Diet composition and prey selectivity of gray wolves (*Canis lupus*) in Prince Albert National Park, Saskatchewan

by

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Abstract

Plains bison (*Bison bison bison*) were nearly driven to extinction in the late 19th century due to overhunting and habitat loss, and populations occurring within their historic range and co-existing with natural predators are exceedingly rare. Studies examining gray wolf (*Canis lupus*) predation on wild, genetically-pure bison populations are limited to only a few areas in North America. We studied wolf predation on plains bison and other ungulates in Prince Albert National Park (PANP), Saskatchewan. The Sturgeon River plains bison (SRPB) are one of only a few wild populations of plains bison in their historical range in Canada, and have experienced a decline of around 50% since 2005. Disease and annual harvests contributed to past bison mortality, but the role of predation in the SRPB decline was unclear. We used stable isotope analysis to examine intra- and inter-annual variation in wolf diet to assess the importance of bison and other ungulates to wolves, relative to the decline of the SRPB. In addition, we measured hair cortisol concentrations (HCC) and marrow lipid content of wolf-killed prey to evaluate the link between chronic stress, body condition, and vulnerability to predation by gray wolves. We found greater variation in proportions of prey consumed by wolves during summer, in comparison to winter when white-tailed deer (*Odocoileus virginianus*) were the main prey. Wolves that had a higher degree of overlap with the SRPB range had more bison in their diet, particularly during winter. Wolf-killed bison had significantly higher HCC compared to human-harvested bison, and bison showed the strongest negative relationship between HCC and marrow lipid content in comparison to moose (*Alces alces*) and deer. Management of the SRPB population should be focused on reducing human-harvests, rather than wolf predation, to lower extinction risk and aid in population recovery.

Preface

This thesis is an original work by Justin R. Shave. Data used in all analyses were generated via stable isotope, marrow lipid, and hair cortisol concentration analyses conducted on wildlife tissue samples. Tissue samples were collected by Prince Albert National Park staff and field technicians, or submitted by wildlife harvesters, First Nations, or landowners in the vicinity of the Park. Stable isotope samples were prepared and analyzed using mass spectrometry at the Great Lakes Institute for Environmental Research, University of Windsor. Marrow was extracted and lipids were analyzed at York University. Hair samples were prepared and analyzed for cortisol concentrations at the Veterinary Biomedical Center, University of Saskatchewan.

To date, chapter two has not been submitted for publication in a peer-reviewed journal, and chapter three has been submitted to Conservation Physiology for review. J. R. Shave was responsible for the data analysis as well as the manuscript composition. Co-authors for chapter two include Andrew E. Derocher, Seth G. Cherry, and Gregory W. Thiemann. Co-authors for chapter three include S. G. Cherry and A. E. Derocher. All co-authors provided valuable feedback and edits throughout the analysis and writing process.

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Chapter 1 : General introduction

Predation can regulate species diversity and alter the community structure of ecosystems (Crawley 1992, Berger et al. 2001, Hawlena and Schmitz 2010). The effects of predators can be direct through predation events (Lima and Dill 1990, Hebblewhite et al. 2002, Heinsohn et al. 2015), as well as indirect through competition or trophic facilitation with other predators, trophic cascades, and apparent competition (Huggard 1993b, Schmitz et al. 2000, Wilmers et al. 2003, Kortello et al. 2007, Wittmer et al. 2013). Furthermore, predation risk can alter the behaviour of prey, resulting in changes to ecosystem dynamics (Sih et al. 2000, Van Dievel et al. 2016, Palmer et al. 2017, Barbosa et al. 2018). Patterns of prey selection can be influenced by predator-prey encounter rates and prey susceptibility (Greene 1986). Encounter rates may be affected by prey density, habitat, and/or landscape characteristics (Greene 1986, Huggard 1993a), while prey vulnerability may be influenced by prey demographics, body condition, and/or landscape features (Quinn and Cresswell 2004, Bergman et al. 2006; McPhee et al. 2012). Insight into predator-prey interactions is important to understand the potential factors influencing prey declines, particularly for small populations at risk for extinction (Sinclair et al. 1998, Wittmer et al. 2005, Mech and Fieberg 2014).

Gray wolves (*Canis lupus*) have been studied to examine the effects of predation at the population, community, and ecosystem level (Schmitz et al. 2000, Kortello et al. 2007, Ripple et al. 2014). Due to the disproportionate effects that wolves can have on ecosystem dynamics, they are considered a keystone species (Paine 1969, Mills et al. 1993, Smith et al. 2003, Ripple et al. 2014). Wolves in Yellowstone National Park (YNP) regulate elk (*Cervus elaphus*) populations (White and Garrott 2005). When wolves were extirpated from YNP, elk overgrazed cottonwood (*Populus* spp.) trees as there was no longer predation to constrain elk populations (Beschta

2003). Upon their reintroduction to YNP, wolves altered elk movements, browsing patterns, and foraging behaviour, which contributed to vegetation re-growth (Ripple et al. 2001; Ripple et al. 2014). A similar example occurred when wolves re-colonized Isle Royale National Park and regulated moose population density, which promoted forest recovery (McLaren and Peterson 1994).

Wolves underwent a vast reduction in their historic range size, and were extirpated from many areas of North America in the 20th century due to their perceived conflict with humans (Young and Goldman 1964). After wolves were listed as *endangered* under the Endangered Species Act (ESA) in the United States and successful reintroductions were implemented, populations began to recover (Mech 1995). Currently, wolf populations are stable in both the United States and Canada (Boitani et al. 2018), but there is still debate on whether wolves should lose their protective status. There are those that view the presence of wolves as a source of pleasure, and reintroductions as a restoration of ecological integrity (Mech 1996). However, increasing wolf populations may result in higher frequencies of conflicts with humans, either directly (Linnell et al. 2000, Geist 2008, Behdarvand and Kaboli 2015) or indirectly through predation on livestock (Meriggi and Lovari 1996). The role of wolves in the decline of ungulate populations is also a contested issue amongst scientists (Seip 1992, Boertje et al. 1996, Hervieux et al. 2014). Removal of protection may make wolves more susceptible to culling, which is controversial in regards to its effectiveness for achieving desired management outcomes (Boutin et al. 2012, Hervieux et al. 2014)

Wolves live and hunt in cooperative packs that consist of up to 20 individuals (Zimen 1976). There are typically two breeding individuals per pack, as well as non-breeding subordinates (Borg et al. 2015). Breeding occurs in winter and pups are born in spring, coinciding with the pulse in ungulate populations (Mech and Boitani 2010b). By autumn, wolf pups are large enough to hunt larger animals that are more difficult to kill (Mech and Boitani 2010b). Pack size can influence the foraging ecology and kill rate of wolves (Thurber and Peterson 1993, Schmidt and Mech 1997). Wolves are opportunistic predators as they may consume a range of food items (Nelson and Mech 1986, Garrott et al. 2007, Metz et al. 2012, Sand et al. 2016).

Wolf predation studies have focused on ungulates, including moose (*Alces alces*; Bergerud et al. 1983, Messier 1994), caribou (*Rangifer tarandus*; Wasser et al. 2011), elk (Carbyn 1983, Hebblewhite et al. 2002), and deer (*Odocoileus* spp.; Kolenosky 1972, Jędrzejewski et al. 1992). In addition, studies have examined wolf predation on livestock (Meriggi and Lovari 1996, Treves et al. 2004) and smaller prey such as fish, beaver (*Castor canadensis*), and sheep (*Ovis* spp.; Szepanski et al. 1999, Darimont and Reimchen 2002, Stanek et al. 2017, O'Donovan et al. 2018). However, fewer studies have examined wolf predation on plains bison (*Bison bison bison*), as there are limited areas where they co-exist (Carbyn and Trottier 1987, Smith et al. 2000, Jung 2011). Historically, bison numbered in the tens of millions, but were nearly driven to extinction in the late 19th century due to overhunting and habitat loss (Samson and Knopf 1994, Isenberg 2001). Wood bison (*B. b. athabascae*) in Wood Buffalo National Park were the main prey of wolves in both the frequency and relative biomass consumed (Carbyn et al. 1993), and wolf predation is relatively common on plains bison in YNP (Smith et al. 2000, Smith et al. 2003). Understanding wolf diet and factors influencing prey selectivity will allow for improved management plans to monitor and conserve plains bison populations in Canada, which were designated as *threatened* in 2004 under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

One method used to quantify consumer diet is stable isotope analysis (SIA), which measures the change in isotopic ratios as nutrients are consumed, metabolized, and reorganized at each trophic level (DeNiro and Epstein 1978; 1981, Peterson and Fry 1987). SIA can be a cost-effective, minimally-invasive technique to estimate diet at various temporal scales (DeNiro and Epstein 1978;1981, Peterson and Fry 1987, Hilderbrand et al. 1996). Three fundamental assumptions must be met before performing SIA. Firstly, prior knowledge of the trophic relationship between consumers and prey must be understood, and only prey selected as potential diet sources should be included in the analysis (Phillips and Gregg 2003, Moore and Semmens 2008). Prior knowledge of source contributions can be obtained through direct observations, scat and/or stomach content analysis, biomass estimation of prey, or previous studies (Votier et al. 2003, Derbridge et al. 2012, Phillips et al. 2014). The second assumption is that prey must be isotopically-distinct from each other (Phillips et al. 2014). The third assumption is that isotope values change predictably during trophic steps. Trophic discrimination is the extent to which isotopic ratios change predictably between trophic levels, due to preferential uptake or excretion of heaver isotopes (Del Rio and Anderson-Sprecher 2008). When SIA is used to estimate diet, a discrimination correction factor is applied to account for the change in isotopic values as it moves through a trophic level (Parnell et al. 2013). Controlled feeding studies have been conducted on wolves and red foxes (*Vulpes vulpes*) to experimentally-derive discrimination factors (Roth and Hobson 2000, Derbridge et al. 2015, McLaren et al. 2015). MixSIAR is a R package that uses Bayesian stable isotope mixing models to estimate the proportional diet of a consumer (Stock and Semmens 2016). MixSIAR includes a multivariate hierarchical component, allowing researchers to estimate the diet of a consumer while accounting for greater variability from sources, trophic discrimination, covariates (e.g., age, region, or time), and individual consumers within a population (Stock and Semmens 2016).

Prey selectivity of wolves may be influenced by a number of factors, including prey abundance or density (Huggard 1993b), environmental conditions (Telfer and Kelsall 1984, Stanek et al. 2017), habitat/landscape characteristics (McPhee et al. 2012b, Torretta et al. 2017), the occurrence of other predators (Atwood et al. 2007), and/or prey vulnerability (McPhee et al. 2012b, Mattisson et al. 2017) . Prey vulnerability may be influenced by the body condition or chronic stress levels of prey (Huggard 1993c), as both factors can negatively affect growth, reproduction, and cognitive ability, increase catabolism of stored energy, and depress immune activity (Boonstra et al. 1998, Sapolsky et al. 2000, Kitaysky et al. 2003, Charmandari et al. 2005, Macbeth et al. 2010). Bio-indicators of chronic stress and body condition include hair cortisol concentration and marrow lipids, respectively, and can be indicative of population status (Sheriff et al. 2011, Meyer and Novak 2012, Raglus et al. 2018). Adverse physiological and morphological effects of chronic stress and poor boy condition may affect population viability (Boonstra et al. 1998, Mumby et al. 2015).

