VALIDATION OF STABLE ISOTOPE ANALYSIS FOR DETERMINING DIETARY PROPORTIONS AND TROPHIC DYNAMICS IN PLAINS SHARP-TAILED GROUSE (*TYMPANUCHUS PHASIANELLUS JAMESI*)

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ABSTRACT

Stable isotopes in the tissue of a consumer organism can be used to estimate the proportional utilization of foods based on different isotopic signals and can also be used to estimate changes to diet over time. In this study, stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) were used to examine the feeding relationships of plains sharp-tailed grouse (*Tympanuchus phasianellus jamesi*). Sharp-tailed grouse are known to consume mostly plant food and utilize insects and spiders as a high-protein food source when available. Food web dynamics are generally poorly understood, and emerging factors such as climate change are likely to alter bird-arthropod trophic relationships. Primary feathers from 40 plains sharp-tailed grouse were analyzed and used to estimate diet proportions of vegetation and arthropods from May to October. Results indicated that plains sharp-tailed grouse may primarily utilize nutrients obtained from insect prey, mainly grasshoppers (Orthoptera: Acrididae), for primary feather synthesis.

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LIST OF ABBREVIATIONS

%C	Percent carbon content
%f	Frequency of occurrence
%n	Number of occurrences
%N	Percept nitrogen content
%w	Percent dry weight
ACA	Alberta Conservation Association
AHY	After hatch-year
ANOVA	Analysis of variance
C	Carbon
CFB	Canadian Forces Base
HY	Hatch-year
IOI	Index of Importance
IOP	Index of Preponderance
IRI	Index of Relative Importance
IRMS	Isotope ratio mass spectrometer
MixSIAR	Stable isotope mixing model package (R stats package)
MRR	Milk River Ridge
N	Nitrogen
P1-P10	Primary feathers 1 through 10
RB	Relative biomass
SD	Standard deviation
SIBER	Stable Isotope Bayesian Ellipses in R (R stats package)
SIDER	Stable Isotope Discrimination Estimation in R (R stats package)
SIMM	Stable isotope mixing model
TDF	Trophic discrimination factor
TP	Trophic position
Twin River	Twin River Heritage Rangeland Natural Area, Alberta, Canada
Wild Rose	Wild Rose Conservation Site, Alberta, Canada
$\delta^{13}C$	Stable isotope ratio of carbon
$\delta^{15}N$	Stable isotope ratio of nitrogen
$\Delta\delta^{13}C$	Trophic discrimination of carbon isotopes
$\Delta\delta^{15}N$	Trophic discrimination of nitrogen isotopes

CHAPTER 1: INTRODUCTION

Abstract

Birds are highly adapted to the environments they occupy and move between and survive on a tight energy budget. Timing of energy-taxing life history events like breeding, feather molt, and migration have in many cases evolved to be synchronous with times of high food availability. Changes to weather and climate threaten the dynamics of these kinds of relationships for many species and increasing pressure from anthropogenic development often compounds the threat. A better understanding of species interactions and trophic dynamics is important to further our understanding of ecosystem function and food web stability. Stable isotope ecology is a growing field in food web research, and the use of stable isotope ratios of carbon and nitrogen can be used as biotracers to estimate diet proportions and other food web metrics. However, not all study systems are well suited for the application of stable isotopes as a research tool. In this study, the utility of stable isotopes for estimating diet proportions and trophic dynamics in plains sharp-tailed grouse was assessed.

1.1 BIRDS AND CLIMATE CHANGE

Birds have a high energy demand. They eat, breathe, and move more than any other vertebrate relative to their weight (Welty 1978) and have an average body temperature that is several degrees higher than mammals (Ruben 1995). Avian species exhibit a broad range of life histories and adaptations across the globe, and a major factor in determining their geographical distributions is their physiological demands (Root 1988). Depending on their adaptations, there are certain times during a bird's life that are more energy-taxing than others. Early development, breeding, egg-laying, migration, and feather molt (loss and regrowth of feathers) are among the most energy intensive times for birds (Murphy and King 1992; Bancroft and Woolfenden 2010). Birds have evolved to manage these challenges in different ways. For many species, molting and reproduction occur at different times in order to reduce acute energy demand (Farner 1964; Kendeigh 1969). Molting in some species takes place over a prolonged period while others undertake a rapid, energy intensive, molt. These energy intensive events are usually synchronized with times of high food availability in seasonal areas (Visser

et al. 1998). The internal anatomy (both physical and chemical), as well as the food selection behaviour of birds, can change with the seasons in order to efficiently utilize available resources (Levey and Karasov 1989; Lepczyk et al. 2000). For example, in American robins (*Turdus migratorius*) and European starlings (*Sturnus vulgaris*) digestive efficiency can be optimized for consuming fruit, or insects, but cannot be optimized for both simultaneously (Levey and Karasov 1989). A notable digestive adaptation that allows many birds to cope with periods of high energy demand, or low-quality diet, is the avian cecum. The cecum consists of a pair of organs (ceca) that protrude from the proximal end of the colon and perform a variety of functions in different species including increasing nutrient absorption, immune function, and water retention. In galliforms (turkeys, grouse, and chickens) the ceca contain microorganisms that break down cellulose (Moss and Hanssen 1980) allowing many of these species, including grouse (Tetraonidae), to subsist on a relatively nutrient-poor diet (Leopold 1953; Remington 1989; Clench 1999).

A major benefit of a high metabolism and high body temperature in birds is that they are able to occupy a diverse array of climates and remain less constrained by low temperatures, provided they can access the food and water resources they need to meet their energy demands (Root 1988; Ricklefs 2000). A great deal of research effort has been dedicated towards studying what birds eat, when they eat it, and why. The fruiting bodies of plants are important food for birds, which in turn act as seed dispersal agents. Fruit and berry foods are often high in sugars or lipids but not rich in protein. They may also contain secondary compounds that protect them from being destroyed by microbes before the seed can be dispersed, which can make them acidic and unpalatable for birds in large quantities. Many birds obtain the protein they need by also consuming arthropods (mostly insects and spiders) or pollen when they are available. The right combination of these food sources is often carefully selected for by birds (Levey and Martinez del Rio 2001; Witmer 2001). The seasonal occurrence of different food sources, and the adaptability of the avian digestive system means that birds have specialized behavioural adaptations that are intrinsically tied to the seasonality and ecological stability (defined in Chapter 4) of their environments. The success of migration, breeding, nesting, brood rearing, and molt all depend on available food supply to meet the energy demands of birds during critical times (Kendeigh 1969; Visser et al. 1998; Crick and Sparks 1999; Dunn and Winkler 1999).

Climate change threatens to disrupt many of the ecological processes and seasonal predictability that birds rely on (Thomas et al. 2004). A report by the National Audubon Society classified more than half of 588 North American bird species as 'climate endangered' or 'climate threatened', meaning they are projected to lose over half of their geographic range within the next 30-60 years (Langham et al. 2015). The consequences of climate change and landscape alteration to birds in the future are difficult to predict exactly (Parmesan and Yohe 2003), however, some impacts are already being noticed by researchers. Reduction in habitat suitability (Jones and Bock 2002), changes to suitable biogeographic range (Langham et al. 2015; Salas et al. 2016), and changes to the complex dynamics of ecological systems are already occurring (Walther et al. 2002). These changes include shifts in plant and insect phenology (Myneni et al. 1997; Ladányi and Horváth 2010; Rafferty and Ives 2011) and the disruption of trophic dynamics (Voigt et al. 2003). Recent studies from around the world have reported declines in insect numbers, related to habitat modification and the use of insecticides, and in some cases these are associated with declines in bird populations (Nebel et al. 2010; Hallmann et al. 2014; Hallmann et al. 2017). A behavioural trend that has been noticed in several bird species is the tendency towards earlier breeding and egg-laying. The effect has been noticed in a range of species both migratory and non-migratory, and with different food habits, and is likely related to increases in average temperatures (Brown et al. 1999; Crick and Sparks 1999; Dunn and Winkler 1999). While it may be tempting to hope that earlier breeding dates in these birds will correspond with similar changes to plant and insect phenology and occurrence of high food availability, this is not likely to be the case as the effects of climate change influence trophic levels differently (Visser et al. 1998; Voigt et al. 2003; Pearce-Higgins 2010; Balzotti et al. 2016). Given the delicate balance of energy demands and timing of food availability for birds relative to their annual life cycle requirements (Carey 2009), it is likely that mismatches between critical life events (e.g. reproduction) and food availability will occur with increasing frequency in many species (Crick and Sparks 1999; Dunn and Winkler 1999). More research is needed with regards to food webs and the changes to trophic interactions that will result from climate change (Prather et al. 2013).

1.2 SHARP-TAILED GROUSE ECOLOGY

Sharp-tailed grouse (*Tympanuchus phasianellus,* Linnaeus 1758) are a gallinaceous bird that inhabits prairie and open forest habitats in central and northern North America. Historically, the species' range was more widespread, but it has declined significantly in the eastern and southern parts of its range (Figure 1) (Connelly et al. 1998). Sharp-tailed grouse prefer mixed habitats that include dense shrub cover for nesting, brood rearing (Roersma 2001), and thermal protection (Raynor et al. 2018). Shrubs provide fruit as an important food source later in the summer and fall, and sharp-trailed grouse also use open habitats with a diversity of herbaceous vegetation that provide plant food and support arthropods upon which they feed during the warm seasons. Display and breeding grounds, called leks, are found in open areas with less vegetation, and often on elevated terrain (Hamerstrom Jr. 1963; Connelly et al. 1998). Sharp-tailed grouse are known to utilize agricultural grains as a food source which may be beneficial, although the overall effects of agricultural development on sharp-tailed grouse tend to be negative (Bird 1961; Manzer and Hannon 2005).

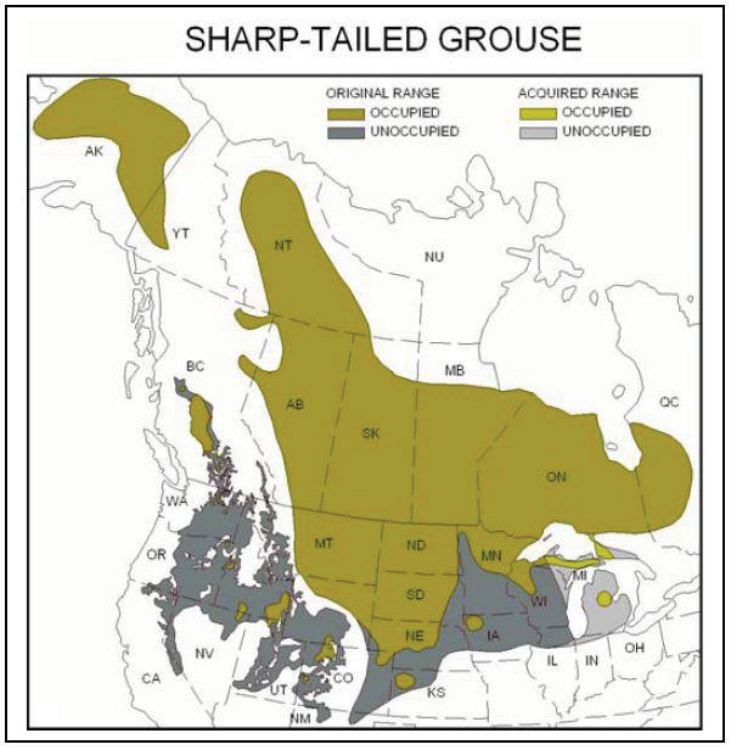

Figure 1 - Sharp-tailed grouse historic distribution, from Schroeder et al. (2004)

Sharp-tailed grouse are non-migratory but will sometimes move short distances between summer and winter ranges (<34 km) (Hamerstrom and Hamerstrom 1951). They congregate in coveys of 2-200 individuals (Ammann 1957) and usually range within 6 km of their breeding and nesting grounds. They remain closer to these areas during nesting and brood rearing (Artmann 1970; Gratson 1988). During the spring sharp-tailed grouse gather at leks and the males compete for courtship of females through

display (Connelly et al. 1998). After they have bred, the females nest within a short distance (0.4 – 1.8 km) of the lek (Artmann 1970), incubate their eggs for 21-23 days (Hillman and Jackson 1973), and rear their precocial brood of 10-12 chicks near the nest throughout the summer. During the first few days of life young chicks are able to feed themselves, however, they are covered in down feathers and require thermal protection from the hen (Hart et al. 1950; McEwen et al. 1969). The chicks can fly short distances after about 10 days (Hart et al. 1950) and are independent after about 3 months, usually around the middle of September (Caldwell 1976). Hatch-year males may attempt to breed the following spring (Bergerud and Gratson 1988). During early development grouse chicks consume mostly insects (Renhowe 1968; Moss 1997; Johnsgard 2016) likely as a source of protein (Sullins et al. 2018) and other essential nutrients to aid in rapid muscle and feather growth (Murphy and King 1992), but possibly also because insects are easier to digest (Savory 1989). The ceca in grouse chicks are not yet fully developed and so they are likely not able to extract the same nutrients from plant foods as adult grouse (Leopold 1953; Remington 1989). Adult grouse also consume arthropods, sometimes in large qualities, when they are available (Marshall and Jensen 1937; Hamerstrom and Hamerstrom 1951; Jones 1966).

There are 6 extant subspecies of sharp-tailed grouse in North America, and they are closely related to other prairie grouse, the greater and lesser prairie-chicken (*T. cupido* and *T. pallidicinctus*). The plains sharp-tailed grouse (subspecies *jamesi*, Lincoln 1917) is the subject of study in this thesis and is the largest subspecies of sharp-tailed grouse. The primary differences between subspecies are in habitat preference and coloration. The northern subspecies appear darker than southern subspecies and favour open boreal forest areas and bogs whereas southern subspecies generally occupy prairies and open steppes (Connelly et al. 1998).

1.3 GROUSE CONSERVATION

Although the species is in widespread decline, sharp-tailed grouse remain a popular game bird species for hunters throughout a lot of their range. Hunting pressure has not been shown to have a significant impact on population numbers in most cases (Ammann 1963), and population declines even persisted in

Utah despite a 25-year closure of the hunting season (Hart et al. 1950). The lack of precise population data and the combined impact of multiple stressors make the reasons for population declines difficult to pinpoint (Connelly et al. 1998). In Alberta, Canada, plains sharp-tailed grouse are listed as a Sensitive species by the provincial government due to decreased habitat availability and pressure from agricultural development in parts of the province (Alberta Environment and Parks 2020). The reasons for the decline of sharp-tailed grouse populations are most often attributed to habitat degradation, loss, and fragmentation from agricultural and oil and gas development (Connelly et al. 1998; Hovick et al. 2014; Hoffman et al. 2015). Inappropriate grazing management of domestic livestock (i.e. overgrazing) has also been attributed as a major driver of decreased habitat suitability (Mcnew et al. 2017), as well as suppression of natural fire regimes (Bartuszevige and Daniels 2016), predator subsidies (Manzer and Hannon 2005; Manzer and Hannon 2007; Howe et al. 2014), invasive plants, shrub removal, pesticides, and climate change (Idaho Department of Fish and Game 2015). The present focus of conservation action emphasizes the need to restore and preserve native grassland habitat, reconnect fragmented habitat, and ensure habitat quality (Schroeder 2004; Hoffman et al. 2015).

Because of their life history requirements and specialized adaptation as a resident upland bird on prairie landscapes, sharp-tailed grouse are considered an indicator species whose success can be used as a barometer for overall ecosystem health (Poiani et al. 2001; Roersma 2001; Spieles 2010). This concept, as well as the conservation status of the species, makes it a worthwhile and interesting subject of study (Roberge and Angelstam 2004). At a habitat management level, there should be a focus on protecting grouse during times that are critical for population success, i.e. nesting and brood rearing (Mcnew et al. 2017). Food quantity and quality in brood rearing habitat are an important factor for both chicks and adults during this stage and are the focus of this thesis. Other grouse species (Tetraonidae) may also benefit from this type of research. Greater sage grouse (*Centrocercus urophasianus*), for example, are an Endangered species in Canada (COSEWIC 2008) and also rely on arthropods as a high nutrient food source during early development (Blomberg 2013). The endangered status of sage grouse makes them a high priority for research pertaining to their survival in the face of climate change. However, the use of hunter harvested birds for the purpose of this study clearly

prohibits its application to sage grouse. Sharp-tailed grouse may serve as a useful proxy in this context, especially given its status as an indicator species.

1.4 DIET STUDIES AND TROPHIC DYNAMICS

Recent trends in grouse research have tended towards species of high conservation concern, and towards studies in population genetics, landscape level ecology, and habitat. Relative effort into studies in behaviour, disease, reproduction, and diet have decreased significantly since the 1980's (Moss et al. 2010). These trends no doubt reflect emerging new technologies that grant valuable insights into population dynamics and large-scale ecological drivers. However, a great deal remains to be learned from studies in grouse diet and nutrition. Most grouse diet studies have been done via esophageal crop analysis of fall harvested birds, reflecting a time of high food availability and relatively low physiological stress to grouse (i.e. not during egg laying or brood rearing, and towards the end of the molt). In addition, food items found in the crops of grouse may not necessarily represent their preferred diet and should not be assumed to be nutritionally adequate. Few studies have been able to link food habits to population trends or individual health metrics. Knowledge about dietary habits during times of high energy demand are likely to be useful in determining relative importance of foods, nutritional demands, and are more likely to relate to limiting factors on distribution and population. However, difficulties arise when overriding factors such as inclement weather during brood rearing obscure the effect of food quality and availability on chick survival (Gullion 1966). Gaps exist in our knowledge of food selection by grouse, especially chicks (Moss et al. 2010). Crop samples from chicks cannot be obtained ethically, and studies that use fecal contents have been found to overrepresent harder, less digestible, food items (Picozzi et al. 1999; Sullins et al. 2018). Arthropod selection by grouse outside of the fall hunting season remains poorly understood as well, as does the effect of landscape alterations and climate change on arthropod abundance, and in turn their availability to grouse chicks as food (Moss et al. 2010; Prather et al. 2013).

