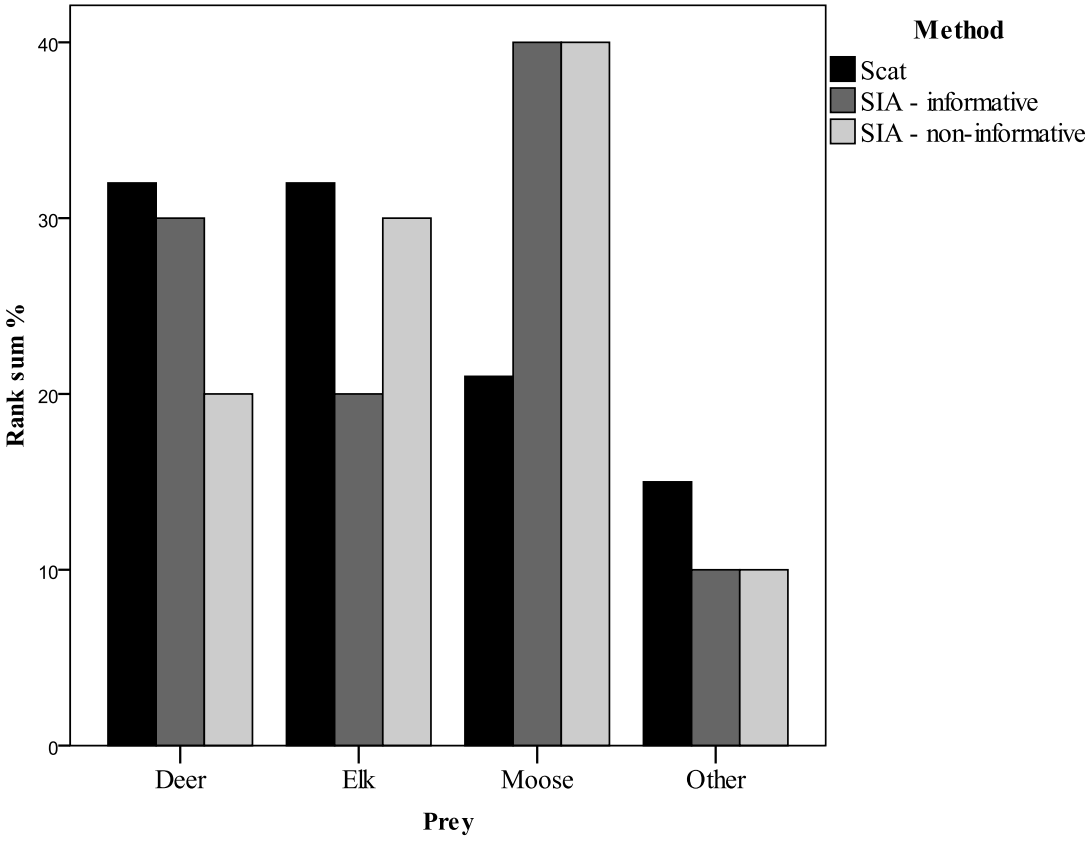

Figure 6. Non-parametric rankings of prey consumed by wolves in northwestern Montana, summer 2008. Scat rankings are for 4 packs. Stable isotope analysis rankings are for 12 packs. Bars represent relative position out of 4, not proportions of prey consumed.