The main objectives of this thesis were to investigate wolf diet and prey selectivity on plains bison and other ungulates in Prince Albert National Park (PANP), Saskatchewan, Canada. The Sturgeon River plains bison (SRPB) population in PANP was established in 1969 from approximately 10-22 founders, which originated from a fenced conservation herd in Elk Island National Park, Alberta. The SRPB population has experienced a decline of around 50% since 2005, and current population estimates are lower than the target management threshold of 400 individuals (Merkle et al. 2015, Cherry et al. in review). Disease and annual harvests are known to contribute to bison mortality, and current plans exist to monitor effects on SRPB population dynamics (Shury et al. 2009, Merkle et al. 2015). No studies have directly examined the role of wolf predation on the SRPB population decline, despite the high degree of overlap between bison and wolves (Harvey and Fortin 2013). As free-ranging populations of bison are reintroduced into their historical range, it will be important to understand the role of predation on bison mortality, particularly when populations are small and at risk for extinction (Merkle et al. 2015, Steenweg et al. 2016, Cherry et al. in review).

In chapter two, titled "Seasonal and inter-annual variation in diet for gray wolves (*Canis lupus*) in Prince Albert National Park, Saskatchewan", we used SIA to examine the intra- and inter-annual variation in diet of two wolf packs in PANP. In chapter three, titled "Chronic stress and body condition of wolf-killed prey in Prince Albert National Park, Saskatchewan", we evaluated the link between chronic stress, body condition, and vulnerability to predation by wolves in bison, moose, and deer. Chapter four provides an overview of the thesis, as well as management implications and areas of future research. Overall, quantifying diet and examining prey selectivity by wolves will provide managers with a greater understanding of predator-prey dynamics within PANP, with applications to wolf-bison populations across North America.

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Chapter 2 : Seasonal and inter-annual variation in diet for gray wolves (*Canis lupus*) in Prince Albert National Park, Saskatchewan

Abstract

Plains bison (*Bison bison bison*) were extirpated from most of their historical range in the late 19th century due to overhunting and habitat loss. Few studies have examined the interactions of bison with gray wolves (*Canis lupus*), as there are limited areas in North America where they co-exist. The Sturgeon River plains bison (SRPB) population in Prince Albert National Park, Saskatchewan is one of only a few populations of plains bison in their historical range in Canada, and have declined around 50% since 2005. This study examined the inter- and intra-annual variation in wolf diet using stable isotope analysis, to assess the importance of bison and other ungulates to wolf diet relative to the decline of the SRPB. We used wolf hair (*n* = 35) and blood (*n* = 29) collected from 30 individuals from 2011 to 2017 to estimate the diet of two wolf packs for summer and winter, visiting potential wolf kill sites (*n* = 270) during the winter from 2013 to 2017 to collect prey samples. We used wolf scats (*n* = 465) collected and analyzed in the winter and summer of 2012 to 2013 as priors for our Bayesian stable isotope mixing models. We found the percentage of bison, deer/elk, and moose consumed in the summer was consistently high for all years, compared to winter when white-tailed deer (*Odocoileus virginianus*) comprised the highest percentage of wolf diet (median range: 40-49%). We observed small inter-annual variation in wolf diet. We examined differences in diet between wolf packs, and found that wolves that had a higher degree of overlap with the SRPB had more bison in their diet, particularly in winter (26-40%). Results from SIA were consistent with proportions of prey found at kill sites, and based on both methods wolves do not appear to be disproportionately contributing to the decline of the SRPB when compared to mortality factors such as harvests.

Introduction

Studying predator-prey dynamics requires an understanding of both predator diet and prey availability (Fryxell and Lundberg 1994, Křivan and Sikder 1999). Predators can affect other species directly through predation events or indirectly through competition or trophic facilitation with other predators, trophic cascades, and apparent competition (Lima and Dill 1990, Schmitz et al. 2000, Wilmers et al. 2003, Kortello et al. 2007, Wittmer et al. 2013). Insights into predator-prey interactions are important for understanding the factors behind prey decline, particularly for small populations at risk of extinction (Sinclair et al. 1998, Wittmer et al. 2005, Mech and Fieberg 2014).

Gray wolves (*Canis lupus*) have been studied to examine both the direct and indirect effects of predation on other species, as well as conflicts with humans through predation on livestock (Wilmers et al. 2003, Kortello et al. 2007, Wittmer et al. 2013, Nelson et al. 2016, Santiago-Avila et al. 2018). Wolf predation has been studied on numerous wild ungulates, including deer (*Odocoileus* spp.), elk (*Cervus elaphus*) and moose (*Alces alces*), and may influence population dynamics of prey (Huggard 1993b, Hebblewhite et al. 2002, Smith et al. 2004). Less-commonly studied are interactions between wolves and plains bison (*Bison bison bison*), as there are fewer areas where they co-exist (Carbyn and Trottier 1988, Lott 1991 Smith et al. 2000, Jung 2011). Historically, bison numbered in the tens of millions but were nearly driven to extinction in the late 19th century due to overhunting and habitat loss (Samson and Knopf 1994, Isenberg 2001). Bison have since increased in abundance, but most herds consist of farmed or captive animals with cattle gene introgression (Halbert and Derr 2006, Freese et al. 2007). Therefore, studies investigating wolf predation on wild, genetically-pure bison are limited to only a few areas in North America (Carbyn et al. 1988, Smith et al. 2000, Freese et al. 2007, Harvey and Fortin 2013).

The diet of wolves can be estimated using direct observation of kills (Boyd et al. 1994, Sand et al. 2005), scat and stomach content analysis (Floyd et al. 1978, Ciucci et al. 1996, Merkle et al. 2009), and stable isotope analysis (SIA; Szepanski et al. 1999, Derbridge et al. 2012, Stanek et al. 2017, O'Donovan et al. 2018). SIA quantifies the change in isotopic ratios as nutrients are consumed, metabolized, and reorganized at each trophic level, which allows for the relative proportion of each food to be determined for a consumer (DeNiro and Epstein 1978;1981, Peterson and Fry 1987). SIA can examine diet at the individual, group, or population level (Urton and Hobson 2005, Derbridge et al. 2012, O'Donovan et al. 2018). As well, tissues used in SIA can provide diet history spanning weeks (e.g. blood) to months (e.g. hair) to lifetimes (e.g. bone collagen; Chisholm et al. 1982, Tieszen et al. 1983, Hilderbrand et al. 1996), allowing researchers to explore temporal differences in diet (Peterson and Fry 1987, Darimont and Reimchen 2002, Hall-Aspland et al. 2005, Gómez et al. 2018).

We used SIA to examine seasonal and inter-annual variation in the diet of wolves for two packs that overlap with plains bison range in Prince Albert National Park (PANP), Saskatchewan. The Sturgeon River plains bison (SRPB) are one of only a few wild populations of plains bison in their historical range in Canada, and have declined by around 50% since 2005, when the population was estimated at ~474 individuals (Merkle et al. 2015). Current population estimates are lower than the target management threshold of 400 individuals (Cherry et al. in review). Disease and annual harvests have contributed to past bison mortality (Shury et al. 2009, Merkle et al. 2015), but the role of predation in the SRPB decline is unclear. Population simulations for the SRPB indicate unsustainable harvest is likely the main factor limiting population recovery; however, these models assume predation rates similar to other bison populations (Cherry et al. in review). No studies have directly investigated the role of predation by gray wolves on the SRPB population. As free-ranging populations of plains bison are reintroduced into their historical range, it is important to understand the effects of predation on bison population dynamics (Steenweg et al. 2016).

We hypothesized that wolf diet would vary seasonally, between summer and winter, due to variation in prey availability and vulnerability. We predicted that wolves would primarily consume wild ungulates in the winter, as ungulate movements are inhibited by deep snow and body condition is generally poorer, making prey more susceptible to predation (Sweeney and Sweeney 1984, Telfer and Kelsall 1984, Metz et al. 2012). Pack cohesiveness is also higher during the winter (Benson and Patterson 2014), potentially allowing wolves to consume larger prey such as bison (Zimen 1976, Metz et al. 2011). During the summer, we expected beaver (*Castor canadensis*) to contribute more to wolf diet, as they are more accessible outside of their lodges. In the summer, there is also overlap between pack territory and summer pasture of cattle, which may increase the occurrence of predation on livestock. We also hypothesized that there would be variation in diet between wolf packs. Since wolves are territorial, and buffer zones that separate adjacent territories can be as wide as 1-2 km, overlap between wolves from different packs is uncommon and often results in inter-pack conflict (Mech 1977, White et al. 1996). We predicted bison would constitute a higher proportion of diet for wolves that show greater overlap with more with the SRPB range (Bergeson 1993).

Methods

Study Area

Our study area was located in the southwest corner of PANP, where wolves overlap with plains bison range (centered at 53.7246 N, 106.6754 W; Fig. 2.1). This area is characteristic of an aspen parkland ecotone, with remnant fescue grassland in the southeast section of our study area. The climate is typified by long, cold winters and short, warm summers. There are two wolf packs in this area (Amyot and Nesslin), that have been monitored since 2006 using GPS-collars.

Wolf kill site visits and sample collection

Wolves were located and captured using a helicopter, and either physically restrained with a net-gun or chemically immobilized with Telazol using a dart gun in November to April from 2011 to 2017 (Proulx et al. 2012). All captures and handling followed Parks Canada protocol and were approved by the Parks Canada Agency Animal Care Task Force. We used wolf GPS-collar data (Argos- and Iridium-linked, Telonics Inc, Mesa, AZ, USA) on two wolf packs (Amyot and Nesslin) to track and identify kill sites (*n* = 270) where prey samples were collected. We identified kill sites using a rule-based algorithm programmed in Python TM language (Python Software, Hampton, NH, USA; Knopff et al. 2009) that identified clusters of GPS points that were within 300m and four days of each other (Sand et al. 2005). This method can identify large-bodied prey consumed by wolves, and up to 83% of deer kills (Webb et al. 2008). We were most interested in detecting bison (large-bodied) kills, and so we preferentially visited larger clusters. We waited a minimum of seven days between the initial cluster formation and our field visit, to ensure enough time had elapsed for the wolves to consume and scavenge their kill (Merrill et al. 2010). Kill sites were visited in November to March from 2013 to 2017. We estimated percentage of biomass consumed by wolves by multiplying each prey item by weight estimates for sex-age class from literature values, and estimates for the percentage of carcass consumed for large- and small-bodied prey (Ackerman et al. 1986, Wilmers et al. 2003, Miller et al. 2013)

Hair samples for white-tailed deer (*Odocoileus virginianus*), moose, bison, and elk were collected by plucking from the carcass or from clumps of hair on the ground at the kill site. Hair from beaver was obtained from trappers west of PANP. Hair from cattle was collected from private landowners within the vicinity of PANP. Hair and blood from wolves were collected during GPS-collaring events from 2011 to 2016. Guard hairs were plucked from the back or shoulder and blood was drawn from the cephalic, saphenous, or jugular vein of immobilized wolves. All samples were stored frozen (-20°C) until analysis.