Most species of grouse consume large amounts of arthropods as chicks, and gradually shift towards a more plant-based diet as they reach maturity (Savory 1989; Connelly et al. 1998). When compared with

other grouse species, sharp-tailed grouse and prairie chickens were reported to consume more arthropods into later stages of development, possibly due to occupying generally warmer habitat (Kobriger 1965; Savory 1989). Arthropod prey are higher in protein than plant foods (Stiven 1961; Sullins et al. 2018) and grasshoppers (Orthoptera: Acrididae) are often the dominant insect prey of sharp-tailed grouse (Renhowe 1968; Mitchell and Riegert 1994). Grasshoppers contain on average 61% protein and 13% fat (Rumpold and Schlüter 2013), and amino acids gained from protein in the diet are essential for muscle and feather development in gallinaceous birds (Blair 2008). Adult grouse may also benefit from increased intake of certain amino acids gained from arthropods, like cystine and methionine, that are essential for feather synthesis (Murphy and King 1992) as they lose and replace their feathers throughout the summer months (Pyle 2008). Although grouse are able to survive on relatively nutrient poor diets (Moss and Hanssen 1980) it is possible that young sharp-tailed grouse are able to achieve their maximum growth rate with less foraging effort by utilizing available arthropods, which are also more easily digested (Stiven 1961; Andreev 1987; Savory 1989). Periods of inclement weather when foraging time becomes limited (Erikstad and Spidsø 1982) may also be less detrimental to grouse that have access to more arthropod prey.

Arthropods are a critical component of healthy grassland ecosystems, performing many ecological functions that contribute to the stability and trophic structure of the grassland environment. Climate, fire, and grazing are the main drivers of arthropod biodiversity and abundance (Laws and Joern 2013; Prather et al. 2013) and vegetative community structure and diversity have a positive relationship with arthropod diversity (Haddad et al. 2011; Welti et al. 2017). Appropriately managed grazing that promotes habitat heterogeneity can have a positive influence on bird-food arthropod availability (Goosey et al. 2019) and herbaceous plant diversity (Mortensen et al. 2018). However, the ecological consequences of losing arthropod biodiversity are poorly understood. Arthropods are sensitive to changes to weather and climate which have a major influence on their timing and phenology, geographic distribution, behaviour, and population genetics. These changes in turn have far-reaching effects on ecosystem functions like primary production (through seed dispersal and pollination), nutrient cycling, control of insect outbreaks and invasive species, and food web stability (Voigt et al.

2003; Prather et al. 2013). Alongside the effects of climate change are the landscape alterations caused by human development. Monoculture cropland and the use of agricultural insecticides alter arthropod population dynamics in significant ways and have the potential to alter arthropod food availability for birds (Johnson et al. 1996; Martin et al. 1998). Grasshoppers, a staple food item for many grassland birds, are often the target of agricultural pest management as certain species (not all) have the potential to cause serious economic damage to crops and hay during outbreak years. Grasshoppers are a valuable food source for many grassland species because of their abundance and differing phenological traits that allow some species to occur at different times during the warm season (Johnson et al. 1996). This diversity allows for a relatively predictable insect food supply for grassland animals. In the event of inclement weather that hinders the success of grasshoppers emerging at a certain time, others will hatch or reach maturity at a different time. In this way, arthropod biodiversity fosters food web stability in the face of variable weather and grasshoppers can act as an important buffer in the food chain (Bird 1961; Naeem 1998).

There are many factors that influence sharp-tailed grouse success on the prairies, and a combination of the factors discussed above are likely responsible for their decline, with some having greater influence than others. This thesis will focus on the influence of weather, climate, and anthropogenic influences on grouse food supply, and the need for maintenance of biodiversity to sustain the diversity of plant and arthropod foods that sharp-tailed grouse require during critical stages of their lives. In the face of a changing climate and increased frequency and severity of weather events it is important to quantify food web structure and dynamics. This information will foster a better understanding ecosystem function (Chamberlain and Pearce-Higgins 2013; Layman et al. 2015) and how both sharp-tailed grouse and their food sources will respond to climate change (Fletcher et al. 2013; Forbey et al. 2014).

1.5 STABLE ISOTOPE ECOLOGY

Stable isotope ecology is the use of isotopes, often those of nitrogen (N) and carbon (C), as bio-tracers to track energy pathways, food-web dynamics, and trophic position in natural and laboratory settings. Sulphur (S), oxygen (O), and deuterium (D) are also used in some cases. Stable isotopes are non-

radioactive, naturally occurring, variations of the same element that have a different number of neutrons, affecting the atomic weight of molecules. The metric of interest in isotope ecology is the ratio between the heavy and light isotopes of an element. For example, N occurs in nature in two stable forms, ^{14}N and ^{15}N, the latter of which has one more neutron in its nucleus than the former, making it slightly heavier. ^{14}N is far more common, making up 99.63% of the nitrogen on earth while ^{15}N makes up the remaining 0.37%. Although the difference is subtle, the weight of the extra neutron is enough that the two isotopes react differently during chemical reactions like evaporation, photosynthesis, digestion, or tissue synthesis. These processes cause the ratio between the heavy and light isotope to change as the element in question cycles through natural systems and organisms (Figures 2 and 3) (Peterson and Fry 1987). This process is referred to as fractionation. Generally, light isotopes react faster in kinetic reactions, and heavier isotopes concentrate where bonds are strongest in exchange reactions (Fry 2008). Carbon has two stable isotopes, ^{12}C (making up 98.89% of carbon on earth) and ^{13}C (making up 1.11%), and is often used in conjunction with nitrogen in food web studies (Layman et al. 2012).

In order to standardize the use and notation of isotope ratios and convert them to values that are easier to interpret, isotope ratios have their own notation: the δ (delta) notation. The δ value denotes the difference between the isotope ratio (i.e. $^{15}N/^{14}N$) of a sample being analysed and the isotope ratio of an international reference standard. For nitrogen the international standard is the heavy/light isotope ratio of atmospheric nitrogen. For carbon the standard is based on the isotope ratio of a Cretaceous belemnite fossil found in the Pee Dee formation in South Carolina and is referred to as the Vienna-PeeDee Belemnite standard. A δ notation is given as the specified element with the mass of the heavy isotope as a superscript. For example, the formula for a nitrogen isotope ratio ($\delta^{15}N$) is:

$$\delta^{15}N = [(R_{sample} / R_{standard}) - 1] * 1000$$

where R is the ratio of the heavy to light isotopes. The formula multiplies the ratio by 1000 in order to amplify differences that are often very small. The values are therefore given in permil (‰) rather than percent (Fry 2008).

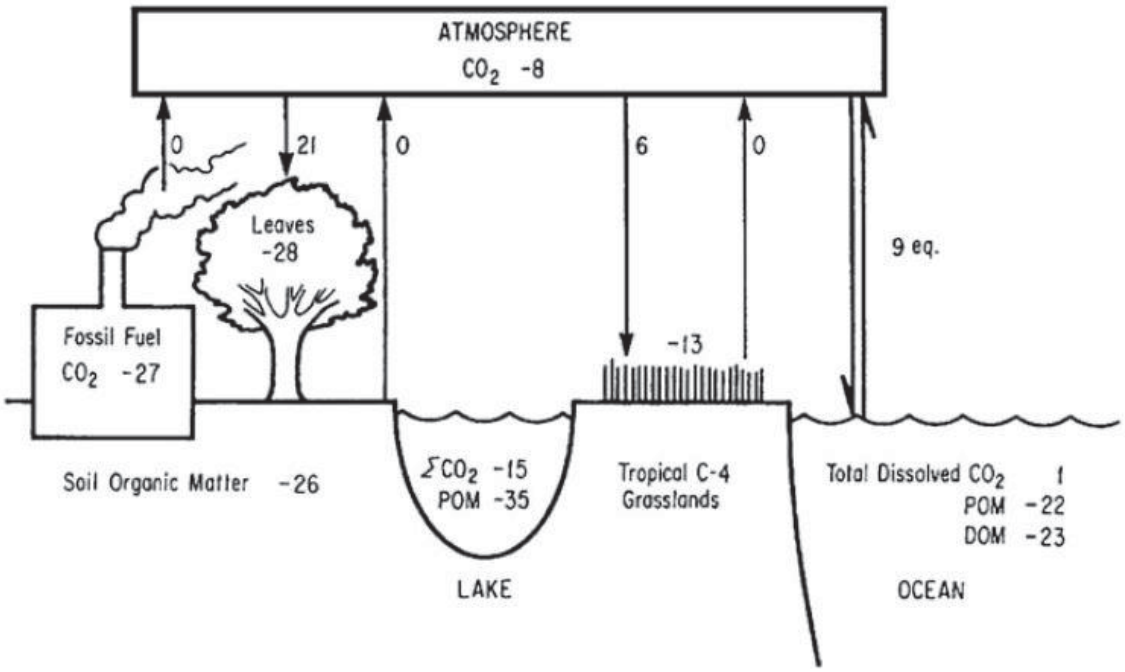

Figure 2 - Nitrogen isotope cycle from Peterson and Fry (1987)

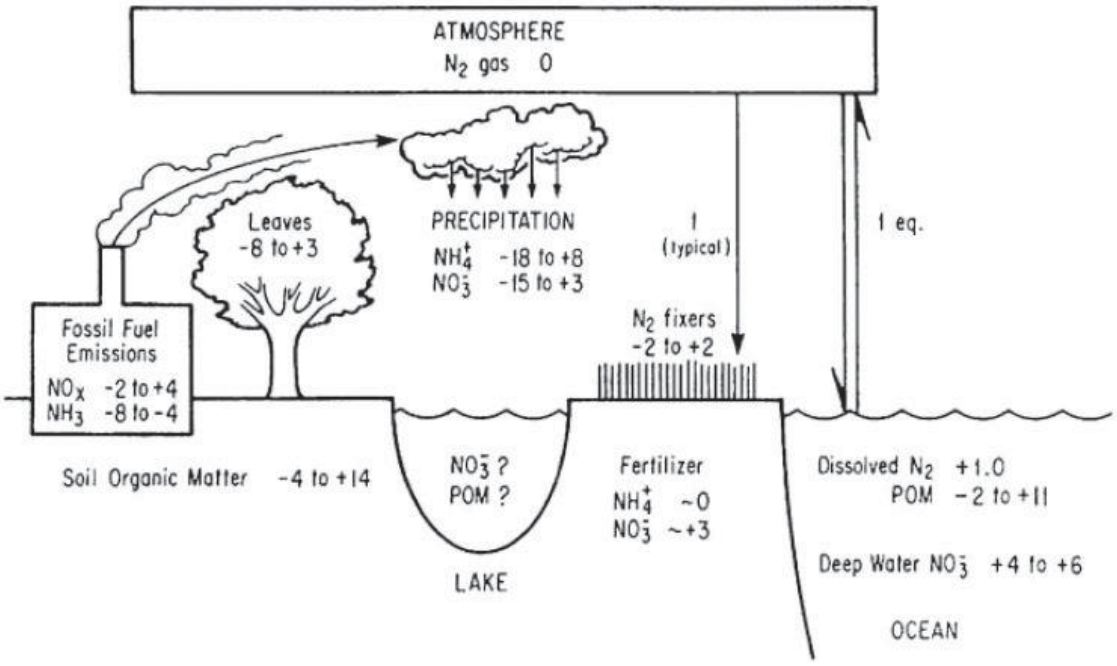

Figure 3 - Carbon isotope cycle from Peterson and Fry (1987)

Stable isotope analysis is usually done using an Isotope Ratio Mass Spectrometer (IRMS) that is carefully calibrated to measure the amount of each isotope in a sample. The principle concept used to separate heavy and light isotopes prior to measurement is inertia. Simply put, a sample is dropped into a chamber where it is combusted at high temperature, turning it to gas. The sample gas is then ionized, causing the molecules to lose electrons. The now positively charged molecules are then accelerated through a magnetic field and separated according to their atomic mass, the heavier isotopes having more inertia than the lighter isotopes, and so travelling farther. The ions are counted in Faraday cups and the isotope ratio is given as a computer counts the amount contributed to each collector. Using algebra, and correction factors established over decades of isotope research, the lab results can then be standardized using the international standards and used in ecological research (Craig 1957; Santrock et al. 1985; Fry 2008).

Isotope ecology has become one of the most popular tools in food web research in recent years. Isotopes can be used to track energy pathways through food-webs, model trophic structure, and track the migration of birds (Inger and Bearhop 2008; Layman et al. 2012). Ratios of nitrogen isotopes ($\delta^{15}N$) can be used to estimate trophic position of an organism within a food web as nitrogen tends to become enriched (fractionates resulting in more of the heavy isotope) as it moves up the food chain (Post 2002). Ratios of carbon isotopes ($\delta^{13}C$) can be used to identify the sources of dietary carbon as carbon varies more along the breadth of a food web, and mostly within primary producers. Ultimately the isotope ratios of a given organism are driven by what it consumed in addition to the biochemical processes, i.e. photosynthesis, digestion, metabolism and tissue growth, wherein fractionation occurs (Layman et al. 2012). If these processes can be accounted for and properly estimated, including temporal considerations, i.e. tissue turnover, useful models can be constructed that can give researchers valuable insights into food web dynamics and diet-reconstruction (Newsome et al. 2007; Layman et al. 2012; Phillips et al. 2014; Nielsen et al. 2017).

Diet reconstruction using stable isotopes is done by obtaining the isotope values of the food items that an organism has available to it as well as the isotope value of the organism itself. Because the isotopes

in the organism had to come from what it ate, mathematical models called stable isotope mixing models (SIMMs) can be used to estimate the proportions of the different food items that contributed to the final isotope value of the organism's tissue (Fry 2008; Phillips et al. 2014). However, there are many caveats and limitations to this process that researchers must be aware of in order to use stable isotopes in a way that is ecologically meaningful (Phillips 2001; Phillips et al. 2014). In order to estimate relative contributions of different food items to a consumer's diet the food items, or groups of food items, must be isotopically distinct, otherwise the SIMM cannot distinguish between sources (Phillips and Gregg 2003). It is also important to know the properties of the kind of tissue that is being sampled from the consumer organism. This is because tissues turn over at different rates and isotopes fractionate differently during synthesis of different tissues. Blood, for example, has a high turnover rate and its isotope value reflects what the consumer ate relatively recently. Muscle tissue has a slower turnover rate than blood, but a faster turnover rate than bone (Hobson and Clark 1992a; Hobson and Clark 1992b; Caut et al. 2009). Feathers have no turnover rate because once they are produced, like mammalian hair, they are metabolically inert. For this reason, feathers can be useful in estimating diet over long periods of time if the pattern and timing of molt of the bird in question is known (Bearhop et al. 2002)

The following two example studies outline how stable isotopes of feathers can be used to estimate the contribution of different foods to bird diets over time. Renfrew et al. (2017) examined the winter diet of migratory bobolinks (*Dolichonyx oryzivorus*) while they were in South America by taking advantage of their unusual molting pattern. Bobolinks go through two complete molts every year, one in North America during the boreal summer, and another in South America during the austral summer. During each molt bobolinks replace all their feathers. Knowledge of their molting pattern allowed the researchers to take clippings from different primary feathers that had grown during the beginning, middle, and end stage of their austral molt. The isotope values from these feather clippings were representative of the bobolinks' diet at three different times: shortly after they arrived in South American, half-way through their stay, and right before they left to migrate north again, respectively. In this way the researchers were able to use $\delta^{13}C$ values of the feather clippings to differentiate proportional contributions of native grasses (that use a C_4 photosynthetic pathway) and agricultural

rice (a C_3 grass). The difference in $\delta^{13}C$ between C_3 and C_4 plants is quite detectable, about 16‰ in their study. Using statistical mixing models, the isotope values of local C_3 plants, C_4 plants, and the bobolinks' feather clippings the researchers were able to reconstruct an estimate of the bobolinks' diet proportions. They determined that bobolinks consumed relatively more C_3 plant material at the end of their molting period, right before migrating north. This coincided with greater availability of rice (close to harvest time) and so it was concluded that bobolinks were taking advantage of the abundant agricultural food source, possibly in preparation for migration. This study has implications for nutritional trade-offs between agricultural rice and native grasses, as well as conservation issues related to conflicts with agricultural producers who may consider the bobolink as a pest (Renfrew et al. 2017).

Another study by Blomberg et al. (2013) demonstrated the use of $\delta^{15}N$ to differentiate proportional contributions of plant foods and arthropod foods in greater sage grouse chicks. Using the principle of trophic enrichment discussed earlier, known local plant and arthropod foods were analysed for $\delta^{15}N$. It was confirmed that arthropods were enriched in $\delta^{15}N$ relative to plant foods, allowing a SIMM to differentiate between the two sources. As with sharp-tailed grouse, arthropods are an important food source for rapidly developing sage-grouse chicks. In this study the researchers used sequential sampling of developing primary feathers, and $\delta^{15}N$ analysis, to estimate the contribution of plant versus arthropod foods during the first 28 days after hatching. It was determined that feather $\delta^{15}N$ became depleted with age as the diet gradually shifted towards more plant foods, as expected. Individual health metrics (tarsus length and overall mass) also demonstrated that chicks that consumed more arthropods, i.e. had more enriched $\delta^{15}N$ values in their feathers, correlated with larger body size and the ability to transition to a plant-dominant diet faster (Blomberg et al. 2013).