SIA of blood and hair samples were performed at the Chemical Tracers Lab (University of Windsor, Windsor, ON, Canada). Blood samples were freeze-dried, homogenized, and lipids were removed, since variation in lipid concentrations can influence measurements of carbon isotope ratios (Rau et al. 1992, Post et al. 2007, Logan et al. 2008). Two milliliters of a 2:1 chloroform methanol mixture was added to dried blood samples, which were then vortexed for two seconds and placed in a water bath for 24h at 30°C. Samples were centrifuged, and the chloroform methanol solution was drained. Another two milliliters of the chloroform methanol solution was then added, and samples were centrifuged and drained again. We removed underfur from hair samples and rinsed samples under a ventilation hood in a 2:1 chloroform/methanol solution to remove fine debris and oils (Darimont et al. 2007). All samples were air dried before weighing.

Samples were weighed (~1 μg) and placed into tin capsules for continuous-flow mass spectrometry analysis using a Delta V Advantage mass spectrometer (Thermo Fisher Scientific, Waltham, MA, USA) coupled to a Costech 4010 elemental combustion system (Costech Analytical Technologies Inc., Santa Clarita, CA, USA) and a ConFlo IV gas interface (Thermo Fisher Scientific, Waltham, MA, USA). During continuous-flow mass spectrometry analysis, samples were combusted, resulting in the separation of CO_2 and N_2, which we used to quantify isotopic ratios (Fry 2006). Isotope values are expressed in delta notation as

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) 1000,$$

where X is ^{13}C or ^{15}N, and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standards used in SIA are Peedee Belemnite limestone for carbon, and atmospheric N^2 for nitrogen (DeNiro and Epstein 1978; 1981).

SIA of wolf hair and blood

We used guard hairs and red blood cells (RBCs) for SIA of wolves. Hair tissue does not turnover, and thus reveals the diet of an individual when it is growing (Roth and Hobson 2000). Wolves undergo an annual moult in the spring, and guard hair is grown from summer to autumn (Young and Goldman 1964, Darimont and Reimchen 2002, Darimont et al. 2009). Therefore, guard hair reflects the summer and autumn diet of wolves. Cellular components of blood differ in their isotopic half-lives, with plasma reflecting diet integrated approximately one to two weeks before collection, and RBCs representing the diet of the previous several months (Hilderbrand et al. 1996, Thomas and Crowther 2015, Rode et al. 2016). Since we used RBC samples collected from wolves in November to April, we expected $\delta^{13}C$ and $\delta^{15}N$ values to be more representative of wolf diet in late autumn and winter.

Aerial wildlife surveys, scat analysis, and wolf kill site visits were used to select prey to include in our mixing models (Szepanski et al. 1999, Darimont and Reimchen 2002, Derbridge et al. 2012, O'Donovan et al. 2018). We used non-parametric Mann-Whitney U tests to examine if species were isotopically distinct, and accounted for error associated with multiple comparisons using a Bonferroni correction (Bland and Altman 1995, Cabin and Mitchell 2000). We used diet-hair and diet-blood discrimination factors (hair: $\delta^{13}C = 2.6\%$, $\delta^{15}N = 3.2\%$; blood: $\delta^{13}C = 0.7\%$, $\delta^{15}N = 2.6\%$) from a captive feeding study on red foxes (*Vulpes vulpes*; Roth and Hobson 2000) to account for isotopic change through trophic levels (Del Rio and Anderson-Sprecher 2008, Parnell et al. 2013, McLaren et al. 2015). We used data analyzed from wolf scat as priors for our mixing models (Merkle et al. 2014). Wolf scat ($n = 465$) was collected opportunistically during the summer and winter of 2012 to 2013, and analyzed for the percent frequency of occurrence of prey. Prey biomass estimates were calculated using a regression equation that accounted for the ratio of indigestible to digestible remains (Table 2.1; Floyd et al. 1978, Weaver 1993).

We ran Bayesian stable isotope mixing models to estimate wolf diet during summer and winter from 2011 to 2017 (Moore and Semmens 2008, Semmens et al. 2009). We included a process*residual error term in our models (Stock and Semmens 2016b). For each model we ran three chains that were 100 000 iterations long, with a burn-in of 50 000 and thinned every 50th iteration. We used Gelman-Rubin diagnostic tests to assess convergence for each model, not allowing more than one value above 1.1 for all variables in the model, as well as trace plots produced by MixSIAR (Stock and Semmens 2016a). We also used a pairs plot to examine trade-offs between any strongly correlated prey before interpreting diet results (Stock and Semmens 2016a). All models were run using JAGS and R software (Plummer 2003, R Core Team 2017) and the R package MixSIAR (Stock and Semmens 2016a).

Results

Parameters validation

Hair samples were obtained from 14 deer, 16 moose, 12 bison, 4 elk, 10 beaver, and 7 cattle. We collected hair (*n* = 35) and blood (*n* = 29) from 30 wolves. The means and standard errors of $\delta^{13}C$ and $\delta^{15}N$ varied between wolf packs as well as diet sources (Table 2.2). Elk could not be isotopically separated from other prey, violating an assumption of stable isotope mixing models. Therefore, we combined deer and elk before running our models, as they shared the same region of the mixing space and are taxonomically closely-related. All other prey were isotopically distinct. Isotopic values for hair and blood samples from wolves were centered on ungulates in the mixing space, and no outliers were observed (Fig. 2.2).

SIA of summer and winter wolf diet

For combined pack data, the percentage of bison, deer/elk, and moose consumed in the summer was consistently high for all years (Table 2.4; bison: median range = 26-39%; deer and elk: 21-24%; moose: 16-33%). Wide 95% credible intervals (CI) for the posterior distribution of models resulted in considerable overlap between prey. Cattle (3-7%) and beaver (1-9%) comprised a lower percentage of wolf diet in the summer for all years. We found similar prey contributions for both wolf packs in the summer. The contribution of bison to the diet of the Amyot pack was higher in 2011, 2013, and 2014 (Table 2.4). However, wide CIs for posterior distributions indicated a large variation in prey contributions.

In winter, we found a higher percentage of deer /elk consumed by wolves for all years, compared to the summer (Table 2.5; 40-49%). We found a similar percentage of bison consumed in the winter compared to the summer (25-45%), and almost no contribution from cattle or beaver. Bison comprised a higher percentage of diet for the Amyot pack (26-40%) compared to the Nesslin pack (20-23%), while the median percentage of moose in wolf diet was higher for the Nesslin pack in 2013, 2014, and 2016 (19-35%).

Wolf kill site visits

Of the kill sites that we visited ($n = 270$), deer were found most frequently during all winters, 77% of the time (Table 2.5). Moose were recorded at kill sites most frequently in 2015 (31% of visits), and on average 15% over all years. Bison were found at kill sites most frequently in 2014 (16% of visits), and on average 7% for all years. Elk were found least frequently at kill sites (1% of visits). When we corrected for the biomass of prey, deer accounted for 45% of wolf diet, moose for 24%, bison for 29%, and elk for 2% (Table 2.5).

Discussion

We found wolf diet varied between summer and winter, with a more equal contribution of wild ungulates to wolf diet in the summer. Deer/elk comprised the highest percentage of wolf diet in winter, supplemented by bison and moose. While we found evidence that wolves consumed beaver and cattle in the summer, diet contributions were minimal overall. Relative proportions of prey contributions were similar among years. Bison comprised a higher percentage of the diet for the Amyot pack in both summer and winter, while diet contributions for other prey were similar between packs.

Wolves were centered on ungulates in the isotope mixing space, which is supported by other studies on wolf diet (Milakovic and Parker 2011, Derbridge et al. 2012). Urton and Hobson (2005) performed SIA on wolves in central Saskatchewan, which overlapped with our study area in PANP, and found elk and deer dominated wolf diet, although they did not include bison in their mixing model. The main prey of wolves shows considerable variation across regions, and includes moose (Ballard et al. 1987, Mech and Fieberg 2014), deer (Ballard et al. 1987, Huggard

1993b), elk (Huggard 1993b, Smith et al. 2000, Hebblewhite et al. 2002, Smith et al. 2004, Atwood et al. 2007, Kortello et al. 2007), and caribou (*Rangifer tarandus*; Ballard et al. 1987, Merkle et al. 2017). Wolves may also supplement their diet with smaller prey (Szepanski et al. 1999, Milakovic and Parker 2011, Derbridge et al. 2012, O'Donovan et al. 2018). The primary prey of wolves can be dependent on habitat overlap between predator and prey, prey density, and therefore the encounter rate between wolves and prey (Huggard 1993b).

Wolves are opportunistic and switch their diet as needed. Prey switching can occur as a result of a number of factors (that are not mutually exclusive), including in response to seasonal and environmental changes (Nelson and Mech 1986, Szepanski et al. 1999), the occurrence of other predators (Kortello et al. 2007, Merkle et al. 2017), prey vulnerability (Bergman et al. 2006, Garrott et al. 2007, Metz et al. 2012), or changes in the abundance of prey (Garrott et al. 2007, Sand et al. 2016). We found that winter diet for wolves centered on ungulates, particularly deer, which is what we had predicted. Deep snow (>70 cm) can inhibit ungulate movement, restricting access to forage and increasing energetic output, making them more susceptible to predation by wolves (Telfer and Kelsall 1984, Huggard 1993a, Mech et al. 2001, Smith et al. 2004). We expected bison contributions to be higher in winter, as wolf pack cohesiveness is higher (Benson and Patterson 2014), and deeper snow may make bison more susceptible to predation by wolves. However, hunting activities occur in the late summer and autumn, and it is likely that wolves scavenge gut piles and/or consume bison that are wounded or stressed during unsuccessful hunting attempts, which may have increased diet contributions of bison for summer SIA. Beaver and cattle are less available to wolves in the winter, as beavers reside in lodges and forage under the ice (Muller-Schwarze 2011), and cattle are on their winter pasture. In summer when there was greater overlap between wolves and cattle pasture, we found little evidence of cattle depredation. Other studies have shown wolf predation on livestock occurs infrequently when wild ungulates are readily available (Meriggi and Lovari 1996, Oakleaf et al. 2003, Treves et al. 2004).

Variation in diet may also be observed between wolf packs, due to differences in prey availability between packs. Prey abundance can differ between packs as a result of habitat and landscape heterogeneity between regions, which can influence foraging and migration patterns of prey (Gustine and Parker 2008, Milakovic and Parker 2011, Muposhi et al. 2016). Variation in habitat type/quality not only influences prey availability and density, but it can also affect prey vulnerability by modifying prey detection, access, and/or the success of an attack (McPhee et al. 2012a;b, Torretta et al. 2017). We found bison comprised a higher percentage of diet for the Amyot pack compared to the Nesslin pack. There is greater overlap between the SRPB population and the Amyot wolf pack (Fig. 2.3; Bergeson 1993), which would have increased the encounter rate between wolves and bison. In addition, landscape characteristics within the SRPB range, including flat, open meadows, may have increased vulnerability of bison to wolf predation (Bergeson 1993, McPhee et al. 2012b, Torretta et al. 2017). Finally, the Amyot pack is larger than the Nesslin Pack, which may increase the acquisition and consumption of larger prey, such as bison, for wolves in the Amyot pack, due to benefits of cooperative hunting (MacNulty et al. 2014)

Overall, SIA, kill sites, and scat analysis, reveal that wolves are consuming bison in PANP. There was considerable variation in the posterior distribution of our stable isotope mixing models, which confounds our interpretation of prey contributions to wolf diet. In our mixing models, we incorporated uncertainty in both our isotope and red fox discrimination factors. While controlled feeding studies have been performed on wolves (Derbridge et al. 2015, L'Hérault et al. 2018), red fox discrimination factors have been commonly-used for wolf diet studies (Darimont et al. 2009, Milakovic and Parker 2011, Derbridge et al. 2012). Derbridge et al. (2015) found that specifying wolf fractionation rates made little practical difference when estimating wolf diet. The red fox discrimination factors placed wolves within the prey hypervolume in iso-space, suggesting that it is accurately representing wolf diet-tissue discrimination. We also incorporated priors into our models using results from wolf scat analysis, which often improves mixing model outputs by guiding parameter estimates and reducing the variance of prey contributions (Moore and Semmens 2008). However, there was considerable overlap among the posterior distributions of our mixing models, which was most likely a result of the similarity of our sources in the isotope mixing space, and is common when using SIA to reconstruct carnivore diet (Derbridge et al. 2012).

Deer and elk could not be isotopically separated, as they display high dietary overlap of browse and grass species, particularly during the summer (Hansen and Reid 1975, Krysl and Bryant 2016). While moose and beaver spend a large portion of time foraging in aquatic habitats, beaver may consume greater quantities of browse, leading to higher δ^{13}C values (Drucker et al. 2003). Bison had higher δ^{13}C, indicating they are foraging primarily on C_3 plants, which is expected in an aspen parkland ecotone (Chisholm et al. 1986). The overlap between combined δ^{13}C and δ^{15}N signatures is normal when all prey are occupying a similar ecological niche, particularly when compared with δ^{13}C and δ^{15}N values from other ecosystems (Chisholm et al. 1982, Szepanski et al. 1999, Webb et al. 2017).

In conclusion, bison constitute a smaller proportion of wolf diet when compared to other ungulates, which is consisten with results from other wolf-bison predator-prey systems (Smith et al. 2000, Jędrzejewski et al. 2002, Smith et al. 2004). However, predation in combination with other mortality factors, such as disease and harvest, may further population decline and increase extinction risk of the SRPB population (Joly and Messier 2004, Merkle et al. 2015, Sigaud et al. 2017). Extinction risk for the SRPB was highest in population simulations when the effects of harvests and disease were combined (Cherry et al. in review). Therefore, management of the SRPB population should focus on reducing harvests, rather than wolf predation, to aid in the population recovery of the SRPB.

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Table 2.1 Percent of total biomass (%) of prey items from wolf scats (n = 465) collected opportunistically during the summer and winter of 2012 to 2013 in the southwest corner of Prince Albert National Park, Saskatchewan. Biomass estimates were calculated using a regression equation, which accounted for the ratio of indigestible to digestible remains (Floyd et al. 1978, Weaver 1993).

	Percent of total biomass (%)	
Species	Summer	Winter
Beaver	6	0
Bison	35	24
Cattle	14	0
Deer/Elk	30	57
Moose	13	18

Table 2.2 Means ($\bar{x}$) and standard errors (SE) of $\delta^{13}C$ and $\delta^{15}N$ values estimated from hair and blood tissue of wolves, and hair tissues from diet sources, collected from 2011 to 2017 in Prince Albert National Park, Saskatchewan.

		$\delta^{13}C$		$\delta^{15}N$	
Species	*n*	$\bar{x}$	SE	$\bar{x}$	SE
Wolf (hair)	35	-23.86	0.08	6.96	0.15
Amyot	23	-23.94	0.10	6.90	0.25
Nesslin	12	-23.73	0.07	7.04	0.22
Wolf (blood)	29	-25.92	0.11	7.46	0.20
Amyot	19	-25.97	0.40	7.87	0.25
Nesslin	10	-26.01	0.13	6.68	0.10
Bison	12	-26.29	0.08	6.24	0.23
Deer	14	-26.51	0.24	4.46	0.33
Moose	16	-26.74	0.11	2.28	0.23
Elk	4	-26.25	0.05	4.21	0.56
Cattle	7	-24.60	0.09	7.68	0.90
Beaver	10	-24.70	0.22	4.53	0.49

Table 2.3 Mann–Whitney U test scores for tests of difference between δ^{13}C and δ^{15}N values of wolf diet sources from hairs collected from 2011 to 2017 in Prince Albert National Park, Saskatchewan.

		Bison	**Deer**	**Moose**	**Elk**	**Cattle**	**Beaver**
Bison (*n* = 12)	δ^{13}C		109	156*	19	0***	4**
	δ^{15}N		148*	192***	42*	61	101
Deer (*n* = 14)	δ^{13}C	109		127.5	16	2***	6**
	δ^{15}N	148*		207**	31	28**	67.5
Moose (*n* = 16)	δ^{13}C	156	127.5		10	0***	3***
	δ^{15}N	192***	207**		8	2***	12.5*
Elk (*n* = 4)	δ^{13}C	19	16	10		0***	0*
	δ^{15}N	42*	31	8		3.5	17
Cattle (*n* = 7)	δ^{13}C	0***	2***	0***	0*		98
	δ^{15}N	61	28*	2**	3.5		114
Beaver (*n* = 10)	δ^{13}C	4**	6**	3***	0*	98	
	δ^{15}N	101	67.5	12.5*	17	114	

*, **, and *** indicate δ^{13}C or δ^{15}N values are statistically different at the 0.05, 0.01, and 0.001 significance levels, respectively.

Table 2.4 Posterior median estimates and 95% credible intervals of summer diet proportions for Amyot (A), Nesslin (N), and combined wolf packs, from Bayesian stable isotope mixing models. Wolf diet was estimated from 2011 to 2017 in Prince Albert National Park, Saskatchewan. Years that data were unavailable are indicated by N/A.

	Median proportion of summer diet (95% CI) from diet source				
Year	Beaver	Bison	Cattle	Deer and Elk	Moose
2011					
Combined	0.09 (0.00, 0.30)	0.26 (0.06, 0.57)	0.07 (0.00, 0.25)	0.21 (0.04, 0.52)	0.29 (0.01, 0.54)
A	0.08 (0.00, 0.30	0.25 (0.05, 0.58)	0.07 (0.00, 0.26)	0.21 (0.03, 0.53)	0.28 (0.00, 0.53)
N	0.03 (0.00, 0.24)	0.19 (0.03, 0.46)	0.04 (0.00, 0.20)	0.29 (0.05, 0.75)	0.34 (0.01, 0.63)
2012					
Combined	0.04 (0.00, 0.25)	0.39 (0.13, 0.74)	0.06 (0.00, 0.25)	0.24 (0.04, 0.58)	0.16 (0.00, 0.41)
A	0.04 (0.00, 0.24)	0.39 (0.13, 0.74)	0.06 (0.00, 0.24)	0.24 (0.03, 0.57)	0.16 (0.01, 0.42)
N	0.03 (0.00, 0.20)	0.43 (0.14, 0.71)	0.05 (0.00, 0.27)	0.23 (0.03, 0.62)	0.16 (0.00, 0.47)
2013					
Combined	0.01 (0.00, 0.17)	0.33 (0.11, 0.60)	0.03 (0.00, 0.18)	0.24 (0.04, 0.60)	0.31 (0.04, 0.53)
A	0.02 (0.00, 0.18)	0.33 (0.12, 0.63)	0.03 (0.00, 0.15)	0.24 (0.05, 0.58)	0.31 (0.05, 0.53)
N	0.03 (0.00, 0.30)	0.28 (0.04, 0.73)	0.04 (0.00, 0.29)	0.24 (0.03, 0.66)	0.26 (0.01, 0.67)
2014					
Combined	0.02 (0.00, 0.19)	0.31 (0.10, 0.57)	0.04 (0.00, 0.16)	0.23 (0.05, 0.54)	0.33 (0.08, 0.56)
A	0.02 (0.00, 0.18)	0.31 (0.07, 0.55)	0.03 (0.00, 0.15)	0.24 (0.03, 0.59)	0.32 (0.04, 0.53)
N	0.03 (0.00, 0.18)	0.19 (0.05, 0.44)	0.04 (0.00, 0.14)	0.19 (0.04, 0.48)	0.50 (0.20, 0.71)
2016					
Combined	N/A	N/A	N/A	N/A	N/A
A	0.00 (0.00, 0.15)	0.14 (0.02, 0.40	0.02 (0.00, 0.13)	0.19 (0.03, 0.59)	0.58 (0.10, 0.82)
N	N/A	N/A	N/A	N/A	N/A
2017					
Combined	0.04 (0.00, 0.28)	0.30 (0.10, 0.58)	0.05 (0.00, 0.23)	0.23 (0.05, 0.55)	0.29 (0.04, 0.50)
A	0.03 (0.00, 0.22)	0.35 (0.10, 0.66)	0.04 (0.00, 0.20	0.24 (0.03, 0.59)	0.32 (0.04, 0.50)
N	0.06 (0.00, 0.34)	0.27 (0.07, 0.63)	0.08 (0.00, 0.32)	0.29 (0.05, 0.66)	0.15 (0.00, 0.43)

Table 2.5 Posterior median estimates and 95% credible intervals of winter diet proportions for Amyot (A), Nesslin (N), and combined wolf packs, from Bayesian stable isotope mixing models. Wolf diet was estimated from 2011 to 2016 in Prince Albert National Park, Saskatchewan.

	Median proportion of winter diet (95% CI) from diet source				
Year	Beaver	Bison	Cattle	Deer and Elk	Moose
2011					
Combined	0.00 (0.00, 0.01)	0.36 (0.10, 0.62)	0.00 (0.00, 0.00)	0.40 (0.15, 0.80)	0.21 (0.02, 0.50)
A	0.00 (0.00, 0.02)	0.35 (0.09, 0.60)	0.00 (0.00, 0.00)	0.41 (0.15, 0.81)	0.20 (0.01, 0.44)
N	0.00 (0.00, 0.00)	0.21 (0.03, 0.49)	0.00 (0.00, 0.03)	0.54 (0.21, 0.90)	0.20 (0.02, 0.52)
2012					
Combined	0.00 (0.00, 0.03)	0.25 (0.03, 0.61)	0.00 (0.00, 0.00)	0.49 (0.19, 0.86)	0.21 (0.01, 0.51)
A	0.00 (0.00, 0.01)	0.26 (0.03, 0.55)	0.00 (0.00, 0.00)	0.48 (0.20, 0.86)	0.21 (0.01, 0.50)
N	0.00 (0.00, 0.00)	0.24 (0.02, 0.55)	0.00 (0.00, 0.00)	0.57 (0.24, 0.90)	0.14 (0.01, 0.46)
2013					
Combined	0.00 (0.00, 0.02)	0.41 (0.07, 0.65)	0.00 (0.00, 0.00)	0.45 (0.19, 0.83)	0.11 (0.01, 0.36)
A	0.00 (0.00, 0.00)	0.40 (0.07, 0.65)	0.00 (0.00, 0.00)	0.45 (0.20, 0.79)	0.11 (0.00, 0.40)
N	0.00 (0.00, 0.00)	0.20 (0.02, 0.43)	0.00 (0.00, 0.00)	0.42 (0.17, 0.77)	0.35 (0.08, 0.56)
2014					
Combined	0.00 (0.00, 0.03)	0.30 (0.03, 0.56)	0.00 (0.00, 0.01)	0.47 (0.18, 0.88)	0.18 (0.01, 0.45)
A	0.00 (0.00, 0.03)	0.30 (0.03, 0.61)	0.00 (0.00, 0.00)	0.46 (0.15, 0.87)	0.18 (0.01, 0.43)
N	0.00 (0.00, 0.01)	0.23 (0.03, 0.49)	0.00 (0.00, 0.00)	0.46 (0.19, 0.86)	0.27 (0.02, 0.52)
2016					
Combined	0.00 (0.00, 0.13)	0.45 (0.05, 0.81)	0.00 (0.00, 0.20)	0.40 (0.10, 0.73)	0.07 (0.01, 0.28)
A	0.00 (0.00, 0.04)	0.34 (0.05, 0.80)	0.00 (0.00, 0.01)	0.30 (0.08, 0.80)	0.05 (0.01, 0.27)
N	0.00 (0.00, 0.01)	0.22 (0.03, 0.50)	0.00 (0.00, 0.00)	0.56 (0.23, 0.86)	0.19 (0.01, 0.48)

Table 2.6 Prey species that were recorded at wolf kill sites visited from November to March in 2013 to 2017 in Prince Albert National Park, Saskatchewan.