Together the above examples of the application of stable isotope ecology to avian diets demonstrate the theoretical principles used in the present study. $\delta^{13}C$ and $\delta^{15}N$ isotope values of sharp-tailed grouse primary feathers grown from May to October were used to estimate relative contribution of plant and arthropod foods over the molting period. Chapter 2 reports the results of esophageal crop content analysis of 164 sharp-tailed grouse from which primary feathers were collected for stable isotope

analysis. The concepts of mixing models, molting patterns in sharp-tailed grouse, and various food web structure metrics are discussed in further detail in Chapter 3, and the utility of using stable isotopes to estimate diet proportions in sharp-tailed grouse is assessed. The ecological implications of the results of this study are discussed in Chapter 4.

1.6 RESEARCH OBJECTIVES AND HYPOTHESES

The objectives of this research were to (1) validate the use of stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ in primary feathers from plains sharp-tailed grouse for estimating diet proportions of plant foods and arthropods foods. And to (2) assess the role of arthropods in the ecology of plains sharp-tailed grouse through empirical study and analysis, field data, and literature review.

Working towards these objectives tested the utility of using stable isotopes to estimate diet in sharp-tailed grouse and has helped to understand ecological links between arthropods and grouse beyond what was already known. Results elucidated differences in diet between age and sex classes and contributed to our understanding of the nutritional value of plant and arthropod foods to sharp-tailed grouse.

CHAPTER 2: FALL DIET OF PLAINS SHARP-TAILED GROUSE ASSESSED USING ESOPHAGEAL CROP CONTENTS

Abstract

Sharp-tailed grouse (*Tympanuchus phasianellus*) are an important component of northern grassland food webs, a reliable indicator species, and considered to be valuable to the preservation of biodiversity of grassland ecosystems. Ecological stressors imposed on this species include habitat alteration, fragmentation, encroachment from agricultural development, insecticides, and the effects of climate change on prairie landscapes, all of which have the potential to alter food availability and trophic dynamics. Insects and spiders are an important food source for many grassland birds. The ecological roles of many arthropod species as prey and as contributors of other important ecosystem services, remain unexplored. This study examined esophageal crop contents from 164 plains sharp-tailed grouse (subspecies *jamesi*) from three sites in southern and central Alberta, Canada. Frequent utilization of Dawson's grasshopper (*Melanoplus dawsoni*) was identified in the fall diet of grouse at all sites. This small flightless insect is common on fescue grasslands in prairie, foothills, and parkland biomes. Grasshoppers (Orthoptera: Acrididae, 18 species) occurred in 80% of esophageal crops collected in September, and 31% in October. Of these 91% and 63%, respectively, were Dawson's grasshopper. Juvenile grouse consumed more grasshoppers than adult grouse at all sites and sampling dates. Studies on other gallinaceous game birds have also identified frequent utilization of single arthropod species, likely due to the range, catchability, and abundance of these species at certain times of year. Species-level arthropod ecology can help to contribute to a better understanding of ecosystem stability, optimal land management practices, and previously unexplored food web connections.

2.1 INTRODUCTION

Sharp-tailed grouse (*Tympanuchus phasianellus*) are the most widespread native prairie grouse in North America and are a popular game bird species for many hunters and bird watchers. This species has

decreased in abundance in many parts of its range (Connelly et al. 1998; Johnsgard 2016). In Alberta, Canada, plains sharp-tailed grouse (subspecies *jamesi*) are listed as a Sensitive Species by the Alberta provincial government due to their continued slow decline (Alberta Environment and Parks 2020). The reasons for decline are attributed to a reduction in habitat availability, connectivity, and quality due to conversion of native prairie for agricultural development, and habitat fragmentation caused by roads, utility lines, and other forms of disturbance (Connelly et al. 1998; Manzer and Hannon 2005).

Sharp-tailed grouse are also an important indicator species in prairie ecosystems (South Dakota Department of Game 2017). A growing need for conservation action concerning grouse (Tetraonidae) has prompted research using new technologies in genetics, telemetry, landscape-scale ecology, and habitat management which have greatly increased our knowledge of grouse conservation. However, relative effort invested in studies in diet and behaviour have since decreased (Moss et al. 2010). Changing climate and increased variability and severity of weather events have the potential to alter food availability and trophic dynamics (Voigt et al. 2003; Pearce-Higgins 2010; Rosenblatt and Schmitz 2016), and there are documented declines in insect abundance and diversity in some regions (Hallmann et al. 2017). This makes it important to increase our knowledge of potentially important food web connections needed to understand and promote ecosystem resilience through the preservation of biodiversity (Naeem 1998; Haddad et al. 2011).

Numerous studies have examined the diets of sharp-tailed grouse in detail (Selko and L.F. 1938; Aldous 1943; Kobriger 1965; Renhowe 1968; Sisson 1976; Mitchell and Riegert 1994). Their diet is mostly plant-based but they also consume terrestrial arthropods, sometimes in large quantities, when they are available likely as a high-nutrient food source. Grasshoppers (Orthoptera: Acrididae) are reported as an important food source for sharp-tailed grouse in many of these diet studies. They are known to be a critical food source for chicks (Renhowe 1968; Johnsgard 2016) and can make up a significant portion of adult grouse diets in the fall (Marshall and Jensen 1937; Hamerstrom and Hamerstrom 1951; Jones 1966). Conventional diet studies using fecal analysis or esophageal crop contents may underestimate the contribution of soft-bodied arthropods that break down quickly after being consumed (Sullins et al. 2018). Studies of other grouse species have shown positive correlations between arthropod

consumption and egg quality, brood survival, and growth rates in chicks (Moss et al. 1972; Johnson and Boyce 1990; Picozzi et al. 1999; Park et al. 2001). Red grouse (*Lagopus lagopus scoticus*) have shown a preference for food items high in nitrogen and phosphorous, of which insects are an excellent source (Moss 1972; Butterfield and Coulson 1975; Moss 1989). Other gallinaceous game birds have been known to focus on specific insect species or groups at times of high availability, such as red grouse on crane flies (*Molophilus ater*), and grey partridge (*Perdix perdix*) and red-legged partridge (*Alectoris rufa*) on aphids (Hemiptera: Aphidoidea) (Savory 1989).

Many of the diet studies that examine arthropod consumption by grouse report prey taxa at the family or order level and do not explore species level relationships among arthropods and their predators. This leaves the ecological relationships between grouse and arthropod species that may have different phenologies, mobility, or nutritional value largely unknown. Recent studies from around the world have reported declines in insect numbers, related to habitat modification and the use of insecticides, and in some cases these are associated with declines in bird populations (Nebel et al. 2010; Hallmann et al. 2014; Hallmann et al. 2017). Arthropods are indeed highly responsive to changes in climate, and our understanding of how climate change will influence the essential ecosystem functions that arthropods carry out is insufficient (Prather et al. 2013). It is therefore prudent to explore the utilization of arthropods by grouse with the highest taxonomic precision possible in order to reveal potentially important ecological relationships (Gullion 1966).

In Alberta, and the Canadian prairies, there are more than 40 species of grasshoppers common to the grasslands, and some possess different phenological traits and life histories that affect their abundance and scarcity at different times during the warm season. Fewer than 10 of these species are potential economic pests of agriculture (Johnson 2001; Johnson et al. 2002; Johnson 2003a; Johnson 2008) making it important to distinguish between pest species and those that may be an important food web component for grassland birds. Grasshoppers as a food source are of interest due to their abundance and seasonal occurrence on prairie landscapes, especially regarding how their distributions will be altered with a changing climate (Johnson et al. 2017) and how their presence, diversity, and abundance are affected by agricultural pest control (Martin et al. 1998). Grasshoppers have been

documented as key food items for grassland birds (Martin et al. 1996; Martin et al. 2000) and some mammals (Kuiken et al. 2003) and can act as an important ecological and nutritional buffer in the event of inclement weather or other factors that have the potential to decrease arthropod bird-food supply (Bird 1961).

The purpose of this study was to examine esophageal crops contents from hunter harvested sharp-tailed grouse in Alberta to make observations about their diet habits, including relative use of plant and arthropod food items, during October 2017 and 2018 and September 2018.

2.2 STUDY AREA

Esophageal crops (hereafter "crops") from sharp-tailed grouse were collected during the 2017 and 2018 hunting seasons (October 1 to October 31) from two sites in southern Alberta, Canada (n = 108): the Wild Rose Conservation Site (Wild Rose), managed by the Alberta Conservation Association (ACA), near the hamlet of Spring Coulee (49°15'39" N, 112°59'12" W), and the other on leased ranch land part of the Twin River Heritage Rangeland Natural Area (Twin River) west of the village of Warner (49°14'29" N, 112°20'43" W) (hereafter "southern Alberta sites"). Crops were also obtained on September 1, 2018, from hunters at Canadian Forces Base (CFB) Wainwright in central Alberta (52°48'30" N, 110°57'49" W) (n = 56), approximately 420km (straight line distance) from the southern sites (hereafter "central Alberta site"). The two southern Alberta sites were on native prairie neighbouring agricultural land where the foothills fescue and mixed grass natural subregions meet, along the Milk River Ridge. Collections from central Alberta were taken by donation at a hunter checkpoint at CFB Wainwright during an early-season hunt, in the central parkland natural subregion (Downing and Pettapiece 2006).

Southern Alberta sites: The Milk River Ridge (MRR) is located in the southernmost part of Alberta, which parallels the north bank of the Milk River, adjacent to the Montana border. The MRR is the continental divide between the Gulf of Mexico drainage to the south and the Hudson Bay drainage to the north. Most importantly, the MRR is one of six internationally significant grasslands left on the North American plains spanning an area of 1,663 km^2. Sixty percent of the MRR (western portion) is

located within the foothills fescue natural subregion. Typical landforms throughout this portion of the ridge are undulating, hummocky, plains comprised of calcareous till, eolian and glaciolacustrine deposits (Downing and Pettapiece, 2006). Dominant soils are Orthic Black and Orthic Dark Brown Chernozems (Alberta Agriculture and Forestry, 2018). Plant communities are dominated by graminoids such as rough fescue (*Festuca campestris*), parry oat grass (*Danthonia parryi*), Idaho fescue (*Festuca idahoensis)* and junegrass (*Koelaria macrantha)*. However, some native grassland communities have been modified with the presence of introduced graminoid species such as timothy (*Phleum pretense)*, Kentucky bluegrass (*Poa pratensis)*, and smooth brome (*Bromus inermis)*. Common forbs present include sticky purple geranium (*Geranium viscosissimum)*, three-flowered aven *(Genum triflorum)*, fringed sagewort *(Artemisia frigida),* and prairie goldenbean *(Thermopsis rhombifolia)*. Shrub communities on moderately drained sites are dominated by species such as silverberry (*Elaeagnus commutata)*, prickly rose (*Rosa acicularis)*, snowberry (*Symphoricarpos occidentalis)* and saskatoon (*Amelanchier alnifolia)* (Downing and Pettapiece 2006; Bradley, 2008).

The mean precipitation in southern Alberta is 482.4 mm with the wettest month being June (112.5 mm). The mean temperature is 5.6° C with the warmest months being July and August (17.7° C) (Government of Canada, 2018).

The Wild Rose site is owned in partnership by the Alberta Conservation Association, Alberta Fish and Game Association, Environment and Climate Change Canada, and the Nature Conservancy of Canada which allow foot access for hiking, fishing, and hunting.

In Alberta, Natural Areas protect sites of regional significance while giving opportunities for nature-based recreational activities such as hunting. Similarly, Heritage Rangelands protect areas which are representative of a native prairie ecosystem. Preservation of the ecological integrity and function of prairie sites is achieved through carefully managed grazing practices (Alberta Parks 2018).

The Twin River Heritage Rangeland Natural Area was established in 2001 and protects a 190 km^2 area of the MRR. Numerous priority and rare plants are found within the boundaries of the Twin River area which include hare-footed locoweed (*Oxytropis lagopus*), Raymond's sedge (*Carex raymondii*), intermediate hawk's-beard (*Crepis intermedia*), few-flowered rush (*Trichophorum planifolium*), prickly

milk vetch (*Astragalus kentrophyta*), tufted hymenopappus (*Hymenopappus filifolius*), and Carolina whitlowgrass (*Draba reptans*).

The native prairie vegetation at both Twin River and Wild Rose provides habitat for mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus)*, pronghorn (*Antilocapra americana)*, rocky mountain elk (*Cervus canadensis),* grizzly bear (*Ursus arctos horribilis*), badger (*Taxidea taxus*), sharp-tailed grouse, grey partridge (*Perdix perdix*) and a variety of passerine and small mammal species. Common raptors to the area include ferruginous hawk (*Buteo regalis*), peregrine falcon (*Falco peregrinus*), prairie falcon (*Falco mexicanus*), and golden eagle (*Aquila chrysaetos*) (Alberta Environment and Parks, 2018).

Central Alberta site: CFB Wainwright, in the central parkland natural sub-region, is characterized by undulating, hummocky, terrain with an average elevation of 610 m and orthic or dark brown to black chernozemic soils (Anderson and Bailey 1980). The dominant vegetation is comprised of upland prairie plants, such as plains rough fescue (*Festuca hallii*), junegrass , needle-and-thread grass (*Hesperostipa comata*), prairie crocus (*Anemone patens*), three-flowered aven, beaked hazelnut (*Corylus cornuta*), bunchberry (*Cornus canadensis*), wild sapsarilla (*Aralia nudicaulis*), and aspen (*Populus spp.*) stands (Downing and Pettapiece 2006).

The mean precipitation at CFB Wainwright is 411.8 mm with the wettest month being June (72.5 mm). The mean temperature is 2.2° C with the warmest months being July (17.0° C) (Government of Canada, 2018).

2.3 MATERIALS AND METHODS

When possible sharp-tailed grouse from which crops were obtained were aged and sexed using wing morphology and molt stage (Pyle 2008), crown and tail feather pattern (Henderson et al. 1967), and ossification of the lower mandible (Linduska 1945). All sites were under active grazing management by the ACA, local ranchers, or the Department of National Defence. Crops were brought to the laboratory at the University of Lethbridge and dissected. Extracted food items were separated and identified as close to the species level as possible and were then counted and weighed to the nearest milligram,

oven dried at 60°C for 48 hours, and weighed again. Fifty-six arthropod taxa were identified. Twenty-four were identified to the species level, 7 to genus, 17 to family, and 8 to order. Those that could not be identified to the species level occurred infrequently and were in poor condition. Plant food items consisted mostly of berries and agricultural seeds and were easily separated and identified. Other plant materials such as leaves and grasses that made up a small dietary contribution were combined into a single category. Sweep netting was done in 100 m transects (one sweep per meter) from May to October 2018 at the southern Alberta sites (n = 222, n = 26 during October) and on September 1, 2018 at the central Alberta site (n = 5) in order to quantify relative abundance of arthropods.

The crop contents data were used to rank food items using the method described in Bogdanoff et al. (2018). Three metrics were used: percent composition by dry weight (%w); frequency of occurrence (%f); and number of occurrences (%n). These metrics were used to calculate three indices of importance: Index of Relative Importance (IRI) (Pinkas et al. 1971); Index of Importance (IOI) (Gray et al. 1997; Hunt et al. 1999); and Index of Preponderance (IOP) (Natajrajan and Jhingran 1961):

$$IRI = \%f \cdot (\%n + \%w)$$

$$IOI = 100 \cdot (\%f + \%w) / \Sigma(\%f + \%w)$$

$$IOP = \%f \cdot \%w / \Sigma(\%f + \%w)$$

Ranks were calculated for individual diet items, as well as when diet items were combined into the following groups: leaves; berries; agricultural seeds; shrub buds and seeds; orthopteran prey; and other arthropod prey. The average was then taken of the three ranks in order to rank diet items and groups by importance (Bogdanoff et al. 2018). Two-way analysis of variance was conducted to examine interactions between diet group composition (%w), age, and sex. This was done separately for the southern and central Alberta sites: southern sites n = 98 (age known), n = 56 (sex known), n = 52 (age and sex known); central site n = 56 (age known), n = 55 (sex known).

2.4 RESULTS AND DISCUSSION

When ranking was calculated by diet group (Table 1), berries ranked as the most important food item for all sites in southern and central Alberta. These consisted mostly of snowberry (*Symphoricarpos occidentalis*), rose hips (*Rosa acicularis, R. woodsii*) and chokecherry (*Prunus virginiana*). The high relative abundance of agricultural food items at the southern Alberta sites, and not at the central Alberta site, was attributed to proximity of grain fields at the southern Alberta sites. High numbers of individual grains in wheat (*Triticium*) and canola (*Brassica*) contributed to a high measure of importance of agricultural seeds, even though they occurred in only 16% of crops. Waste grain has been reported to be of benefit to sharp-tailed grouse as an easily accessible supplemental food source (Bird 1961), however, intensely cultivated areas likely negate that benefit by fragmenting native prairie habitat and reducing overall nest success (Manzer and Hannon 2005).