Prey Species	Number of kills located	% of total kills	% biomass[a]
Deer	207	77	45
Moose	41	15	28
Bison	20	7	25
Elk	2	1	2
Total	270	100	100

[a] Percent biomass was calculated by multiplying each prey item by weight averages for each sex-age class from the literature, and estimates for the percentage of carcass consumed for large- and small-bodied ungulates (Ackerman et al. 1986, Wilmers et al. 2003).

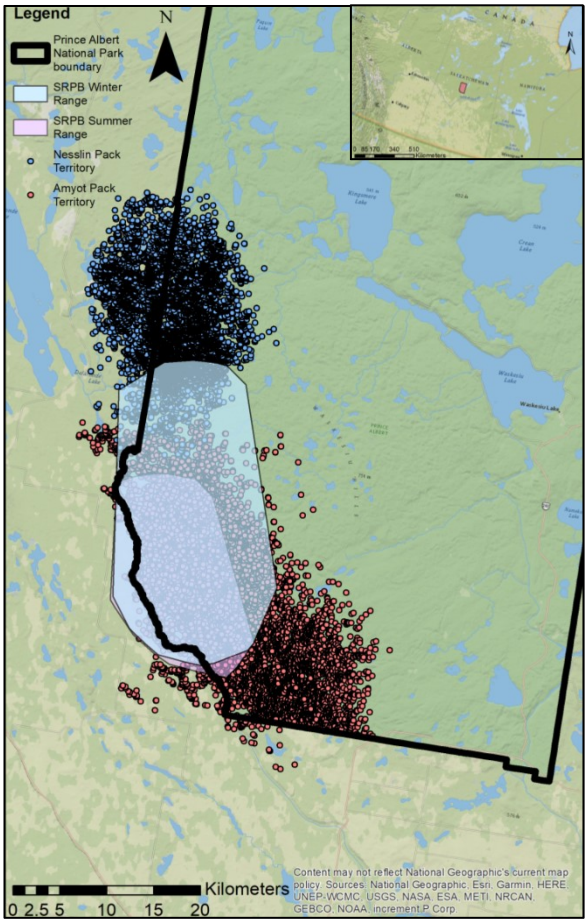
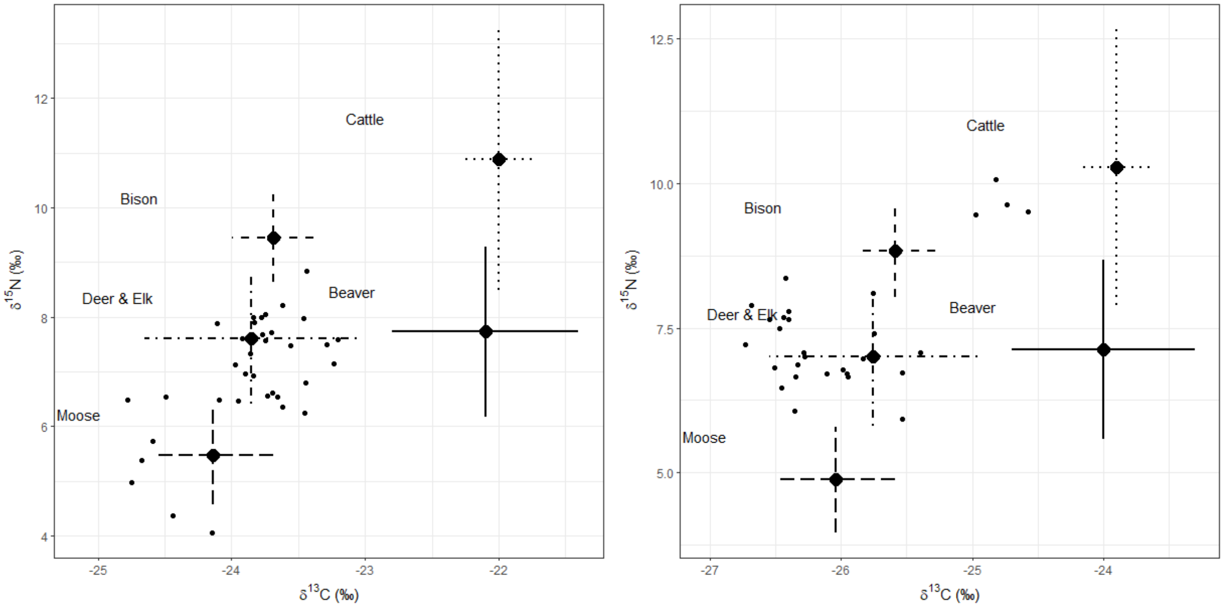


Fig. 2.1 The approximate range and territory size of plains bison and gray wolves, respectively, in Prince Albert National Park. The summer and winter range of bison was estimated using 95% minimum convex polygons. Location data for bison were collected from GPS-collars deployed from 2011 to 2017 over both the summer/fall (June to October) and winter (November to March). Location data for wolves were collected from GPS-collars deployed from 2013 to 2017 over the winter (November to March).



a) Summer

b) Winter

Fig. 2.2 The mixing space of δ^{15}N values and δ^{13}C values, using discrimination values of 2.6% and 3.2% for hair, respectively, and discrimination values of 0.7% and 2.6% for blood, respectively, for potential wolf prey (±SE). Wolf isotope values represent summer and winter diet from 2011 to 2017 in Prince Albert National Park, Saskatchewan.

Chapter 3 : Chronic stress and body condition of wolf-killed prey in Prince Albert National Park, Saskatchewan

Abstract

Chronic stress and poor body condition of prey can cause adverse physiological and behavioural responses, and may make animals more vulnerable to predation. We examined hair cortisol concentration (HCC) and marrow lipid content, as bio-indicators of chronic stress and body condition, respectively, of bison (*Bison bison bison*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) killed by wolves (*Canis lupus*) in Prince Albert National Park, Saskatchewan. The Sturgeon River plains bison population in PANP is one of only a few wild populations of plains bison in their historical range in Canada, and has experienced a decline of around 50% since 2005. We expected wolf-killed prey to have elevated HCC compared to human-harvested animals, and that there would be a negative relationship between HCC and marrow lipids amongst wolf-killed animals. We compared HCC between different mortality sources for bison (wolf-killed or human-harvested; *n* = 43) and found that HCC was elevated in wolf-killed bison (7.56 ± 1.35 pg/mg). We found that HCC, species, sex, and snow depth were all significant predictors of marrow lipid content of bison (*n* = 14), moose (*n* = 11), and deer (*n* = 27). Bison displayed the strongest negative correlation between HCC and marrow lipid percentage ($r^2 = 0.31$). Our results suggest that chronic stress and poor body condition make prey more vulnerable to predation by wolves. HCC and marrow lipid content can provide reliable indicators of the physiological response of animals to stressors, and may provide information on expected predator success which can be used to predict predator population dynamics.

Introduction

In vertebrates, adverse stressors cause the release of glucocorticoids (GC) from the adrenal cortex via the hypothalamic-pituitary-adrenal (HPA) axis (Creel et al. 2009). The release of GC is a component of the stress response and plays a key role in allostasis, which is the active process of maintaining and/or reestablishing homeostasis (McEwen 1998). GCs, such as cortisol, cause behavioural and/or physiological responses which form an adaptive stress response (Le et al. 2005). Stressors that stimulate GC release in wildlife can include parasitism, habitat disturbance, reduction in habitat quality, predation, human hunting pressure, and climate change (Kunkel and Pletscher 2000, Chapman et al. 2006, Lankester 2010, Wasser et al. 2011, Jaimez et al. 2012, Mislan et al. 2016). Acute stress is an immediate adaptive response to adverse stimuli with short-term physiological effects, but chronic or repeated activation of the stress response can be maladaptive and negatively affect growth, reproduction, and cognitive ability, increase catabolism of stored energy, and depress immune activity (Boonstra et al. 1998, Sapolsky et al. 2000, Kitaysky et al. 2003, Charmandari et al. 2005, Macbeth et al. 2010).

Measurement of circulating GC in wildlife can be invasive (e.g. capture and restraint), which can initiate the stress response and alter GC levels (Kersey and Dehnhard 2014). Minimally-invasive methods of GC quantification often use feces, urine, feathers and hair as alternatives (Lafferty et al. 2015, Carlsson et al. 2016, Dantzer et al. 2016, Di Francesco et al. 2017, Seeber et al. 2018). Quantification of fecal glucocorticoids has been conducted on a wide range of taxa, and provides a measure of stress during the time of gut passage (Bonier et al. 2004, Schwarzenberger 2007, Kersey and Dehnhard 2014, Rolland et al. 2017). Cortisol is incorporated into hair during growth, and hair cortisol concentration (HCC) is advantageous for examining chronic stress as it provides a long-term record of stress (e.g. weeks to months) without the need for repeated sampling (Sheriff et al. 2011, Meyer and Novak 2012). HCC has been analyzed in numerous mammals, but fewer studies examine the relationship between HCC and body condition (Mislan et al. 2016, Di Francesco et al. 2017, Ewacha et al. 2017; Heimbürge et al. 2019)

Body condition can be assessed using a variety of morphological or physiological indices, including internal or external fat repositories and measurements such as mass or size (Cattet 1990, Stephenson et al. 1998, Labocha and Hayes 2012, Risco et al. 2018). Another commonly-used method to assess body condition in large mammals is marrow lipids (Neiland 1970, Mech 2007, Yamanaka et al. 2011, Borowik et al. 2016). Marrow lipids are the last energy stores to be metabolized in times of food shortage, and low marrow lipid percentage (10-30%) is indicative of poor body condition (Cheatum 1949, Raglus et al. 2018). The marrow core in nutritionally-stressed individuals appears gelatinous and/or red or yellow, due to higher water content, low red blood cell formation and anemia (Cheatum 1949). Poor body condition can result from low food quality, reproduction, parasitism and environmental factors such as winter severity (Delgiudice et al. 2001, Tollefson et al. 2010, Debeffe et al. 2016, Gardner et al. 2016). In turn, prey body condition, in addition to age, sex and encounter rates, can influence vulnerability to predation (Huggard 1993b;c). Animals killed by predation may have less marrow fat than the same species killed by car accidents (Mech 2007) or human-harvests (Sand et al. 2012).

Understanding the relationship between ungulate stress response and body condition using HCC and marrow lipid content as bio-indicators, respectively, is useful for assessing environmental stressors affecting population status. Negative correlations between GC concentrations, body condition, and immunocompetence are common across taxa (Boonstra 2004, Rich and Romero 2005, Charbonnel et al. 2007, Mislan et al. 2016). Consequently, the combined effect of low reproductive output, poor body condition, and reduced immunocompetence of individuals in a population as a result of chronic stress may impact population viability (Boonstra et al. 1998, Mumby et al. 2015).