Table 1 - Food groups ranked by frequency (%f), number (%n), and dry weight (%w) for sharp-tailed grouse in southern and central Alberta using ranking methods from Bogdanoff et al. 2018

Southern Alberta sites (October 1 - 31, 2017 and 2018)

Diet Groups	%f	%n	%w	Average Rank
Berries	88.0	17.1	54.5	1.0
Agricultural seeds	15.7	68.6	35.1	2.3
Leaves	78.7	<1.0	4.4	3.0
Shrub buds and seeds	39.8	11.5	2.4	4.0
Orthoptera	30.6	1.9	3.4	4.7
Other insects and arachnids	15.7	<1.0	<1.0	6.0

Central Alberta site (September 1, 2018)

Diet Groups	%f	%n	%w	Average Rank
Berries	73.2	35.3	55.9	1.3
Orthoptera	80.4	54.4	37.4	1.7
Leaves	92.9	2.6	6.0	3.0
Other insects and arachnids	50.0	5.8	<1.0	4.0
Seeds	5.4	1.8	<1.0	5.0
Agricultural seeds	0.0	0.0	0.0	-

When all individual diet items were ranked by relative importance (Tables 2 and 3) Dawson's grasshoppers (*Melanoplus dawsoni*) (Figure 4) ranked as the most important food item at the central Alberta site and ranked 7th at the southern Alberta sites. Grasshoppers were the most common family of arthropods present in all sharp-tailed grouse crops. The earlier sampling time (September 1 versus October 1-31) could account for a higher rate of arthropod utilization at the central Alberta site because arthropod abundance would likely have been lower in October due to decreased temperatures and snow.

Figure 4 - Male Dawson's grasshopper (*Melanoplus dawsoni*) in southern Alberta (Photo: Dan Johnson)

Juvenile (hatch-year) grouse consumed more grasshoppers than adults (after hatch-year) at all sites, consistent with previous findings (Renhowe 1968; Johnsgard 2016). At the southern Alberta sites juveniles had on average 472 mg, or 5.3 times, more grasshoppers in their crop than adults (P = 0.0057), and 1143 mg, or 5.1 times, more grasshoppers in their crop at the central Alberta site (P = 0.0006). Male grouse consumed on average 82 mg, or 0.8 times, more grasshoppers than females (P = 0.0264) (Table 4). The difference in mean total crop contents weight between the southern and central sites was attributed to the mild weather on the day of sampling at the central Alberta site (13°C, partly overcast and light rain in the morning). Grouse generally feed less intensely during cold and wet conditions (Erikstad and Spidsø 1982).

Table 2 - Food items ranked by frequency (%f), number (%n), and dry weight (%w) for southern Alberta sharp-tailed grouse (October 1 - 31 2017 and 2018) using ranking method from Bogdanoff et al. 2018

Prey item			**Ranking Metrics**			
Common name	**Scientific name**	**Diet Group**	**%f**	**%n**	**%w**	**Average Rank**
Snowberry	*Symphoricarpos occidentalis*	Berries	74	11.0	10.0	1.3
Rose hip	*Rosa acicularis, R. woodsii*	Berries	59	2.7	23.2	2.0
Chokecherry	*Prunus virginiana*	Berries	23	3.2	21.1	3.7
Green leaf matter		Leaves	79	0.5	4.4	4.0
Wheat grain	*Triticum*	Ag. crops	12	28.0	25.2	4.7
Shrub bud		Shrub buds	38	11.3	2.4	5.3
Dawson's grasshopper	*Melanoplus dawsoni*	Orthoptera	25	1.2	1.7	7.3
Marsh meadow grasshopper	*Pseudochorthippus curtipennis*	Orthoptera	21	0.4	0.7	8.7
Canola seed	*Brassica*	Ag. crops	3	39.3	3.7	9.0
Chickpea	*Cicer*	Ag. crops	3	1.4	6.2	9.0
Bruner's spur-throat	*Melanoplus bruneri*	Orthoptera	6	0.2	0.7	11.3
Saskatoon	*Amelanchier alnifolia*	Berries	4	0.2	0.3	12.3
Damsel bug	*Nabis*	Insects	6	0.1	<0.1	14.0
Clear-winged grasshopper	*Camnula pellucida*	Orthoptera	2	<0.1	0.1	14.3
Migratory grasshopper	*Melanoplus sanguinipes*	Orthoptera	*2*	*<0.1*	*0.1*	*15.7*
Cow grasshopper	*Chloealtis abdominalis*	Orthoptera	2	<0.1	<0.1	16.0
Red-legged grasshopper	*Melanoplus femurrubrum*	Orthoptera	2	<0.1	<0.1	17.3
Curly dock seed	*Rumex crispus*	Seeds	2	0.2	<0.1	17.7
Two-striped grasshopper	*Melanoplus bivittatus*	Orthoptera	1	<0.1	0.1	20.7

Mound ant	*Formica*	Insects	3	<0.1	<0.1	21.0
Seven-spot ladybird	*Coccinella septempunctata*	Insects	2	<0.1	<0.1	21.7
Shield-back bug	Scutelleridae	Insects	2	<0.1	<0.1	23.0
Large-headed grasshopper	*Phoetaliotes nebrascensis*	Orthoptera	1	<0.1	<0.1	24.0
Crab spider	*Xysticus*	Arachnids	2	<0.1	<0.1	24.3
Striped willow leaf beetle	*Disonycha alternata*	Insects	1	<0.1	<0.1	25.3
Wolf spider	Lycosidae	Arachnids	2	<0.1	<0.1	25.7
Wolf-willow	*Elaeagnus commutata*	Berries	1	<0.1	<0.1	26.0
Grass spider	*Agelenopsis*	Arachnids	2	<0.1	<0.1	26.7
Weevil	Curculionidae	Insects	2	<0.1	<0.1	27.0
W. cloud grasshopper	*Encoptolophus costalis*	Orthoptera	1	<0.1	<0.1	27.0
Running crab spider	Philodromidae	Arachnids	1	<0.1	<0.1	31.0
Beetle	Coleoptera	Insects	1	<0.1	<0.1	31.3
Dung beetle	Scarabaeidae	Insects	1	<0.1	<0.1	32.7
Ground beetle	Carabidae	Insects	1	<0.1	<0.1	34.0
Moth	Lepidoptera	Insects	1	<0.1	<0.1	35.0

Table 3 - Food items ranked by frequency (%f), number (%n), and dry weight (%w) for central Alberta sharp-tailed grouse (September 1, 2018) using ranking method from Bogdanoff et al. 2018

Prey item			**Ranking Metrics**			
Common name	**Scientific name**	**Diet Group**	**%f**	**%n**	**%w**	**Average Rank**
Dawson's grasshopper	*Melanoplus dawsoni*	Orthoptera	80.4	49.6	33.0	1.0
Chokecherry	*Prunus virginiana*	Berries	30.4	13.9	28.0	2.3
Green leaf matter		Leaves	92.9	2.6	6.0	2.7
Snowberry	*Symphoricarpos occidentalis*	Berries	35.7	11.6	5.6	4.0
Rose hip	*Rosa acicularis, R. woodsii*	Berries	19.6	1.3	6.6	5.7
Juniper	Juniperus	Berries	12.5	5.0	9.9	6.0
Marsh meadow grasshopper	*Pseudochorthippus curtipennis*	Orthoptera	30.4	1.9	1.2	6.3
Kinnikinnick	*Arctostaphylos uva-ursi*	Berries	7.1	1.0	2.1	9.7
Saskatoon	*Amelanchier alnifolia*	Berries	5.4	2.1	2.4	10.0
Wolf-willow	*Elaeagnus commutata*	Berries	8.9	0.4	1.2	11.0
Prairie spittlebug	*Philaenarcys bilineata*	Insects	16.1	0.9	0.1	12.0
Large-headed grasshopper	*Phoetaliotes nebrascensis*	Orthoptera	7.1	0.8	0.6	13.0
Ant	Formicidae	Insects	14.3	1.0	<0.1	14.3

Four-spotted tree cricket	*Oecanthus quadripunctatus*	Orthoptera	10.7	0.3	0.1	15.0
Migratory grasshopper	*Melanoplus sanguinipes*	Orthoptera	5.4	0.3	0.3	15.3
Two-striped grasshopper	*Melanoplus bivittatus*	Orthoptera	3.6	0.4	0.7	16.3
Curly dock	*Rumex crispus*	Seeds	5.4	1.8	0.1	16.3
Bruner's spur-throat	*Melanoplus bruneri*	Orthoptera	5.4	0.2	0.2	16.7
Seven-spot ladybird	*Coccinella septempunctata*	Insects	7.1	0.2	0.1	19.0
Huckleberry grasshopper	*Melanoplus fasciatus*	Orthoptera	3.6	0.2	0.3	19.7
Packard's grasshopper	*Melanoplus packardii*	Orthoptera	3.6	0.1	0.3	20.7
Prairie meadow katydid	*Conocephalus saltans*	Orthoptera	5.4	0.2	0.1	22.0
Clear-winged grasshopper	*Camnula pellucida*	Orthoptera	3.6	0.1	0.1	24.0
Ichneumonid wasp	Ichneumonidae	Insects	5.4	0.2	<0.1	24.0
Spinach flea beetle	*Disonycha xanthomelas*	Insects	1.8	1.8	0.1	25.0
Cow grasshopper	*Chloealtis abdominalis*	Orthoptera	1.8	0.2	0.3	25.3
Caterpillar	Lepidoptera	Insects	1.8	0.1	<0.1	27.0
Fly larva	Diptera	Insects	5.4	0.2	<0.1	28.0
Buffalo treehopper	Membracinae	Insects	3.6	0.1	<0.1	29.7
Tiger moth	Arctiidae	Insects	1.8	0.1	0.1	31.7
Spider	Araneae	Arachnids	3.6	0.1	<0.1	32.3
White-whiskered grasshopper	*Ageneotettix deorum*	Orthoptera	1.8	0.1	<0.1	32.7
Green flathead leafhopper	Cicadellidae	Insects	3.6	0.2	<0.1	33.3
Weevil	Curculionidae	Insects	3.6	0.1	<0.1	33.3
Funnel web spider	*Agelenopsis*	Arachnids	1.8	0.1	<0.1	34.0
Tiger moth caterpillar	Arctiidae	Insects	1.8	0.1	<0.1	35.0
Wolf spider	Lycosidae	Arachnids	1.8	0.1	<0.1	36.3
Red-shanked grasshopper	*Xanthippus corallipes*	Orthoptera	1.8	0.1	<0.1	37.3
False milkweed bug	*Lygaeus turcicus*	Insects	1.8	0.1	<0.1	38.0
Millipede	Julida	Insects	1.8	0.1	<0.1	38.3
Robust ground cricket	*Allonemobius*	Orthoptera	1.8	0.1	<0.1	39.7
Flea beetle	*Disonycha latifrons*	Insects	1.8	0.1	<0.1	41.3
Moth/butterfly	Lepidoptera	Insects	3.6	0.1	<0.1	42.0
Leaf beetle	Chrysomelidae	Insects	1.8	0.1	<0.1	43.3
Braconid wasp	Braconidae	Insects	1.8	0.1	<0.1	44.3
Funnel weaver spider	Agelenidae	Arachnids	1.8	0.1	<0.1	46.0
Black carpenter ant	*Camponotus pennsylvanicus*	Insects	1.8	0.1	<0.1	47.0
Cricket	Gryllidae	Orthoptera	1.8	0.1	<0.1	48.0

Crab spider	*Xysticus*	Arachnids	1.8	0.1	<0.1	49.0
Running crab spider	Pentatomidae	Arachnids	1.8	0.1	<0.1	50.0
Black grass bug	*Labops*	Insects	1.8	0.1	<0.1	51.0
Black stink bug	*Proxys punctulatus*	Insects	1.8	0.1	<0.1	52.0
Lygus bug	*Lygus*	Insects	1.8	0.1	<0.1	53.0
Harvestmen	Opiliones	Arachnids	1.8	0.1	<0.1	54.0

Table 4 - Average sharp-tailed grouse diet group proportion differences between age and sex (%w)

Southern Alberta sites (October 1-31, 2017 and 2018)

Diet Group	♀ **AHY**	♂ **AHY**	♀ **HY**	♂ **HY**
n	23	9	12	8
Berries	42.7	93.2	79.4	77.4
Leaves	3.8	1.8	3.8	4.4
Shrub buds and seeds	3.3	2.2	6.2	5.0
Agricultural seeds	48.2	0	0	0
Orthoptera	2.0	2.8	10.5	13.2
Other insects and arachnids	0	<1	<1	<1
Mean total crop contents (g)	4.35	5.88	5.71	4.17

Central Alberta site (September 1, 2018)

Diet Group	♀ **AHY**	♂ **AHY**	♀ **HY**	♂ **HY**
n	12	11	20	12
Berries	81.8	73.2	49.2	26.0
Leaves	7.5	14.8	2.6	1.6
Shrub buds and seeds	0	0	<1	<1
Agricultural seeds	0	0	0	0
Orthoptera	10.2	11.2	47.4	71.6
Other insects and arachnids	<1	<1	<1	<1
Mean total crop contents (g)	2.53	2.65	2.36	2.69

AHY = After hatch-year, HY = Hatch-year

Other statistically significant interactions were that females consumed more shrub buds and seeds than males (P = 0.0263) at the southern sites, and at the central Alberta site adult grouse consumed more leaves (P = 0.0045) and more berries (P = 0.0139) than juvenile grouse.

Out of all grouse that potentially had access to agricultural seeds (southern Alberta sites only) and where age or sex was known (n = 97), 17 crops contained wheat, canola, or chickpeas (an average of 1085 mg). Of those only 1 was a juvenile grouse (1 of the 17 was of undetermined age). Only female grouse were observed to have consumed agricultural seeds (10 of the 17 were of undetermined sex), however, due to the small sample set of male grouse where age was known the effect was not statistically significant (P = 0.0504 for age, and P = 0.2165 for sex).

Mean dry weight per individual food item (Table 5) between central and southern sites differed only with chokecherries (44% lighter at the central Alberta site, P = 0.001) and female Dawson's grasshoppers (13% lighter at the central Alberta site, P = 0.017). The earlier seasonal stage (beginning of September versus October 1-31) and more northern cline could explain these differences. It is also possible that more female Dawson's grasshoppers were carrying eggs and had accumulated more body weight later in the season at the southern Alberta sites.

Crop dissections yielded 1070 individual grasshoppers from the 56 crops collected at the central Alberta site in September, of which 976 (91%) were Dawson's grasshoppers. At the southern Alberta sites 305 grasshoppers were recovered from 108 crops collected in October, 191 (63%) of which were Dawson's grasshoppers (Table 6). Dawson's grasshopper is common on the Alberta prairies, especially on fescue grassland where it reaches its highest numbers. It also occurs in lower numbers in short-grass, mixed-grass, and aspen parkland ecoregions. It is short-winged and flightless (very rare occurrences, less than 0.01% in the region where this study took place, have long wings and fly) and persists later into the fall than many other grasshoppers (Johnson 2003b). The size and flightless nature of Dawson's grasshoppers may make them an ideal prey item for ground foraging grouse in the fall, although some research into the susceptibility to predation of different grasshopper subfamilies suggests that flying grasshoppers may in fact be more vulnerable to predation (Belovsky et al. 1990). Dawson's grasshoppers were the most common species collected from sweep netting at all sites from August to October. In October,

however they were not present in high numbers: an average of 0.3 Dawson's grasshoppers collected per 100 sweeps at the southern Alberta sites. At the central Alberta site 2.2 Dawson's grasshoppers were caught per 100 sweeps.

Table 5 – Mean weight and moisture content of individual food items found in sharp-tailed grouse crops (n = 164)

Food item			Summary statistics			
Common name	**Scientific name**	**Sex of grasshopper**	**n**	**Mean dry weight per individual (mg)**	**SD (mg)**	**Moisture content (%)**
Rose hip	*Rosa acicularis, R. woodsii*		446	338	138	52
Snowberry	*Symphoricarpos occidentalis*		1953	35	10	68
Chokecherry	*Prunus virginiana*		780	188	67	46
Juniper	*Juniperus*		98	118	34	52
Curly dock	*Rumex crispus*		72	4	2	38
Saskatoon	*Amelanchier alnifolia*		66	75	19	66
Kinnikinnick	*Arctostaphylos uva ursi*		20	143	43	60
Wolf-willow	*Elaeagnus commutata*		9	192	53	48
Shrub bud			1788	7	3	52
Green leaf matter						73
Wheat grain	*Triticum*		5342	26	3	30
Canola seed	*Brassica*		6155	4	1	38
Chickpea	*Cicer*		218	162	13	45
Dawson's grasshopper	*Melanoplus dawsoni*	♀	611	57	11	65
Female/male weight ratio: 1.5		♂	535	39	6	65
Marsh meadow grasshopper	*Pseudochorthippus curtipennis*	♀	57	67	19	62
Female/male weight ratio: 2.1		♂	47	32	10	61
Bruner's spur-throat grasshopper	*Melanoplus bruneri*	♀	10	146	24	60
Female/male weight ratio: 1.3		♂	24	115	16	60

Large-headed grasshopper	*Phoetaliotes nebrascensis*	♀	6	87	42	63
		♂	9	50	2	65
Two-striped grasshopper	*Melanoplus bivittatus*	♀	1	288		65
		♂	8	158	20	65
Cow grasshopper	*Chloealtis abdominalis*	♀	3	171	7	60
		♂	5	43	9	60
Migratory grasshopper	*Melanoplus sanguinipes*	♀	4	132	46	56
		♂	4	76	5	66
Clear-winged grasshopper	*Camnula pellucida*	♀	5	123	44	66
		♂	2	59	11	61
Huckleberry grasshopper	*Melanoplus fasciatus*	♀	2	98	11	65
		♂	2	105		68
Red-legged grasshopper	*Melanoplus femurrubrum*	♀	2	139	32	67
Packard's grasshopper	*Melanoplus packardii*	♀	2	199	28	61
White-whiskered grasshopper	*Ageneotettix deorum*	♀	1	56		54
W. clouded grasshopper	*Encoptolophus costalis*	♀	1	105		67
Immature grasshopper	Acrididae		24	18	7	67
Beetle	Coleoptera		61	11	9	50
True bug	Hemiptera		47	5	4	46
Ant	Formicidae		24	2	2	44
Spider and Harvestmen	Arachnida		14	11	13	54
Cricket	Gryllidae		12	16	10	50
Larvae	Coleoptera/Diptera/ Lepidoptera		6	17	21	73
Wasp	Ichneumonidae/Braconidae		5	5	3	58
Moth	Lepidoptera		3	30	37	72
Millipede	Myriapoda		1	35		8