We evaluated the link between chronic stress, body condition, and vulnerability to predation by gray wolves (*Canis lupus*) in bison (*Bison bison bison*), moose (*Alces alces*) and deer (*Odocoileus virginianus*) in Prince Albert National Park (PANP), Saskatchewan. The Sturgeon River plains bison (SRPB) population in PANP is one of only a few wild populations of plains bison in their historical range in Canada, and has experienced a decline of around 50% since 2005 (Merkle et al. 2015). Therefore, we examined how stress and body condition may be increasing bison vulnerability to predation. We used prey HCC and marrow lipids as bio-indicators to assess chronic stress and body condition, respectively. We hypothesized that chronic stress levels in prey measured by HCC would differ based on the cause of mortality. We tested this hypothesis by comparing HCC collected from human-harvested versus wolf-killed bison. We predicted that wolf-killed bison would have elevated HCC, as the effects of chronic stress would increase vulnerability of bison to predation. We also hypothesized that HCC would predict body condition of ungulates killed by wolves, when accounting for environmental factors (snow depth and minimum temperature), and age class of prey. We predicted that there would be a negative correlation between HCC and marrow lipid content in wolf-killed ungulates.

Methods

Study Area

Our study area was in the southwest corner of PANP (centered at 53.7246 N, 106.6754 W; Fig. 3.1). This area is characterized by aspen parkland and remnant native fescue grassland in the south, boreal forest in the north, and agricultural land outside of PANP to the west. The upland areas are dominated by trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*), and the lowland areas are dominated by black spruce (*Picea mariana*) and larch (*Larix laracina*; Fortin et al. 2002). The area has long, cold winters (daily mean temperature for January: -16.5°C) and short, warm summers (daily mean temperature for July: +17.7°C), and receives an average of 450 mm of annual precipitation, the majority of which falls as rain.

Sample Collection

We used wolf GPS-collar data on wolves to track and identify kill sites where bison (*n* = 20), moose (*n* = 11), and deer (*n* = 23) samples were collected. We identified kill sites using a rule-based algorithm programmed in Python TM language (Python Software, Hampton, NH, USA; Knopff et al. 2009) that identified clusters of GPS points that were within 300m and four days of each other (Sand et al. 2005). Kill sites were visited during November to March from 2013 to 2017. We used skeletal or hair remains from prey carcasses to identify species and sex-age class (young of year, yearling, or adult). Remains of prey that we could not sex in the field were sexed using DNA extraction and single-locus analysis at Wildlife Genetics International (Nelson, BC, Canada) from ~50mg of muscle sample. A 10-12cm section from the middle of the femur was cut using a handsaw for marrow lipid analysis. Hair samples for cortisol analysis were collected by plucking from the prey carcass or from clumps of hair on the ground at the kill site.

Hair samples from bison (*n* = 23) were also collected during legal harvesting events that occurred outside of PANP (Bergeson 1993). At the harvest location we collected hair and muscle tissue samples, and determined age and sex of bison using the horns and teeth (Fuller 1959). We collected samples during late summer to late autumn from 2013 to 2015, when most harvests occur as bison are more likely to leave PANP to graze on agronomic species (Sigaud et al. 2017). All samples were stored frozen (-20°C) until analysis.

Marrow lipid analysis

We determined marrow lipid content by scooping marrow out of a cross-sectional cut and discarding the exposed surface, which may have been subject to oxidation during storage. We quantitatively extracted the marrow lipid using a modified Folch extraction (Folch et al. 1957, Iverson et al. 2001), with a 2:1 chloroform-methanol (Chl:MeOH) solution and 0.1 mg/ml butylated hydroxytoluene (BHT) to prevent oxidation. Marrow lipid content was expressed as the percent of total sample wet weight.

Hair cortisol concentration analysis

We used guard hairs for cortisol analysis as there is less variation among and within body regions in comparison to underfur (Macbeth et al. 2010). Bison, moose and deer undergo an annual moult in the spring, after which the winter coat of underfur and overlying guard hair is grown over the summer to late fall (Peterson 1978, Meagher 1986). Guard hairs reflect cortisol levels during the summer and fall before sample collection, as cortisol is integrated during hair growth. We removed surface contaminants from hair by performing two 3-min methanol washes (0.1 mL of methanol/mg hair) per sample and drying the samples underneath a fume hood for two days. HCC was extracted and analyzed at the Veterinary Biomedical Center (University of Saskatchewan, Saskatoon, SK, Canada) following Macbeth et al. (2010). We conducted assay validation on bison samples, as this is the first record (that we know of) of HCC analysis for this species. The cortisol extraction efficiency was >95% (Macbeth et al. 2010). Parallelism between serially-diluted bison hair extracts and standard cortisol concentrations was observed (R^2 =

0.994, p = 0.19). The intra-assay coefficient of variability (*n* = 6) was 9.36% and the inter-assay coefficient of variability (*n* = 12) was 11.78%.

Hair cortisol concentrations of wolf-killed versus human-harvested bison

We examined the difference between HCC (log-transformed) of wolf-killed and human-harvested bison. We tested assumptions of normality and homogeneity of variance of our transformed data, and we used a t-test to examine the HCC of wolf-killed or human-harvested bison if assumptions were not violated. We also compared a series of linear mixed effects models to determine which factors best predicted HCC in bison. Variables in our models included mortality source (wolf-killed or human-harvested), age (young of year, yearling, and adult) and sex of bison. We included an interaction term between age and sex, and year as a random effect. Because all of our models were nested, we used Likelihood Ratio Tests (LRT) to examine whether the more complex model was justified by the reduction in likelihood.

Factors affecting prey body condition

We examined the relationship between marrow lipid content and HCC in prey samples from wolf kill sites. We used generalized linear mixed effects models to examine the relationship, using a binomial family for our models and a log-odds link function. We included the variables HCC, species, sex, mean snow depth from the two weeks before sample collection, and mean low temperature from the two weeks before sample collection. We included year and site as a random effect, to account for variation between years and wolf pack. We used Spearman's test of correlation to determine and exclude highly correlated variables ($r^2 > 0.60$). Since all of our models were nested, we used LRTs to examine whether the more complex model was justified by the reduction in likelihood, and accounted for the error associated with multiple comparisons using a Bonferroni correction (Bland and Altman 1995, Cabin and Mitchell 2000).

All analyses were conducted in R (R Core Team 2017) using the package lme4 (Bates et al. 2014), with an alpha (α) value of 0.05.

Results

Hair cortisol concentrations of wolf-killed versus human-harvested bison

The transformed data followed a normal distribution (Shapiro-Wilk test: W = 0.96, $p > 0.05$) and had equal variance across samples (Bartlett test: $K^2 = 1.31$, $p > 0.05$), so we used a t-test to compare HCC of wolf-killed ($n = 20$) to harvested bison ($n = 23$). HCC was significantly higher in wolf-killed bison (Fig. 3.2; Two-sample t-test: t = 8.36, $p < 0.001$). We constructed four different models of varying complexity to explain HCC, including the null model (Table 3.1). Source of mortality (human-harvested versus wolf-killed) was the best predictor of HCC in bison (Likelihood ratio test: D = 7.86, $p < 0.01$; Table 3.2). Males had elevated HCC in both harvested and wolf-killed bison, but sex and age variables were not significant.

Factors affecting prey body condition

HCC and marrow lipids ranged from $\bar{x} = 6.2\pm1.5$ to 9.1 ± 1.3 pg/mg and $\bar{x} = 55.3\pm9.1$ to 77.2 ± 4.1%, respectively, between species (Table 3.3). We constructed five models of varying complexity to explain marrow lipid, including the null model, and we included site and year as random effects to account for variation between wolf packs and years of the study (Table 3.4). Mean snow depth and mean minimum temperature were negatively correlated (Spearman's correlation: $r^2 = -0.64$, S = 38 535, $p < 0.001$), so we used snow depth as a measure of winter severity. We found that the addition of all variables (HCC, species, sex, and snow depth) significantly added to the fit of the models, with species explaining the least in regards to marrow lipid content (Table 3.5). Bison displayed the strongest negative correlation between

HCC and marrow lipid percentage (Fig. 3.3). Females had on average higher marrow lipid content than males, and marrow lipid content decreased with increasing snow depth.

Discussion

Wolf-killed bison had significantly higher HCC than harvested bison, and mortality source was the best predictor of HCC in bison. The range of HCC in bison is comparable to other taxa (Table 3.6). There is considerable inter-individual variation in HCC within a species, which may indicate the health status of individuals (Lafferty et al. 2015, Caslini et al. 2016). Because most hair samples were collected from wolf-killed animals, we were unable to sample the same body region on each individual, as it was dependent on prey remains. HCC can vary between body regions (Sharpley et al. 2010, Terwissen et al. 2013, Carlitz et al. 2015), but we would expect our range of HCC to be larger if this was biasing our results. Marrow lipid analysis provided information over the autumn and winter, based on the period of sample collection, whereas HCC provided measurement of stress over the summer and autumn, based on hair growth in ungulates. While the measurement period of each bio-indicator differed, both quantify stress and body condition over weeks to months. Ideally, stress and body condition would be analyzed concurrently, to better examine a finer-scale relationship between the two variables.

Chronic stress can result in adverse physiological responses, and individuals with high circulating GC concentrations may experience muscle wasting, immunosuppression, a decrease in reproductive ability, growth suppression, and reduced body condition (Boonstra and Singleton 1993, Boonstra et al. 1998, Charbonnel et al. 2007). However, few studies have identified the effects of chronic stress on the fitness of free-ranging populations, and high levels of circulating GC do not necessarily indicate a stress response or that an animal is in poor health (Beehner and Bergman 2017). Although baseline GC levels can estimate the relative fitness of individuals, the relationship varies between species, within populations, and at different life stages (Bonier et al. 2009). We found the strongest negative relationship between HCC and marrow lipid content in bison, with little to no relationship in moose or deer. Such differences across taxa are common (Charbonnel et al. 2007, Mislan et al. 2016, Rakotoniaina et al. 2017, Wolf et al. 2018).

Wolves often select prey that are less fit, including young, old, diseased and injured individuals (Huggard 1993c, Mech and Peterson 2003, Garrott et al. 2007). Prey that are consumed by wolves may have elevated cortisol and low marrow lipid content, because it is easier for wolves to chase, subdue and kill weaker prey (Smith et al. 2000, Husseman et al. 2003). Vulnerability associated with weakness may be particularly important for prey species such as bison, because the risk of injury to wolves is higher during predation events with bison compared to other ungulates (Huggard 1993c, MacNulty 2002, Tallian et al. 2017). Studies on other predators found that individual kill rate was negatively correlated with prey body condition (Mattisson et al. 2017), indicating that the body condition of prey may help to predict predator success rate.

It is difficult to differentiate if poor body condition causes an increase in circulating GC, or if chronic stress causes a decrease in body condition. Animals in poor body condition may exhibit elevated GC concentrations as they must metabolize protein, rather than fat, for energy, resulting in catabolism of muscle tissue (Cherel et al. 1988, Heath and Dufty 1998). Alternatively, experimentally increasing GC concentrations can adversely affect body condition and lead to muscle wasting (Boonstra 2004, Rich and Romero 2005, Charbonnel et al. 2007). Therefore, the effects of chronic stress and body condition on each other are most likely correlated and confounding.