Table 6 – Orthopteran prey ranked by frequency (%f), number (%n), and dry weight (%w) for sharp-tailed grouse in Alberta using ranking method from Bogdanoff et al. 2018

Southern Alberta sites (October 1-31, 2017 and 2018)

Prey Species		Ranking Metrics			Average Rank
Common name	**Scientific name**	**%f**	**%n**	**%w**	
Dawson's grasshopper	*Melanoplus dawsoni*	25.0	62.6	48.7	1.0
Marsh meadow grasshopper	*Pseudochorthippus curtipennis*	21.3	21.6	19.7	2.0
Bruner's spur-throat grasshopper	*Melanoplus bruneri*	5.6	10.2	20.8	3.0
Clear-winged grasshopper	*Camnula pellucida*	1.9	1.6	2.7	4.0
Migratory grasshopper	*Melanoplus sanguinipes*	1.9	0.7	1.6	5.3
Cow grasshopper	*Chloealtis abdominalis*	1.9	1.3	1.4	6.0
Two-striped grasshopper	*Melanoplus bivittatus*	0.9	0.7	2.4	7.3
Red-legged grasshopper	*Melanoplus femurrubrum*	1.9	0.7	1.4	7.3
Large-headed grasshopper	*Phoetaliotes nebrascensis*	0.9	0.3	0.8	9.0
Western clouded grasshopper	*Encoptolophus costalis*	0.9	0.3	0.5	10.0

Central Alberta site (September 1, 2018)

Prey Species		Ranking Metrics			Average Rank
Common name	**Scientific name**	**%f**	**%n**	**%w**	
Dawson's grasshopper	*Melanoplus dawsoni*	80.4	91.2	88.3	1.0
Marsh meadow grasshopper	*Pseudochorthippus curtipennis*	30.4	3.5	3.3	2.0
Large-headed grasshopper	*Phoetaliotes nebrascensis*	7.1	1.5	1.6	3.3
Two-striped grasshopper	*Melanoplus bivittatus*	3.6	0.7	2.0	5.0
Migratory grasshopper	*Melanoplus sanguinipes*	5.4	0.6	0.9	5.0
Four-spotted tree cricket	*Oecanthus quadripunctatus*	10.7	0.6	0.1	6.0
Bruner's spur-throat grasshopper	*Melanoplus bruneri*	5.4	0.3	0.6	6.3
Huckleberry grasshopper	*Melanoplus fasciatus*	3.6	0.4	0.8	8.0
Packard's grasshopper	*Melanoplus packardi*	3.6	0.2	0.8	9.0
Prairie meadow katydid	*Conocephalus saltans*	5.4	0.3	0.2	10.0
Cow grasshopper	*Chloealtis abdominalis*	1.8	0.4	0.9	11.0
Clear-winged grasshopper	*Camnula pellucida*	3.6	0.2	0.4	11.3
White-whiskered grasshopper	*Ageneotettix deorum*	1.8	0.1	0.1	13.0
Red-shanked grasshopper	*Xanthippus corallipes*	1.8	0.1	0.1	14.0
Robust ground cricket	*Allonemobius*	1.8	0.1	<0.1	15.0
Fall field cricket	*Gryllus pennsylvanicus*	1.8	0.1	<0.1	16.0

When relative biomass was considered, Dawson's grasshoppers were not the highest ranking, due to their size. Dawson's grasshoppers occurred at an average of 35 mg biomass per 100 sweeps where Bruner's spur-throat grasshoppers (*Melanoplus bruneri*) occurred at 50 mg, and marsh meadow grasshoppers (*Pseudochorthippus curtipennis*) at 20 mg at the southern sites. Sharp-tailed grouse utilization of Dawson's grasshoppers during the fall cannot be considered a specialization (Devictor et al. 2010) based on the present data since the grouse were likely capturing the insect prey that was most abundant and easiest to catch. However, it is of ecological interest and possibly nutritionally beneficial to grouse that Dawson's grasshopper persists later into the fall than other grasshoppers and is more common on fescue grasslands than other grasslands. It appears to be an ideal insect prey species for sharp-tailed grouse during that time, much like other game birds that have been known to take advantage of certain arthropods during times of high availability (Savory 1989).

Research into the effect of cattle grazing on fescue grasslands suggests that changes to grassland microhabitats can have major effects on grasshopper populations. Heavy stocking rates have been attributed to declines in some species like lesser migratory grasshoppers (*Melanoplus sanguinipes*) and slant-faced grasshoppers (Acrididae: Gomphocerinae) while simultaneously causing an increase in Dawson's grasshopper numbers. The effect measured was great enough that the increase in Dawson's grasshopper abundance was enough to increase the overall number of grasshoppers present in most cases (Holmes et al. 1979). Arthropod diversity in general has also been shown to increase as a result of ecologically appropriate grazing practices, potentially increasing the number of arthropods available to grassland birds as food (Goosey et al. 2019). Intermittent disturbance, i.e. grazing, can be beneficial to grouse by increasing forb diversity, which in turn supports a more diverse array of arthropod species (Sullins et al. 2018; Goosey et al. 2019). However, management recommendations often emphasize the need for moderation and re-evaluation of grazing regimes in order to be of benefit to grouse and other grassland birds (Mattise 1978; Kirby and Grosz 1995; Winder et al. 2018). A review on the subject points out that the effects of grazing on grouse warrants further research with a more detailed emphasis on stocking rates, timing and frequency of disturbance, and livestock type (Dettenmaier et al. 2017).

Most grouse species consume large amounts of arthropods as chicks, and gradually shift towards a more plant-based diet as they reach maturity (Savory 1989). Adult grouse have exceptionally large caeca that allow uptake of greater amounts of nitrogen from their diet (Leopold 1953; Sedinger 1997). However, when compared with other grouse species, sharp-tailed grouse and prairie chickens (*Tympanuchus cupido*) were reported to consume more arthropods into later stages of development, possibly due to occupying generally warmer habitat (Kobriger 1965; Savory 1989). Arthropod prey are higher in protein than plant foods (Stiven 1961; Sullins et al. 2018) and grasshoppers contain on average 61% protein and 13% fat (Rumpold and Schlüter 2013). Amino acids gained from protein in the diet are essential for muscle and feather development (Blair 2008), and certain amino acids like cystine and methionine are important for feather growth (Murphy and King 1992). Although grouse are able to survive on relatively nutrient poor diets (Pendergast and Boag 1971) and may not strictly require access to a lot of arthropods after the first few months of life, it is possible that young sharp-tailed grouse are able to achieve their maximum growth rate with less foraging effort by utilizing available arthropods, which are also more digestible (Stiven 1961; Andreev 1987; Savory 1989). Periods of inclement weather when foraging time becomes limited (Erikstad and Spidsø 1982) may be less detrimental to grouse that have access to more arthropod prey. Adult grouse may also benefit from increased amino acid intake as they lose and replace their feathers throughout the summer months (Pyle 2008).

Changes to our climate are likely to increase the environmental stressors on sharp-tailed grouse in North America (Flanders-Wanner et al. 2004; Thomas et al. 2004; Pearce-Higgins 2010; Forbey et al. 2014). Changes to arthropod communities, abundance, and biodiversity may be a contributing factor if arthropod prey availability becomes limited, or if timing of availability is altered (Lactin et al. 1995). Grazing regimes and agricultural pest management practices have the potential to influence arthropod abundance, especially grasshoppers which are often the target of pest control (Martin et al. 1998; Johnson et al. 2017). Potential effects on arthropod food sources for grouse, and grasslands birds in general, should be considered at the species level when possible as there may be important food web connections, such as food web interactions between sharp-tailed grouse and Dawson's grasshoppers, that would otherwise be overlooked.

CHAPTER 3: ESTIMATING FEEDING RELATIONSHIPS OF SHARP-TAILED GROUSE IN MIXSIAR USING STABLE ISOTOPES $\delta^{15}N$, $\delta^{13}C$, AND CONCENTRATION DEPENDENCE

Abstract

Stable isotopes of a consumer organism can be used to estimate the proportional utilization of food items that have different isotopic signals, and can also be used to estimate changes in diet over time. Using stable isotopes as biotracers in ecological research has become a useful tool for investigating trophic dynamics in ecosystems. Recent advances in stable isotope theory and modeling have extended the utility of natural abundance stable isotope data. However, as a growing field some potentially useful approaches to using stable isotopes remain untested. In this study stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) were used to validate their utility in examining the feeding relationships of plains sharp-tailed grouse (*Tympanuchus phasianellus jamesi*) in southern Alberta, Canada. Sharp-tailed grouse are known to consume mostly plant food and opportunistically utilize insects and spiders as a high protein food source during the warm season. Primary feathers obtained from hunter harvested grouse were analysed and used to estimate diet proportions of vegetation and arthropods from May to October. Stable isotope measurements of primary feathers were able to show seasonal changes in sharp-tailed grouse diet. Results indicated that sharp-tailed grouse may primarily utilize nutrients obtained from insect prey (mainly grasshoppers) for feather synthesis during molt, and that the isotope signals found in primary feathers may be a result of isotopic routing. Stable isotope data also reflected known differences among adult female and male, and juvenile grouse feeding ecology. However, model uncertainty existed due to a wide range of $\delta^{13}C$ values in plant foods. This research points towards the utility of compound-specific isotope analysis, rather than the two-tracer model used here, for future investigations into the feeding relationships of omnivorous grouse.

3.1 INTRODUCTION

Sharp-tailed grouse (*Tympanuchus phasianellus*) are an important indicator species on prairie landscapes in North America and have declined in many parts of their range in recent years (Connelly et al. 1998). Grouse population declines have been attributed to habitat loss, degradation, and fragmentation (Manzer and Hannon 2007), inappropriate grazing management of domestic livestock (Mcnew et al. 2017), and climate change (Forbey et al. 2014). Recent trends in grouse research have seen a decrease in the number of studies examining diet in favour of new areas of focus in conservation made possible with technological advances, i.e. genetics and landscape-scale ecology (Moss et al. 2010). Information about feeding relationships may help in identifying changes to grouse ecology and potential limiting factors as climate change alters plant and arthropod phenology and biodiversity, and consequently affects food availability (Walther et al. 2002; Booth et al. 2012). Arthropod prey are an important high protein food source for many birds, including grouse (Sullins et al. 2018), and some studies indicate alarming rates of arthropod decline around the world (Nebel et al. 2010; Hallmann et al. 2017).

Conventional diet studies on plains sharp-tailed grouse (subspecies *jamesi*) have detailed the types of food items grouse utilize at different times of the year from esophageal crop contents and fecal analysis (Aldous 1943; Kobriger 1965; Renhowe 1968; Sisson 1976; Mitchell and Riegert 1994). However, these types of studies have several limitations (Votier et al. 2003). Soft food items are often underestimated as they are quickly broken down and become unrecognizable (Sullins et al. 2018), tracking diet over large spatial or temporal scales may be difficult, and they only provide a snapshot of the animals' diet at the time of collection (Layman et al. 2015) which may be weather dependant (Erikstad and Spidsø 1982). As an alternative to conventional diet studies stable isotope ecology has shown great promise in elucidating many aspects of food web ecology and is a widely accepted technique for diet reconstruction and food web analysis. Nitrogen (N) and carbon (C) are the most common elements used in food web analysis as $\delta^{15}N$ generally shows a stepwise increase with trophic level, and $\delta^{13}C$ can be used to trace carbon sourcing from isotopically distinct sources (Fry et al. 1978; Post 2002; Layman et al. 2012). Stable isotopes have been used to estimate diet proportions in greater

sage grouse chicks (Blomberg et al. 2013) and Atwater's prairie chicken (*Tympanuchus cupido attwateri*) (Torres-poche 2017), and these studies have revealed important information about the trophic ecology of grouse. Torres-poche (2017) found that historic prairie chicken feathers from museum specimens had significantly higher $\delta^{15}N$ values than contemporary feathers. Given that higher $\delta^{15}N$ values are an indicator of feeding at a higher trophic level (Hobson 1990), as well as the results from Torres-poche's model, this suggested a potentially higher utilization of arthropods by prairie chicken's in the past.

Grasshoppers (Orthoptera: Acrididae) are of particular interest as their abundance, diversity, and varying phenology (Lactin et al. 1995) on grasslands provides many birds with a reliable food source during the spring and warm season (Johnson et al. 1996; Martin et al. 2000). Sharp-tailed grouse are known to utilize grasshoppers as a significant component of their diet (Jones 1966; Mitchell and Riegert 1994), and arthropod prey are critical for grouse chicks during the first weeks of life (Connelly et al. 1998; Johnsgard 2016). Given the impact of climate change on arthropods (Prather et al. 2013) and the influence of agricultural pest management on grasshoppers (Martin et al. 2000), its is prudent to explore trophic relationships between birds and arthropods.

Stable isotope ecology is a powerful tool for exploring trophic dynamics and has undergone rapid development in recent years. The MixSIAR package (Stock et al. 2018) made available for use in R (R Core Team 3.6.1 2019) is one such tool used in ecological modeling. MixSIAR uses Markov chain Monte Carlo (MCMC) sampling and Bayesian inference to estimate answers to ecological questions through the analysis of biotracers (i.e. isotopes). MixSIAR was built on several years of mixing model advances in MixSIR (Moore and Semmens 2008) and SIAR (Parnell et al. 2010). The advantage of using a Bayesian approach is the ability to account for uncertainty around the isotope values of the sources and trophic discrimination, as well as the incorporation of informative priors that inform the model of previously known information (Moore and Semmens 2008). MixSIAR provides further improvements by allowing the inclusion of fixed and random effects, and the incorporation of both residual and process error in a 'multiplicative error' formulation that is more reflective of actual biological processes than previous model error structures (Stock et al. 2018).

Several important factors must be carefully considered for a stable isotope mixing model (SIMM) to produce reliable and ecologically meaningful results. SIMMs function on the premise that dietary isotope values are reflected in the isotope values of consumer tissues after a number of biological processes have been accounted for (Phillips 2012). The trophic discrimination factor (TDF), which is the estimated change in isotope ratio between the food item and the tissue it is incorporated into (expressed as $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$), is likely the most important factor to be accounted for in a SIMM (Phillips et al. 2014). The TDF is determined by multiple processes like fractionation and metabolic routing that occur between the time a food item is consumed and tissue synthesis. As such, the TDF is variable depending on the type of tissue being analysed (McCutchan et al. 2003) and can also vary between prey types (Bastos et al. 2017). Ideally, a TDF value is derived experimentally for the consumer in question, however, in most studies involving diet estimation using isotopes an approximate value is obtained from the literature (Caut et al. 2009). An R package has also been developed to estimate the TDF of a given consumer from a compiled dataset using a phylogenetic regression model. The SIDER package (Stable Isotope Discrimination Estimation using R) uses Bayesian inference to incorporate information about the animal's feeding ecology and the tissue being sampled (Healy et al. 2017). As with other important model parameters, it is recommended that a sensitivity analysis is done with SIMMs using different TDF values (Martinez Del Rio et al. 2009; Phillips et al. 2014).

The effects of lipid on carbon isotope values for both consumer and prey in SIMMs remains a debated issue among isotope ecologists (Arostegui et al. 2019). Lipids are depleted in ^{13}C relative to other tissues due to fractionation during lipid synthesis (DeNiro and Epstein 1977). This results in samples with higher lipid content having more negative $\delta^{13}C$ values, and some researchers argue that variation in lipid content may obscure variation in diet (Elliott et al. 2017). Techniques have been developed to exclude lipids from SIMMs either by extracting lipids prior to analysis (Bligh and Dyer 1959), or by arithmetically correcting for lipid content using the C:N ratio as a proxy for lipid content (Kiljunen et al. 2006; Logan et al. 2008). Other isotope ecologists argue that excluding lipids from the analysis results in misleading interpretations (Arostegui et al. 2019). Prey items with high or variable lipid content can indeed cause misleading model output when estimating diet, particularly if the carbon

from prey lipids is not sourced in the synthesis of the consumer tissue being analysed, as is likely the case with feathers (Bearhop et al. 2002). There is no consensus to date on best practices for lipid treatment in SIMMs, however, testing the sensitivity of the model to lipid correction is recommended (Tarroux et al. 2010).

Isotopic routing is another factor that can complicate the interpretation of diet estimates. SIMMs make the inherent assumption that ingested food items are broken down into their elemental components, and thereafter reassembled evenly during tissue synthesis. This is not a realistic assumption, particularly for omnivorous animals that may obtain dietary protein and carbohydrates from different sources. This may lead to isotopes preferentially being sourced from one food source, i.e. a high-protein source, in the synthesis of a consumer tissue. Consequently, the mixing model will overestimate the contribution of the high protein food source when that tissue is analysed and modeled (Podlesak and McWilliams 2006). While this process can make accurate estimation of diet difficult, isotopic routing can also be useful in understanding metabolic processes and nutrient allocation (Martinez Del Rio et al. 2009).

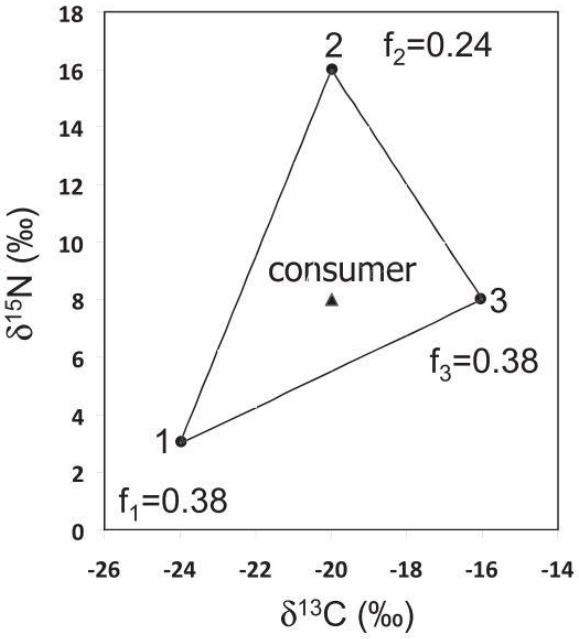

Figure 5 – Figure from Phillips (2012) illustrating a mixing polygon in an isotope biplot. The numbers 1-3 represent diet sources, and diet proportions (f) are estimated from the consumer's position within the polygon

Other modeling parameters that warrant careful consideration in SIMMs are the use of informative or uninformative priors in Bayesian approaches (Stock et al. 2018), consideration of concentration dependence (Phillips and Koch 2002), appropriate source grouping, and avoiding fitting a nonsensical model, i.e. one where the consumer's isotope value lies outside of the mixing polygon (Figure 5) (Phillips 2012). The latter point also illustrates one factor that supersedes all other mixing model

concerns: the quality of the input data. Good quality data includes a comprehensive isotopic baseline of all potential food items, and isotope values from consumer tissues with consideration given to tissue turnover rate, and spatial and temporal scale (Boecklen et al. 2011; Phillips et al. 2014). A good understanding of the system under question is critical, including appropriate accounting of all potential diet sources. Plants that use a C_4 photosynthetic pathway have substantially different $\delta^{13}C$ values than C_3 plants (around a 15‰ difference) (Peterson and Fry 1987). This difference can be useful in estimating diet contributions between C_3 and C_4 sources (Renfrew et al. 2017), but the choice of including C_4 plants as a potential food source in a mixing model can also change the model results (Torres-poche 2017). Lastly, an understanding of any physiological processes undergone by the study organism is also vital. For example, nutritional stress such as fasting during egg-laying can positively influence $\delta^{15}N$ values of an organism (Hobson et al. 1993; Vanderklift and Ponsard 2003).

Stable isotope data can also be used to quantify food web structure in interesting ways. Trophic position can be estimated relative to the isotope values of primary producers or primary consumers (Post 2002). Ecological inferences can also be made using 'isotopic niche' to explore food web dynamics, intrapopulation trophic variability, and community wide food web characteristics (Layman et al. 2007; Layman et al. 2012).

In this study of plains sharp-tailed grouse, feeding relationships were estimated between plant food and arthropod prey (insects and spiders) over a 6-month period using primary feathers. Feathers provide a practical repository of isotope data that represent the isotope values of nutrient contributions to feather synthesis during the time in which the feather was grown, after the application of an appropriate TDF. After synthesis, feathers are metabolically inert, making it relatively simple to estimate temporal scale if the molting pattern of the bird is known (Hobson and Clark 1992b; Renfrew et al. 2017). Adult sharp-tailed grouse molt their 10 primary feathers between May and October (Pyle 2008) which provides a convenient overlap with the time during which arthropods become available as prey. Given the principles around trophic discrimination of $\delta^{15}N$, and differential values of $\delta^{13}C$ depending on source contribution of carbon (Layman et al. 2012), it was hypothesised that diet proportions of plant foods and arthropod prey could be estimated from feather

$\delta^{15}N$ and $\delta^{13}C$ over the molting period. Since grouse utilize arthropods opportunistically (Jones 1966) it was expected that $\delta^{15}N$ values would increase as arthropod prey became available, and that juvenile grouse feathers would reflect high arthropod consumption early in the season.

3.2 STUDY AREA

Collection sites were located near Spring Coulee (Wild Rose Conservation Site: 49.26° N, 112.98° W) and Warner (Twin River Heritage Rangeland Natural Area: 49.24° N, 112.35° W), Alberta, approximately 46 km apart. Sites were located on native prairie neighbouring agricultural land where the foothills fescue and mixed grass natural subregions meet, along the Milk River Ridge (Downing and Pettapiece 2006). Both sites were dominated by native grasses, forbs, and shrubs (Appendix 1) and were under grazing management by the Alberta Conservation Association (Wild Rose) and local ranchers (Twin River) (See Chapter 2 for a detailed description of the study sites). Sites were known to have one or more leks in their vicinity and were both popular hunting areas for sharp-tailed grouse. These locations were chosen because they represented some of the last remaining vestiges of native prairie habitat in southern Alberta.

3.3 METHODS

3.3.1 Feather Sampling and Preparation

Plains sharp-tailed grouse primary feathers were obtained from wings donated by hunters in the study area during the 2017 and 2018 fall hunting seasons. Grouse from which wings were donated were aged and sexed using wing morphology and molt stage (Caldwell 1980; Pyle 2008) (Appendix 2), crown and tail feather pattern (Henderson et al. 1967), and ossification of the lower mandible (Linduska 1945).

Grouse were separated into 4 classes based on age and sex: female after-hatch-year (AHY) (adult female) (n = 15); female hatch-year (HY) (juvenile female) (n = 9); male AHY (adult male) (n = 8); and male HY (juvenile male) (n = 8). Wings were stored frozen at -20°C prior to extraction of feathers.

Primaries 1-10 (P1-P10) were removed from each wing and cleaned following recommendations from Paritte and Kelly (2009) (Figure 6).

Cleaning was done by first rinsing each feather in deionized water with 1% Alconox detergent (Cat. 1104-1). Feathers were individually shaken in a 500 ml Erlenmeyer flask containing 300 ml of Alconox solution for 30 s and then rinsed 3 times in clean deionized water in the same manner. The Alconox solution and clean water were replaced after every 5 feathers. Feathers were then dried at 60°C for

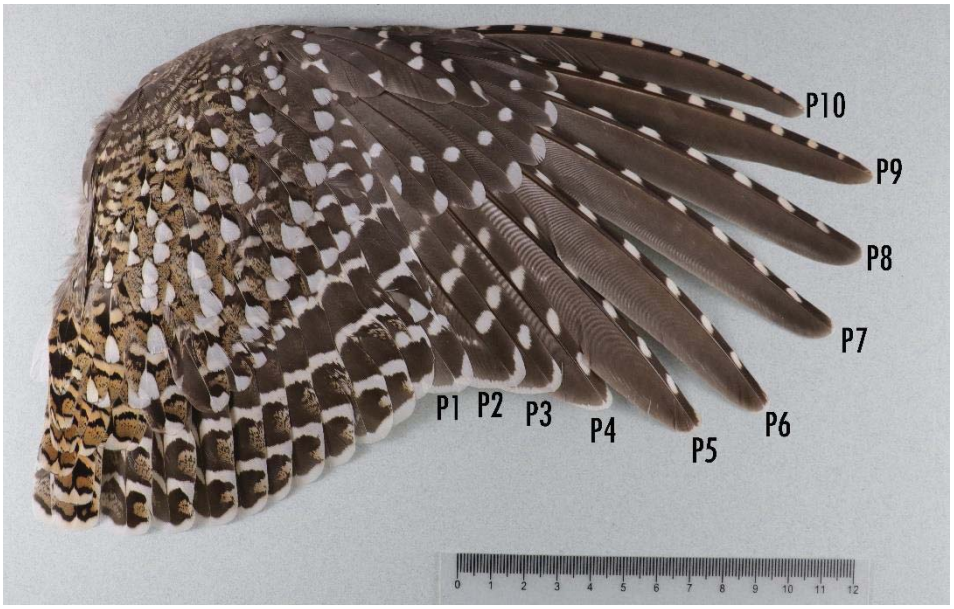

Figure 6 - A sharp-tailed grouse wing with labelled primary feathers 1-10

24 hr. Following drying, each feather was sealed in a 50 ml test tube with a screw cap containing 15 ml of 2:1 chloroform:methanol solution and shaken for 30 s under a fume hood to remove surface oils. The solvent was replaced after every 5 feathers. Feathers were then allowed to air dry under the fume hood for 24 hr (Paritte and Kelly 2009).

Following cleaning, feathers (n = 418) were prepared for stable isotope analysis following guidelines from Hobson (2006) and Bontempo et al. (2014). Material from the posterior vane of each feather was sampled to obtain the most consistent measurements across feathers. In order to account for potential variability along the length of the feather vane (Bontempo et al. 2014) a narrow strip of feather material, uniform in width and from the center of the posterior vane, was cut from each feather using

surgical scissors. Using a modified pipette tip and metal plunger, each feather strip was placed into an 8 x 5 mm tin capsule for stable isotope analysis. In order to obtain an appropriate target weight for isotope analysis (5 mg), the width of the strip necessarily varied (1-2 mm) according to its length. In

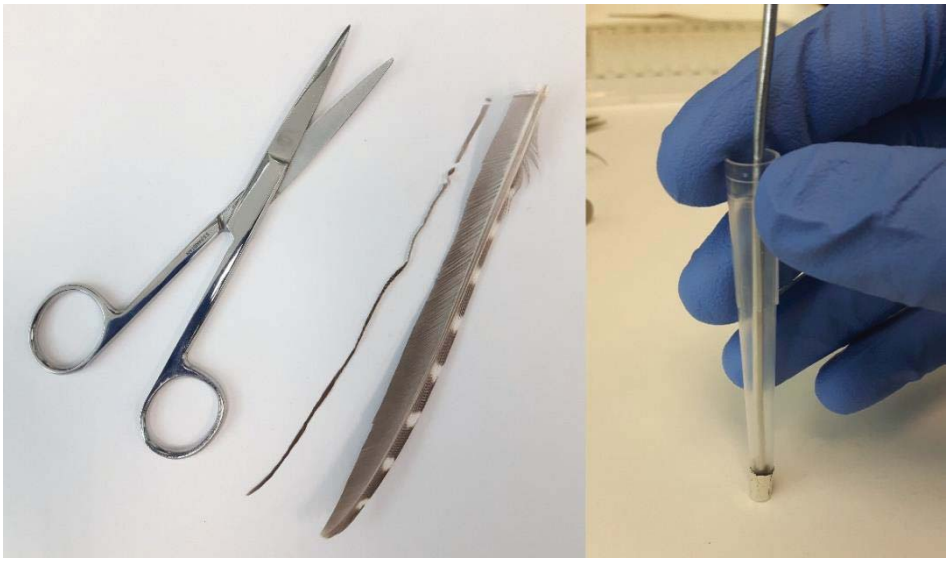

Figure 7 - A strip of feather material was cut from the middle of the posterior vane of each primary feather for stable isotope analysis

order to avoid potential contribution of yolk nutrients to prejuvenal feathers (Romanoff 1944; Blomberg et al. 2013), i.e. P9 and P10 in juvenile grouse (Pyle 2008), 2 mm of the distal portion of the vane was excluded when sampling juvenile P9 and P10 feathers. Duplicate feather samples were included (i.e. sampling the same feather twice and sampling the same primaries from opposing wings of the same bird) in order to ensure that methods were yielding consistent results (Appendix 3.1 – 3.3).

3.3.2 Baseline Sampling and Preparation

In order to establish reliable baseline isotope values of potential food items for sharp-tailed grouse, arthropod and vegetation sampling was conducted over a period of 6 months, from May to October 2018. This time period coincided with the time period during which sharp-tailed grouse molt their primary feathers (Pyle 2008).

Plant sampling for isotope analysis was done intermittently throughout the sampling period as plants emerged, and at different stages of maturity. Wild plants were sampled (n = 139) as well as

agricultural seeds from nearby cultivated fields (n = 17). Vegetation surveys were done in May as well as in July-August in order to obtain a comprehensive list of plant species available to foraging grouse. Vegetation surveys were done using a modified Daubenmire method (Daubenmire 1959). Ten 100 m transects (10 ¼ m^2 quadrats each) were completed at each of the two sites during May and July-August (n = 400 plots). Height of dominant vegetation and litter depth was measured at each plot (Appendix 1). To the extent possible, all plants available to grouse as forage were sampled, and plants that were dominant or were known to be eaten by grouse were sampled multiple times. Prior knowledge of sharp-tailed grouse diet preference was obtained by analysing esophageal crops obtained from hunters in the study area (n = 106) (Chapter 2) as well as from previous diet studies specific to plains sharp-tailed grouse (Aldous 1943; Kobriger 1965; Renhowe 1968; Sisson 1976; Mitchell and Riegert 1994). When possible, plant samples were taken directly to the lab and placed in a drying oven at 60°C for 48 hr prior to sample preparation. Occasionally, plant samples were initially stored frozen at -20°C until they could be placed in a drying oven.

Arthropod sampling was conducted via sweep netting from May to October 2018. Sites were visited intermittently (30 times over the sampling period, roughly once a week, n = 222 transects) and 5-10, 100 m sweep transects (1 sweep per meter with a 38 cm diameter sweep net) were done during each visit. Sweep collections were stored in perforated plastic bags and placed in a freezer at -20°C the same day. All arthropods (insects and spiders) were extracted from the sample bags in the lab, identified, counted, and weighed (Appendix 4). Identification precision varied between taxa, however, all arthropods were separated to taxonomic order at a minimum. Representative arthropods (n = 136) were selected for isotope analysis from each order, depending on knowledge of feeding behaviour (i.e. herbivorous or predaceous), phenology, and if the species or taxon was known to be utilized by sharp-tailed grouse. Ten arthropod orders were represented in the isotope analysis for this study: Orthoptera (n = 34); Hemiptera (n = 30); Araneae (n = 29); Coleoptera (n = 20); Hymenoptera (n = 9); Lepidoptera (n = 6); Diptera (n = 4); Opiliones (n = 2); Odonata (n = 1); and Lithobiomorpha (n = 1). Each sample prepared for analysis was comprised of several homogenized individuals, and arthropod samples were separated based on three collection periods: May-June; July-August; and September-October (Appendix

5.1). This was done in order to track potential changes to arthropod prey isotope values through the study period. Arthropods selected for isotope analysis were placed in a drying oven at 60°C for 48 hr after identification and weighing.

After desiccation, plant and arthropod samples were homogenized in a Retsch Mixer Mill Type MM 301. Sample material was placed in a 50 ml stainless steel grinding jar containing a 20 mm stainless steel grinding ball and vibrated for 5 minutes at 15 Hz. Homogenized samples were stored at -20°C in 2 ml microcentrifuge tubes.

Some arthropods likely contained high amounts of lipid (Rumpold and Schlüter 2013), also reflected in the C:N ratio (Post et al. 2007) (Appendix 5.1). In order to asses the effect of lipids on the $\delta^{13}C$ values of arthropod samples in this study, a subset of 28 samples were reanalysed after lipid extraction. Lipid extraction followed guidelines from Bligh and Dyer (1959) and lab protocols from SINLAB (Stable Isotopes in Nature Laboratory, University of New Brunswick): Approximately 50 mg of homogenized sample material was placed into a 2 ml microcentrifuge tube, and 1 ml of 2:1 chloroform:methanol solution was added under a fume hood. Samples were agitated for 30 s using a Fisherbrand Analog Vortex Mixer (CAT 02-215-365) and left to settle for 30 minutes. After settling, the supernatant was pipetted out, and the process was repeated. The treatment was repeated until the supernatant appeared clear (3 times for most samples, 4 times for some). Results from these analyses were used to derive a linear regression equation to correct all arthropod $\delta^{13}C$ values ($\Delta\delta^{13}C = -0.724 + 0.3692 * C:N$, $R^2 = 0.629$, $P = < 0.001$) (Appendix 6).

3.3.3 Stable Isotope Analysis

All samples were analyzed for $\delta^{15}N$, $\delta^{13}C$, percent nitrogen content (%N), and percent carbon content (%C) using Delta V Plus isotope ratio mass spectrometer with Thermo-Fisher Scientific instrumentation at the Lethbridge Research Center. IsoDat software (Thermo Electron Corp.) was used to determine elemental concentrations and calculate delta (δ) values. Experimental error determined from isotope standards within the sample sets (n = 235) was 0.40 ‰ for $\delta^{15}N$, 0.23 ‰ for $\delta^{13}C$, 0.38% for %N, and 1.67

% for %C (Appendix 7). All isotope measurements in this thesis pertain to molar measurements, and elemental concentration measurements pertain to their mass.

3.3.4 Statistical Analysis

Before analysis could be done using MixSIAR, isotope data were examined and manipulated to ensure that the model input was reliable, accurate, and ecologically coherent. Statistical analyses were conducted in JMP 14 (JMP®, Version 14.3.0. SAS Institute Inc.). Shapiro-Wilk tests were used to test for normality of source groups prior to using parametric tests.

Source grouping – In order to avoid bias from plants that were sampled more often than others, a single average value was determined for each plant species that was sampled at each site, during each season (n = 103) (Appendix 8). A two-way ANOVA was conducted to test differences in $\delta^{15}N$, $\delta^{13}C$, and elemental concentrations between plants by collection site and season (Appendix 9.1). For C_3 plants $\delta^{13}C$ varied across seasons and sites (P = 0.0033 by season, P = 0.0008 by season*site) and %N varied across seasons (P = < 0.0001). No difference was detected in $\delta^{15}N$ or %C. When plants were compared by growth form (i.e. forbs, agricultural seeds, berries, buds, grass seeds, and grass-likes), differences were again detected in $\delta^{13}C$ values (P = < 0.001) and %N concentrations (P = 0.0004). Given the research objectives and since the species composition of plant samples was not consistent enough across seasons to allow for a rigorous comparison, these sources were combined with the exception of grass seeds, which had average $\delta^{15}N$, $\delta^{13}C$ values very close to that of Orthoptera and Lepidoptera (Figure 8). Some anomalously high $\delta^{15}N$ values were detected in the seeds of curly dock (*Rumex crispus*). Four samples were analysed and values were 2.76, 4.94, 10.71, and 11.68 $\delta^{15}N$.