Environmental factors that affect cortisol concentration and body condition of ungulates include parasites and disease, disturbance and habitat quality, seasonality, starvation, and/or injury. Body condition can be negatively related to parasite infection, although the effect size is variable (Carlsson et al. 2016, Sánchez et al. 2018). We did not examine the effect of parasites on body condition on ungulates in our study area, although there was an outbreak of anthrax due to *Bacillus anthracis* that killed 28 bison in our study area in 2008 (Shury et al. 2009). Human disturbance and a reduction in habitat quality can increase GC concentrations in free-ranging wildlife (Boonstra et al. 1998, Creel et al. 2002, Ewacha et al. 2017). Our study area was located in a relatively remote area of a national park, so sustained human disturbance and habitat degradation was minimal. Hiking trails and roads in our study area, as well as human disturbance (vehicle traffic and hazing off of agricultural land) when animals ranged outside of PANP, may have initiated an acute stress response in individuals (Fortin and Andruskiw 2003). Severe weather, such as prolonged, cold winters can decrease forage quality for ungulates and result in poor body condition late in the winter (Cederlund et al. 1991, Delgiudice et al. 2001). We found that deeper snow was correlated with reduced marrow lipid content. Deep snow (>70 cm) can inhibit ungulate movement, restricting access to forage and increasing energetic output, which can lead to malnutrition and starvation (Kelsall 1969, Sweeney and Sweeney 1984, Telfer and Kelsall 1984, Huggard 1993a). Overall, there are varying effects of seasonality on cortisol and body condition, which may be related to behavioural and environmental differences, such as offspring care and protection, food availability, and temperature (Mislan et al. 2016, Uetake et al. 2018, Heimbürge et al. 2019). Future studies should consider sectioning ungulate hair samples to examine temporal differences in HCC over the growing period.

Sex and age can influence body condition and to a lesser extent chronic stress, although the effects of both varies between and within species (Heimbürge et al. 2019). Sex may interact with other factors, such as reproductive status and sexual dimorphism, to influence body condition and chronic stress levels (Lafferty et al. 2015, Mislan et al. 2016). Male bison had elevated HCC and were in poorer body condition compared to females, but the results were not significant for HCC. GC concentrations may peak during the breeding season of ungulates, when there is an increase in the number of agonistic encounters between males (Reyes et al. 1997, Romero and Butler 2007, Pavitt et al. 2015), which overlapped with HCC measurements in our study (late summer to autumn). Cortisol levels may also increase later in pregnancy, or during parturition and/or lactation (Bocci et al. 2014, Edwards and Boonstra 2018).

Our results identify a potential link between body condition and chronic stress, particularly in wolf-killed bison, that suggests wolves may be killing prey in poorer condition. Understanding the relationship between body condition/chronic stress and environmental stressors may allow managers to reduce harvest rates during and after years when prey condition is expected to be low. It may also provide information on expected predator success, which can be used to predict predator population dynamics. Finally, the lower HCC observed in human-harvested bison, relative to wolf-killed bison, indicates that hunting may have relatively larger impacts on population dynamics, as hunters appear to remove healthier individuals that are more likely to survive and reproduce successfully.

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Table 3.1 Linear mixed effects models used to investigate factors affecting hair cortisol concentration (HCC) for plains bison in Prince Albert National Park, Saskatchewan. Variables included in the most complex model are mortality source (human-harvested or wolf-killed), age, sex, and an interaction between age and sex, with the simplest model being the null model. All models included a random effect of year.

Model Number	Model Description
1	HCC ~ 1+ (1|Year)
2	HCC ~ Mortality Source + (1|Year)
3	HCC ~ Mortality Source + Age + (1|Year)
4	HCC ~ Mortality Source + Age + Sex + (1|Year)
5	HCC ~ Mortality Source + Age + Sex + Age:Sex + (1|Year)

Table 3.2 Likelihood ratio tests (LRT) of linear mixed effects models used to investigate the relationship between hair cortisol concentration and mortality source, age, and sex of plains bison in Prince Albert National Park, Saskatchewan, using an alpha (α) = 0.05. If p < α then the more complex model was justified by the reduction in likelihood.

Models compared	D	df	p-value
1 vs 2	7.86	1	< 0.01
2 vs 3	1.26	1	> 0.05
3 vs 4	0.08	1	> 0.05
4 vs 5	0.95	1	> 0.05

Table 3.3 Ranges of hair cortisol concentrations and marrow lipids measured from hair and femur samples, respectively, from wolf-killed bison, deer, and moose collected during the winter from 2013 to 2017 in Prince Albert National Park, Saskatchewan.

Species	Hair Cortisol Concentration (Mean x̄ pg/mg ± SE)	Marrow Lipid Content (Mean x̄ % ± SE)
Bison	6.15 ± 1.46	74.57 ± 6.34
Deer	6.81 ± 0.48	77.22 ± 4.09
Moose	9.11 ± 1.25	55.27 ± 9.05

Table 3.4 Generalized linear mixed effects models used to investigate factors affecting body condition for bison, moose and deer killed by wolves in Prince Albert National Park, Saskatchewan. Variables included in the most complex model are hair cortisol concentration (HCC), species, sex and snow depth, with the simplest model being the null model. All models included a random effect of site (i.e. wolf pack) and year.

Model Number	Model Description
1	% Marrow Lipid ~ 1 + (1 | site) + (1 | year)
2	% Marrow Lipid ~ HCC + (1 | site) + (1 | year)
3	% Marrow Lipid ~ HCC + Species + (1 | site) + (1 | year)
4	% Marrow Lipid ~ HCC + Species + Sex + (1 | site) + (1 | year)
5	% Marrow Lipid ~ HCC + Species + Sex + Snow Depth + (1 | site) + (1 | year)

Table 3.5 Likelihood ratio tests (LRT) of generalized linear mixed effects models used to investigate the relationship between marrow lipid percentage and hair cortisol concentration of bison, moose and deer in Prince Albert National Park, Saskatchewan, using an alpha (α) = 0.05. If $p < \alpha$ then the more complex model was justified by the reduction in likelihood.

Models compared	D	df	p-value
1 vs 2	53.40	1	< 0.001
2 vs 3	22.35	1	< 0.001
3 vs 4	62.77	1	< 0.001
4 vs 5	28.53	1	< 0.001

Table 3.6 Ranges of hair cortisol concentrations previously determined in free-ranging or captive wild mammalian species (adapted from Di Francesco et al. 2017).

Species	Median (Md) or mean x̄ pg/mg (range)	Sample Size	Reference
Rhesus macaque (*Macaca mulatta*)	x̄ = 110.3 (32.1-254.3)	20	Davenport *et al.* 2006
Caribou (*Rangifer tarandus*)	Md = 2.31 (1.57-3.86)	12	Macbeth 2013
Reindeer (*R. tarandus*)	Md = 2.88 (2.21-3.40)	12	Macbeth 2013
Wolves (*Canis lupus*)			
Tundra-taiga	females: Md = 17.3 (9.95-32.2)	48	Bryan *et al.* 2015
	males: Md = 15.8 (8.91-40.4)	55	
Northern boreal forest	females: Md = 14.6 (7.6-34.0)	24	Bryan *et al.* 2015
	males: Md = 12.3 (4.8-26.8)	21	
Polar bears (*Ursus maritimus*)	x̄ = 9.5 (5.5-19.9)	17	Bechshoft *et al.* 2011
	x̄ = 12.75 (3.98-24.42)	88	Bechshoft *et al.* 2011
	Md = 0.48 (0.16-2.26)	185	Macbeth *et al.* 2012
	Md = 0.62 (0.10-9.97)	729	Mislan *et al.* 2016
Grizzly bears (*Ursus arctos*)	Md = 2.84 (0.62-43.33)	151	Macbeth *et al.* 2010
	Md = 8.1 (5.3-26.1)	113	Bryan *et al.* 2013
Black bears (*Ursus americanus*)	females: Md = 4.5 (0.6-10.7)	58	Lafferty *et al.* 2015
	males: 6.2 (0.5-35.1)	58	
Muskoxen (*Ovibos moschatus*)	Md = 11.7 (3.5-48.9)	150	Di Francesco *et al.* 2017
Alpine ibex (*Capra ibex ibex*)	x̄ = 22.40 ±1.44	35	Prandi *et al.* 2018
Red deer (*Cervus elaphus*)	females: 4.77 ± 0.69	98	Caslini *et al.* 2016
	males: 5.75 ± 0.63	76	

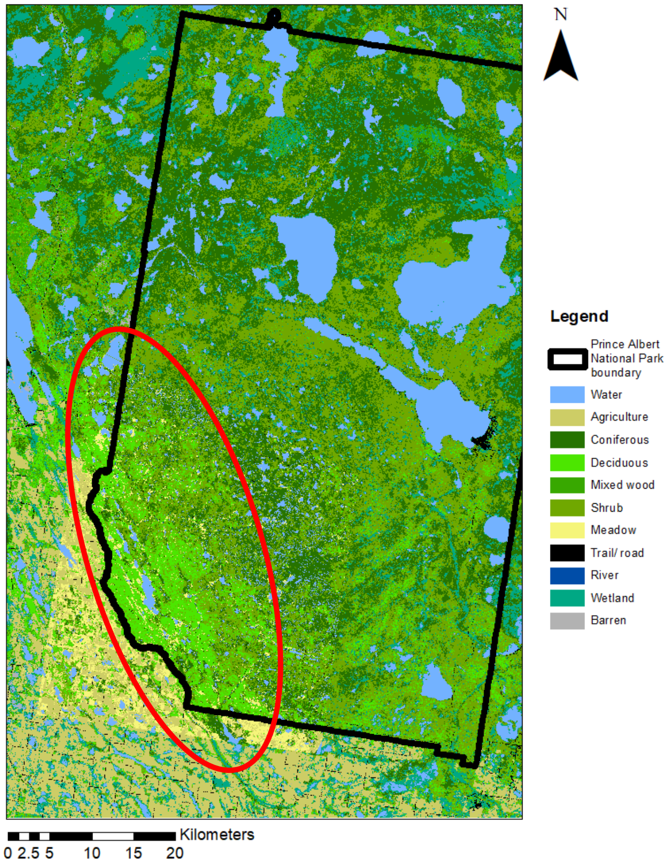

Fig. 3.1 Map of Prince Albert National Park, Saskatchewan with our study area indicated by the red ellipse.

Fig. 3.2 Comparison of hair cortisol concentrations between human-harvested (*n* = 23) and wolf-killed (*n* = 20) plains bison. Mean values (± SE) are shown for each group. Samples from wolf-killed bison were collected at wolf kill sites visited from November to March in 2013 to 2017 in the SW corner of Prince Albert National Park, Saskatchewan. Samples from human-harvested bison were collected from harvest events that occurred outside of the Park from August to November in 2013 to 2016.