The only plants found in the study area that used a C_4 photosynthetic pathway were grasses, which were not dominant in the area (Wang et al. 2006; Osborne et al. 2014). Grasses are not reported to be a common diet item for sharp-tailed grouse, and including C_4 sources as a separate mixing source when not appropriate would affect the model outcome (Torres-poche 2017). For this reason, model iterations were run both with and without C_4 plants as a mixing source (Table 7). The only C_4 plant analysed in

this study was blue grama grass (*Bouteloua gracilis*), therefore a simulated dataset of 10 samples was created using the isotope and elemental concentration values from blue grama grass and a standard deviation of 1.0 around the $\delta^{15}N$ and $\delta^{13}C$ values.

Isotope values for arthropods were separated by collection site, taxonomic order, and by 3 different sampling periods (May-June, July-August, and September-October) (Appendix 5.1). Two-way ANOVA of $\delta^{15}N$, $\delta^{13}C$, and elemental concentrations detected differences between orders ($P = < 0.0001$), as well as with %N between seasons ($P = 0.0004$), but not by site (Appendix 9.2). Given the study objectives and the amount of overlap in niche space (Figure 8), arthropod sources were grouped in the following manner (hereafter referred to as *trophic* separation): a weighted average of $\delta^{15}N$, $\delta^{13}C$, and C and N concentration for each arthropod order excluding Orthoptera and Lepidoptera was calculated using relative biomass (RB) data gathered from sweep netting (averaged across the study period) (Appendix 5.3). Due to their isotopic similarity an average was also determined for Orthoptera (weighted by species RB), Lepidoptera, and wild grass seed. Between the trophically separated groups there was a significant difference in $\delta^{15}N$ but not in $\delta^{13}C$ or elemental concentrations (Appendix 9.4). This method of separation roughly reflected trophic separation within the arthropod samples: the first group contained many predatory arthropods (Araneae, Coleoptera, Hemiptera, Opiliones, Hymenoptera, Diptera, and Odonata) and the second group contained mostly herbivorous prey insects (Orthoptera and Lepidoptera). The reference to "predatory" and "prey" arthropods is not strictly accurate as both groups contain arthropods that engage in both types of feeding behaviour, however, separation was based on average $\delta^{15}N$ values which is reflective of trophic level (Post 2002). Standard deviations for all groups were calculated from the entire respective datasets in order to appropriately capture the spread of the isotope values for modeling purposes (Appendix 10).

Two main source grouping methods were employed and compared (Table 7):

Three-source trophic model: Using the *trophic* separation method described above for arthropod sources (1) and (2), and (3) C_3 plants (Figure 10a).

Four-source trophic model: Using the *trophic* separation method described above for arthropod sources (1) and (2), and (3) C_3 leaf material (forbs, grass-likes, and buds) separated from (4) berries (snowberry, rose hips, chokecherry, saskatoon) and agricultural seeds (Figure 10b).

Four additional source grouping methods were employed to asses model sensitivity (Table 7):

Two-source model: A two-source approach with (1) all arthropods grouped together using a weighted average based on overall RB of each order, and (2) C_3 plants (Appendix 11.1).

Three-source C_4 model: A three-source approach including (1) C_3 plants, (2) C_4 plants, and (3) all arthropods grouped together (Appendix 11.2).

Four-source trophic C_4 model: A four-source approach that used the *tropic* separation method described above for arthropod source (1) and (2) and included (3) C_3 and (4) C_4 plants as separate sources (Appendix 11.3).

Six-source model: A six-source approach that used the *tropic* separation method described above for arthropod source (1) and (2) excluding (3) Hemiptera as its own source, (4) C_3 leaf material, (5) berries and agricultural seeds, and (6) C_4 plants (Appendix 11.4).

Differences between these source groupings were assessed using a Welch's t-test (Appendix 9.4).

Table 7 - Summary of model iterations and source groupings used in MixSIAR

Model name	**Number of sources**	**Source Separation**
Three-source trophic	3	"Predatory" arthropods; "prey" arthropods; C_3 plants
Four-source trophic	4	"Predatory" arthropods; "prey" arthropods; C_3 leaf material; berries and agricultural seeds
Additional model iterations used in sensitivity analysis		
Two-source	2	All arthropods combined; C_3 and C_4 plants combined
Three-source C_4	3	All arthropods combined; C_3 plants; C_4 plants[1]
Four-source trophic C_4	4	"Predatory" arthropods; "prey" arthropods; C_3 plants; C_4 plants[1]
Six-source trophic	6	"Predatory" arthropods[2]; "prey" arthropods; Hemiptera; C_3 plants; C_4 plants[1]; berries and agricultural seeds

[1] Simulated dataset based on 1 sample of *Bouteloua gracilis*

[2] Excluding Hemiptera

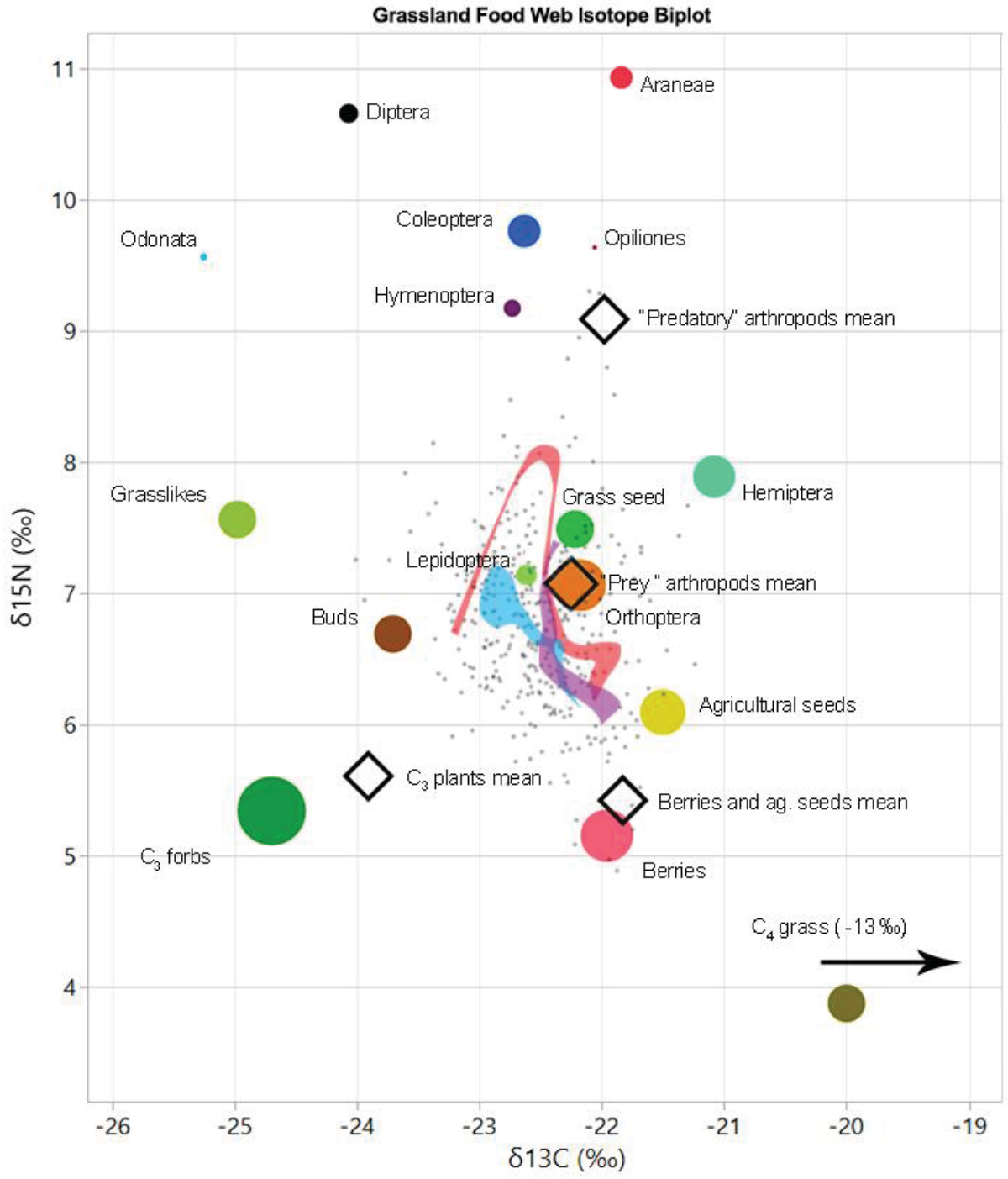

Figure 8 - Isotope biplot of a grassland ecosystem food web. Points are average source values, and size corresponds to relative biomass. Black diamonds represent averages used in the SIMM. The thickened lines track the isotope measurements of sequentially grown primary feathers in adult female (purple), adult male (red), and juvenile (blue) (shown in more detail in Figure 9). Semi-transparent black dots are individual feather isotope values. Source isotope values are corrected for trophic discrimination using TDF from Caut (2009)

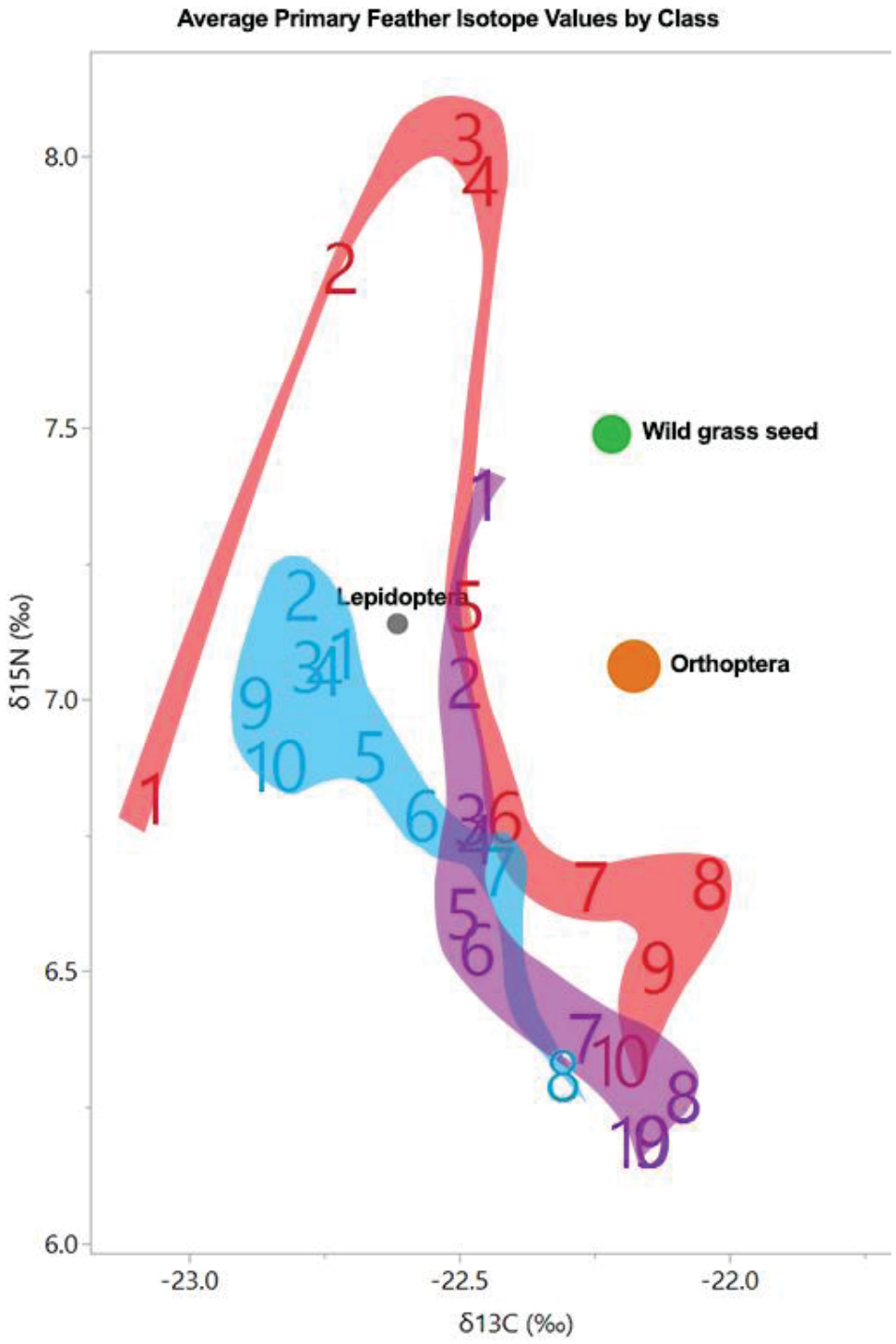

Figure 9 - Isotope biplot showing seasonal changes to sharp-tailed grouse primary feather isotope signals. Colours correspond to adult female (purple), adult male (red), and juvenile (blue) grouse. The numbers represent the biplot position of the average isotope value of the corresponding primary feather. Note that P9 and P10 in juvenile grouse are grown during the prejuvenal molt, before P1-P8 (preformative molt), see text for full explanation (Pyle 2008). Source isotope values are corrected for trophic discrimination using TDF from Caut (2009)

Feather isotope data – Each primary feather was assigned a Julian date according to when it was estimated to have grown. Molting of primary feathers occurs from May – October for adult grouse (Pyle 2008), as such P1 was estimated to have grown May 1, P10 on October 31, and P2-P9 at equal time intervals in between. During their first year of life, following their prevjuvenal molt (first set of pennaceous feathers), juvenile grouse undertake an incomplete performative molt during the summer. During this molt only P1-P8 are replaced from June – October (Pyle 2008). As such, P9 and P10 in juvenile grouse were treated as having been grown in the spring (May 12), and P1-P8 at equal intervals from June 1 – October 31 (Appendix 12).

When testing for differences between grouse classes, only primaries grown during the same time period were compared. A two-way ANOVA detected no difference between collection site regarding $\delta^{15}N$ and $\delta^{13}C$. Significant differences were detected in $\delta^{15}N$ and $\delta^{13}C$ between age classes ($P = 0.0073$ and at $P = 0.0014$ respectively) and in $\delta^{15}N$ between sexes in adult grouse ($P = 0.0003$). Among juvenile grouse, no significant differences were detected between sexes. For this reason, sex classes were combined for juveniles, and kept separate for adult grouse (Appendix 9.3).

Layman metrics – The SIBER package (Stable Isotope Bayesian Ellipses in R) (Jackson et al. 2011) was used to calculate isotopic niche dimensions (Layman et al. 2007) to compare relative resource use in iso-space. Bayesian ellipses were compared by calculating the probability that the posterior distributions of ellipse sizes were different. This was done by determining the proportion of posterior draws that were different from another ellipse as a proxy for the probability of a difference (Jackson et al. 2011). Trophic position (TP) estimates were calculated for each grouse class for 3 time periods during the study period using the formula from Post (2002):

$$TP = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{baseline}) / \Delta\delta^{15}N$$

Where λ is the trophic level of the baseline (i.e. 1 for primary producers, or 2 for primary consumers) and $\Delta\delta^{15}N$ is the trophic discrimination factor for nitrogen per trophic level, assumed to be 3.4 ‰ (Post 2002).

Protein factor for nitrogen – Percent protein content was calculated from nitrogen concentrations using a nitrogen to protein conversion factor (*k*p) for arthropods (*k*p = 4.76) (Janssen et al. 2017) and plants (*k*p = 4.43 for dicots; *k*p = 4.37 for monocots) (Yeoh and Wee 1994). The conventional *k*p value of 6.25 overestimates protein content of whole-body arthropods due to the presence of nonprotein nitrogen in chitinous materials, nucleic acids, phospholipids, and ammonia in excreta (Janssen et al. 2017).

3.3.5 Model Structure

MixSIAR (Stock et al. 2018) was used to estimate diet proportions of plant material and arthropod prey in three classes of grouse: adult female (n = 15), adult male (n = 8), and juvenile grouse (n = 17). The mixing model was run separately for each class, treated each grouse as a random variable, and Julian date as a continuous effect. Iterations of the model were run for all grouse classes using the *three-source trophic* and *four-source trophic* source grouping approaches in the main analysis. These approaches to source grouping where the most ecologically representative ways to separate known important food sources for sharp-tailed grouse that were isotopically distinct, i.e. forbs, prey arthropods, and berries and agricultural seeds in late summer and fall. Four additional source grouping approaches were run to test model sensitivity (Table 7).

MCMC parameters were set to 300,000 iterations with 3 Markov chains, a burn-in of 200,000 iterations, and a thinning ratio of 1:100. If the model failed to converge with these parameters it was run again at 1,000,000 iterations with 3 chains, a burn-in of 500,000, and a thinning ratio of 1:500. Convergence of MCMC chains was assessed using Gelman-Rubin and Geweke diagnostic tests (Geweke 1992; Gelman et al. 2014) built into the MixSIAR package.

Sensitivity analysis – A series of repeat model iterations were run to assess model sensitivity to changes in important parameters. The *three-source trophic* model structure using the adult female grouse feather dataset was used in a sensitivity analysis that assessed the influence of changes to TDF, lipid correction, and informative/non-informative priors (Appendix 14.1 -14.5).