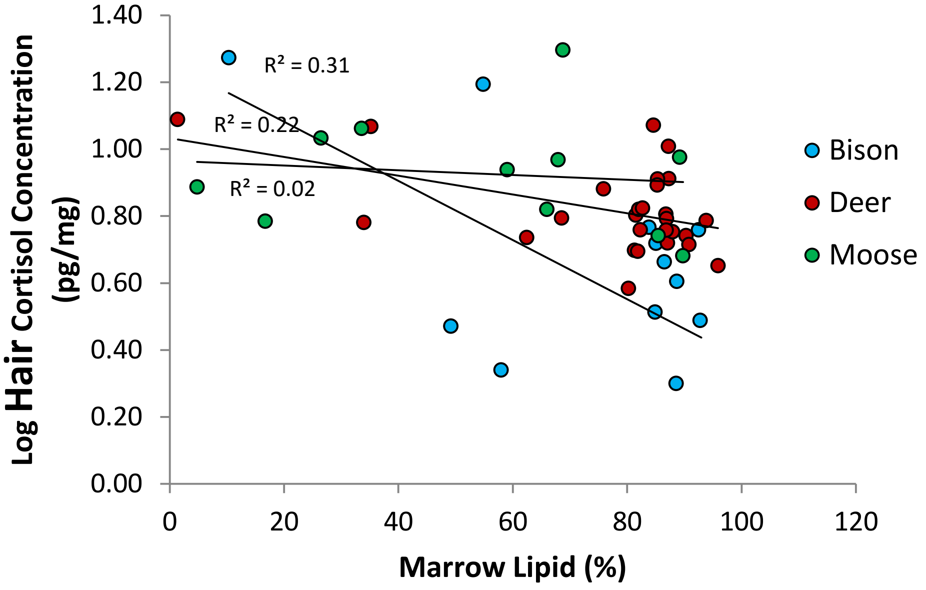

Fig. 3.3 Linear regressions examining the relationship between marrow lipid content and hair cortisol concentration for wolf-killed bison (*n* = 14), moose (*n* = 11), and deer (*n* = 27). Hair and femur samples were collected from wolf kill sites visited from November to March in 2013 to 2017 in the SW corner of Prince Albert National Park, Saskatchewan.

Chapter 4 : General discussion

We aimed to a) examine inter- and intra-annual variation in wolf (*Canis lupus*) diet to quantify the proportion of bison and other ungulates consumed by wolves in PANP, and b) examine how chronic stress and body condition of prey may be linked to wolf predation. We found white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*) comprised the highest proportion of wolf diet, particularly in the winter. We observed seasonal differences in wolf diet, with greater variation in prey contributions in the summer compared to the winter, when deer/elk were the main prey of wolves. We found inter-pack variation in diet, as wolves that overlapped with plains bison (*Bison bison bison*) range had a higher proportion of bison in their diet. Hair cortisol concentrations (HCC) were elevated in wolf-killed bison compared to human-harvested bison, and mortality source was the best predictor of HCC in bison. Wolf-killed bison also had the strongest negative correlation between HCC and marrow lipids, when compared to wolf-killed deer and moose (*Alces alces*).

Ungulates are the main prey for wolves in PANP, and continued monitoring of ungulate populations is recommended. An accurate estimate of the prey base may help to predict patterns of prey selection by wolves (Huggard 1993a), as changes to prey availability may result in shifts in predation (Garrott et al. 2007, Sand et al. 2016). Currently, abundance estimates for ungulates in our study area are performed via aerial surveys, predominantly to monitor the population size of the Sturgeon River plains bison (SRPB). One of the primary biases of aerial surveys is that it can miss smaller-bodied prey, including deer or elk (Caughley 1974, Cook and Jacobson 1979, Pollock and Kendall 1987). Camera traps may be a more accurate measure of population size in our study area, using indices of relative abundance, such as detection rates, or occupancy modelling for surveys of unmarked individuals (Burton et al. 2015). Population size may also be estimated indirectly through life-table methods based on population demographics (Rabe et al. 2002). There are biases or assumptions that are violated for most population estimates; therefore, it can be beneficial to use multiple methods to obtain reliable estimates (Buckland et al. 2000, Rönnegård et al. 2008, Corlatti et al. 2017).

The role of wolves in ungulate population declines is still a contested issue amongst scientists (Wasser et al. 2011, Boutin et al. 2012, Mech and Fieberg 2014). For example, caribou (*Rangifer tarandus*) populations across North America have been decreasing, and numerous studies have examined the effect of wolves on their decline (Bergerud et al. 1983; Seip 1992; Boertje et al. 1996; Boutin et al. 2012; Serrouya et al. 2017). While caribou are the main prey of wolves in some regions (Ballard et al. 1987; Merkle et al. 2017), habitat loss, degradation, and disturbance are other factors most likely contributing to decreases in caribou populations (Dickie et al. 2017; Mumma et al. 2018). Wolf control methods have been implemented in a number of areas to reduce conflicts with humans, and facilitate the recovery of ungulate populations (Theberge and Gauthier 1985, Cluff and Murray 1995, Boertje et al. 1996). While wolf culls may be somewhat effective at reducing population declines of prey, long-term landscape management is often needed for viable population recovery (Boutin et al. 2012, Hervieux et al. 2014). Furthermore, wolves will often regulate ungulate population levels, and removal of wolves may have negative cascading effects on other trophic levels in an ecosystem (Messier 1994, Schmitz et al. 2000, Winnie and Creel 2017). Wolves may also select prey that are less fit, including young, old, diseased, and injured individuals in poor body condition (Huggard 1993b, Mech and Peterson 2003, Garrott et al. 2007, Mattisson et al. 2017), which would leave healthier individuals to survive and reproduce. However, effects of predation may be exacerbated when prey populations are already small, leading to further declines as a result of predation (Wittmer et al. 2005).

Plains bison were designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as *threatened* in 2004. The target population size for the management of the SRPB population in Prince Albert National Park (PANP) is 400 individuals, to maintain sufficient genetic diversity (Merkle et al. 2015). The population size estimate for the SRPB in 2017 was 180 bison, and the SRPB has been below the target management threshold since 2007 (Merkle et al. 2015. Cherry et al. in review). Small populations are of conservation concern, as low genetic variability within a population may lead to inbreeding depression, which can have negative effects on birth weight, survival, reproduction, and susceptibility to disease (Keller and Waller 2002, Freese et al. 2007, Sanderson et al. 2008). Our diet analysis indicated that wolves were consuming bison in both the summer and winter, and wolves that overlapped more with the SRPB range had a higher proportion of bison in their diet. Therefore, the SRPB decline may be somewhat attributed to wolf predation. In addition, an anthrax outbreak in 2008 and annual harvests by humans have contributed to past bison mortality (Shury et al. 2009, Sigaud et al. 2017), and extinction risk for the SRPB was highest in population simulations when the effects of hunting and disease were combined (Cherry et al. in review). The number of bison killed by human-harvests compared to wolf predation was consistently high for all years of observation (Fig. 4.1). While wolves alone do not appear to be the primary cause of the SRPB decline, predation in combination with other mortality factors may increase the extinction risk for the SRPB population.

The SRPB population provides a unique management challenge, as they inhabit the interface between a protected national park, agricultural, and crown lands (Sigaud et al. 2017). Working with local stakeholders and landowners to develop conservation and management strategies will be integral to the persistence of the SRPB population. Strategic exclusionary fencing may lower bison conflict with humans outside of PANP and reduce damage to agricultural crops (Hofman-Kamińska and Kowalczyk 2012, Sigaud et al. 2017). Because bison leave PANP to graze on high-quality agronomic species (Sigaud et al. 2017), seasonal land conservation easements may allow bison to forage outside PANP for short periods of time (Cherry et al. in review). Only Indigenous hunters are legally permitted to harvest bison in the area, and only when bison are outside of PANP. Continued unrestricted hunting practices outside of PANP will most likely result in undesirable levels of extinction risk for the SRPB (Cherry et al. in review). Therefore, a temporary moratorium on hunting may allow the population to recover to its social carrying capacity, while allowing for harvests to continue in the future. Wild plains bison populations occurring within their historic range and co-existing with natural predators are exceedingly rare in North America, and thus have high conservation value (Freese et al. 2007, Sanderson et al. 2008). As free-ranging populations of bison are reintroduced into their historical range, it will be important to understand potential sources of mortality, including natural predators, on bison population dynamics (Steenweg et al. 2016).

In conclusion, wolves are consuming a variety of ungulates in PANP, including bison, and wolf diet varies seasonally. Stable isotope analysis provides an additional method to quantify predator diet, and in combination with other techniques can be an effective method to reconstruct diet at various temporal scales. In addition, chronic stress and poor body condition may make prey more vulnerable to predation by wolves. HCC analysis is a non-invasive method to quantify chronic stress, and results may be used to assess the status of populations, or provide information on expected predator success. In our study area, management of the SRPB population should be focused on human-harvests, rather than wolf predation, to lower extinction risk and aid in population recovery.

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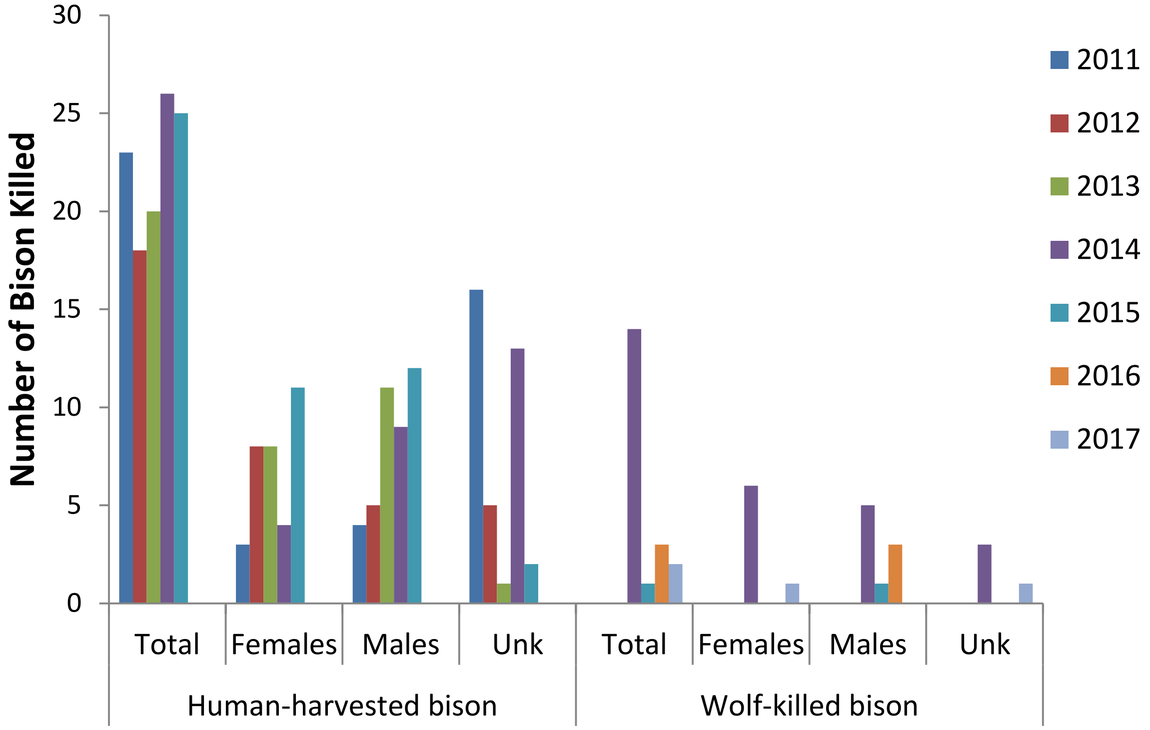

Fig. 4.1 Comparison of the number of bison killed by human-harvests versus wolf predation using observations from harvest events and wolf kill sites from 2011 to 2017 in Prince Albert National Park, Saskatchewan.

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