Trophic discrimination factor – The TDF for feathers derived by Caut et al. (2009) was used in the main analysis of this study ($\Delta\delta^{15}N = 3.84 \pm 0.26$ ‰ and $\Delta\delta^{13}C = 2.16 \pm 0.35$ ‰). Two other TDFs were also used

in the sensitivity analysis: Torres-poche (2017) developed and experimental TDF from congeneric captive Attwater's prairie chickens (*Tympanuchus cupido attwateri*) ($\Delta\delta^{15}N$ = 3.46 ± 0.53 ‰ and $\Delta\delta^{13}C$ = 1.14 ± 0.28 ‰); and SIDER (Healy et al. 2017) was used to estimate a TDF using a phylogenetic regression model that accounted for tissue type (feather) and feeding ecology (omnivore) ($\Delta\delta^{15}N$ = 2.82 ± 1.40 ‰ and $\Delta\delta^{13}C$ = 1.64 ± 1.42 ‰) (Appendix 14.3).

Priors – Informative priors were used in the mixing model that were derived from analysing previous literature on sharp-tailed grouse summer feeding ecology specific to the plains subspecies (Aldous 1943; Kobriger 1965; Renhowe 1968; Sisson 1976; Mitchell and Riegert 1994). From this literature a prior was developed using a Dirichlet distribution (Table 8) estimating that grouse consumed 70% plant material, 25% "prey" arthropods, and 5% "predatory" arthropods (Table 9). A sensitivity analysis was conducted on the influence of different informative priors, as well as using an uninformative prior (Appendix 14.1).

Lipid correction - Arthropod $\delta^{13}C$ values were corrected using the experimentally derived formula from this study ($\Delta\delta^{13}C$ = -0.724 + 0.3692 * C:N), and plant materials were corrected for lipids using the formula derived by Post et al. (2007) for plants with > 40% carbon content (Eq. 13: $\Delta\delta^{13}C$ = -5.83 + 0.14 * %Carbon, R^2 = 0.841, P = < 0.001) (Appendix 6).

Concentration dependence – Unless otherwise specified, SIMMs assume that proportional contribution of C and N from sources are the same. This is only a reasonable assumption in the case where food sources have similar C and N concentrations (Phillips and Koch 2002). MixSIAR allows for the incorporation of elemental concentrations of sources which are used to weight the proportional contributions of sources in the model estimate in scenarios where elemental concentrations are significantly different among sources (Stock et al. 2018). Given the differences in elemental concentration between plant and arthropod sources in this study (Appendix 5.1 and 9.4), concentration dependence was used during modeling.

Table 8 - Informative prior weighting for source groupings used in all model iterations

Model	C_3 plants	C_4 plants	"Predatory" arthropods	"Prey" arthropods	Berries and ag. seeds	All arthropods	C_3 and C_4 plants	Hemiptera
Three-source trophic	2.1		0.15	0.75				
	70%		5%	25%				
Four-source trophic	1.4		0.2	1	1.4			
	35%		5%	25%	35%			
Two-source						0.5	1.5	
						25%	75%	
Three-source C_4	1.2	0.9				0.9		
	40%	30%				30%		
Four-source trophic C_4	2.4	0.4	0.2	1				
	60%	10%	5%	25%				
Six-source	1.9	0.2	0.15	1.5	2.1			0.15
	32%	3%	3%	25%	35%			3%
Three-source trophic with uninformative prior	1		1	1				
	33%		33%	33%				

Table 9 - Summary of plains sharp-tailed grouse diet analysis from five literature sources

	Sharp-tailed grouse summer diet proportions		
	Range (%)	Mean (%)	Median (%)
Vegetation	64 - 79	68	64
Orthoptera	6 - 34	25	33
Other arthropods	2 - 9.5	5	3

3.4 RESULTS

Model outcomes were different depending on the type of source grouping employed. In the main analysis that compared the *three-source trophic* approach to the *four-source trophic* approach uncertainty was introduced with the inclusion of berries and agricultural seeds as an additional source. In the *three-source trophic* model, arthropod utilization was estimated to be much higher than expected through the entire study period. The *four-source trophic* model also estimated high utilization of arthropods and estimated a high utilization of berries and agricultural seeds in the fall. However, estimation uncertainty was high with the *four-source trophic* model (Table 10).

Three-source trophic model – This model estimated the highest proportion of arthropod utilization for adult grouse. Adult female grouse were estimated to utilize the highest proportion of "prey" arthropods, and all classes were estimated to utilize other "predatory" arthropods less. The time series estimation showed a large increase in utilization of "prey" arthropods for all classes through the study period. The adult male grouse model had the most uncertainty, reflected in the credible intervals, as well as the most variability in diet proportions over the study period (Figures 11 -13; Tables 12 -14).

Four-source trophic model – This model showed high levels of uncertainty in estimates for adult grouse, but not for the juvenile grouse model. All models estimated high arthropod utilization in the early season, and a high proportional utilization of berries and agricultural seeds in the late summer and fall for all classes. The adult male grouse model was the most uncertain (Figures 11 -13; Tables 12 -14).

Table 10 - Comparison of overall average diet proportion estimates for all models with standard deviation in parentheses (does not include time series estimates)

		Model				
Class	**Source**	**Three-source trophic**	**Four-source trophic**	**Two-source**	**Three-source (with C_4)**	**Four-source trophic (with C_4)**
Adult female	"Predatory" arthropods	0.08 (0.03)	0.04 (0.02)	-	-	0.04 (0.02)
	"Prey" arthropods	0.68 (0.07)	0.32 (0.13)	-	-	0.30 (0.10)
	Berries and ag. seeds	-	0.44 (0.16)	-	-	-
	C_3 Plants	0.23 (0.07)	0.19 (0.07)	0.92 (0.03)	0.77 (0.03)	0.60 (0.09)
	C_4 Plants	-	-		0.08 (0.02)	0.05 (0.02)
	Arthropods	-	-	0.08 (0.03)	0.15 (0.03)	-
Adult male	"Predatory" arthropods	0.18 (0.10)	0.16 (0.09)	-	-	0.18 (0.09)
	"Prey" arthropods	0.55 (0.14)	0.19 (0.15)	-	-	0.46 (0.14)
	Berries and ag. seeds	-	0.46 (0.15)	-	-	-
	C_3 Plants	0.24 (0.13)	0.15 (0.08)	0.72 (0.13)	0.65 (0.08)	0.32 (0.13)
	C_4 Plants	-	-		0.08 (0.03)	0.01 (0.02)
	Arthropods	-	-	0.28 (0.13)	0.26 (0.08)	-
Juvenile	"Predatory" arthropods	0.17 (0.05)	0.16 (0.05)	-	-	0.11 (0.03)
	"Prey" arthropods	0.45 (0.08)	0.50 (0.09)	-	-	0.36 (0.09)
	Berries and ag. seeds	-	0.10 (0.05)	-	-	-
	C_3 Plants	0.38 (0.07)	0.23 (0.06)	0.63 (0.05)	0.69 (0.05)	0.51 (0.09)
	C_4 Plants	-	-		0.05 (0.01)	0.02 (0.01)
	Arthropods	-	-	0.37 (0.05)	0.26 (0.05)	-

Model Comparison: Three-source Trophic vs. Four-source Trophic

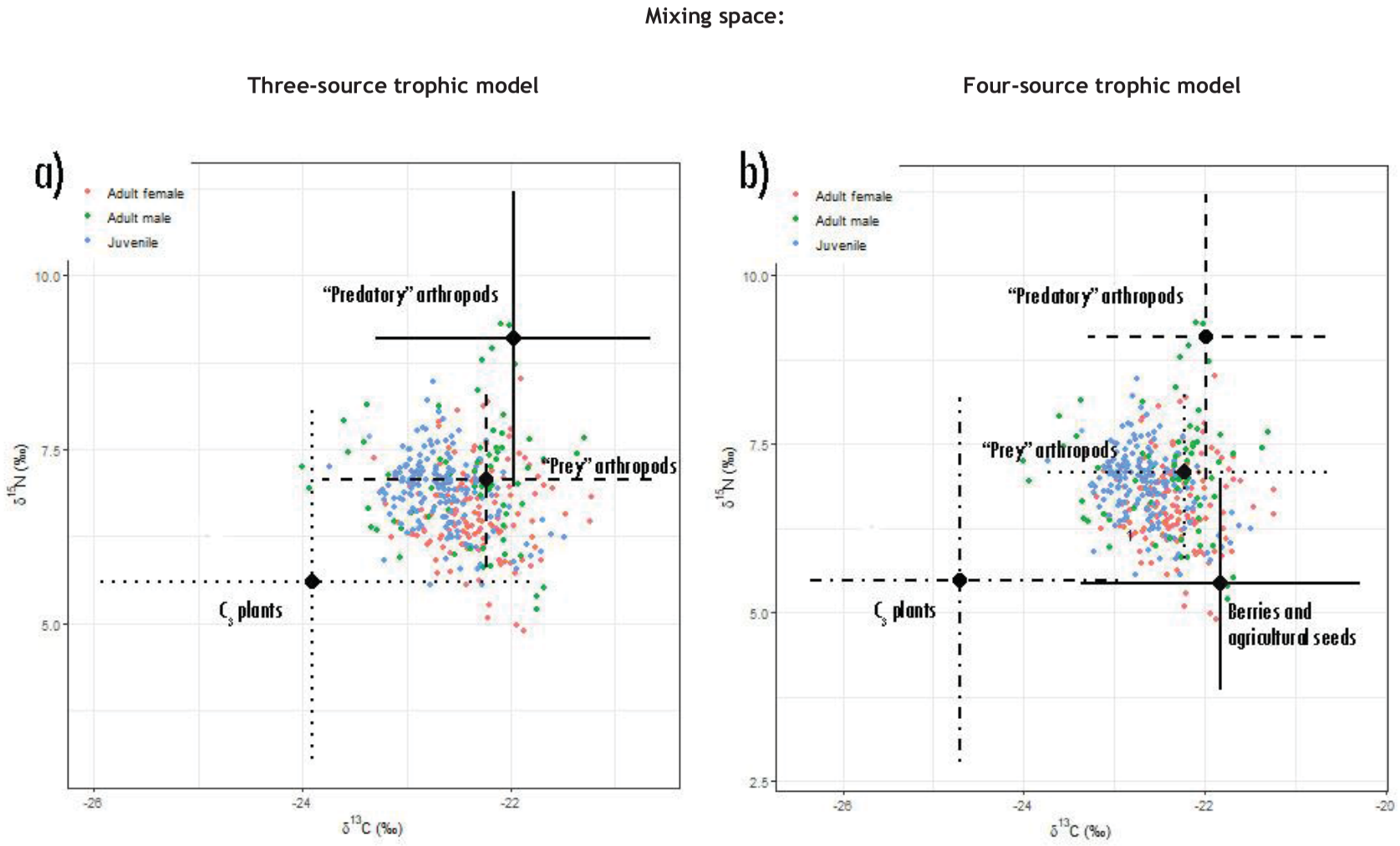

Figure 10 - Mixing space biplots for the respective models. Points represent averages calculated for source groups, and extending lines indicate standard deviation around the mean. Corrected for trophic discrimination using TDF from Caut et al. (2009).

Table 11 - Source summary statistics used in models, corresponding to biplots shown in Figure 10

Three-source trophic model

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Concentration	C Concentration	n
"Predatory" arthropods	5.248	2.104	-24.138	1.266	0.107	0.520	96
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
C_3 plants	1.767	2.543	-26.066	2.058	0.027	0.466	102

Four-source trophic model

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Concentration	C Concentration	n
Berries and ag. Seeds	1.582	1.544	-23.987	1.498	0.022	0.481	21
"Predatory" arthropods	5.248	2.104	-24.138	1.266	0.107	0.520	96
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
C_3 plants[1]	1.641	2.695	-26.858	1.706	0.029	0.466	75

[1] excluding berries

Adult female three- source trophic model **Adult female four-source trophic model**

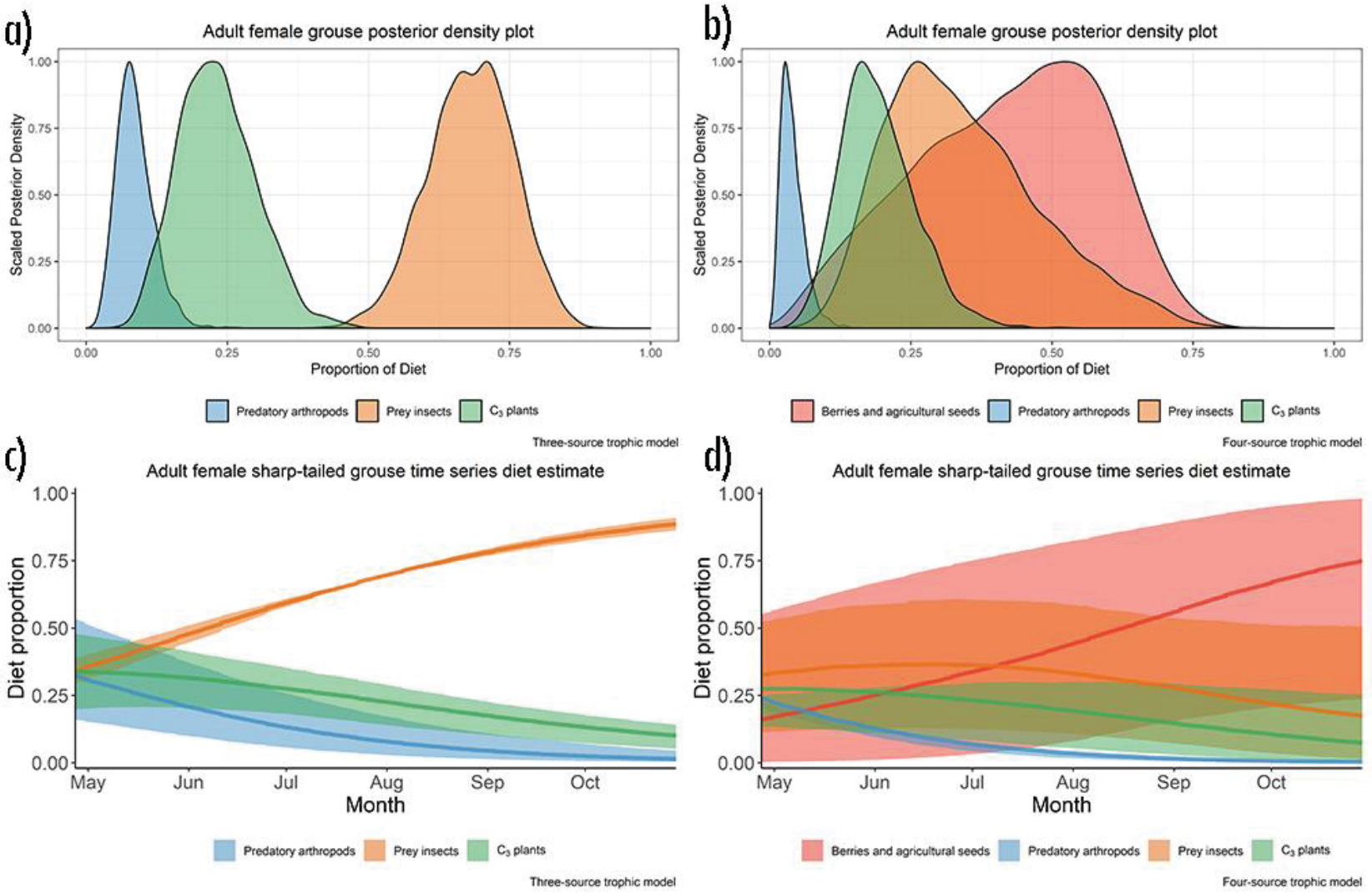

Figure 11 - Comparison of posterior density plot and time series estimate for adult female grouse models. The posterior density plot is a probability distribution for the proportions of each diet source. Time series estimates are given via the median estimated value (line) and the 95% credible interval (ribbon)

Table 12 - Summary of model estimates for adult female grouse corresponding to Figure 11 with standard deviation (SD) and Bayesian credible intervals (CI)

Three-source Trophic model overall average diet proportions

Source	Median	SD	95% CI
"Predatory" arthropods	0.08	0.03	0.03 - 0.16
"Prey" arthropods	0.68	0.07	0.53 - 0.82
C_3 Plants	0.23	0.07	0.11 - 0.37

Four-source Trophic model overall average diet proportions

Source	Median	SD	95% CI
Berries and ag. seeds	0.44	0.16	0.10 - 0.69
"Predatory" arthropods	0.04	0.02	0.01 - 0.09
"Prey" arthropods	0.32	0.13	0.14 - 0.65
C_3 Plants	0.19	0.07	0.08 - 0.34

Time series diet proportions

Month	Source	Median	95% CI
May	"Predatory" arthropods	0.32	0.16 - 0.53
	"Prey" arthropods	0.34	0.27 - 0.36
	C_3 Plants	0.34	0.20 - 0.48
August	"Predatory" arthropods	0.08	0.03 - 0.18
	"Prey" arthropods	0.68	0.67 - 0.67
	C_3 Plants	0.23	0.14 - 0.30
October	"Predatory" arthropods	0.01	0.00 - 0.04
	"Prey" arthropods	0.89	0.86 - 0.90
	C_3 Plants	0.10	0.05 - 0.14

Time series diet proportions

Month	Source	Median	95% CI
May	Berries and ag. seeds	0.16	0.00 - 0.55
	"Predatory" arthropods	0.24	0.20 - 0.23
	"Prey" arthropods	0.33	0.11 - 0.52
	C_3 Plants	0.27	0.13 - 0.25
August	Berries and ag. seeds	0.43	0.07 - 0.82
	"Predatory" arthropods	0.04	0.02 - 0.04
	"Prey" arthropods	0.34	0.11 - 0.59
	C_3 Plants	0.20	0.06 - 0.30
October	Berries and ag. seeds	0.75	0.24 - 0.98
	"Predatory" arthropods	0.00	0.00 - 0.01
	"Prey" arthropods	0.17	0.01 - 0.51
	C_3 Plants	0.07	0.01 - 0.25

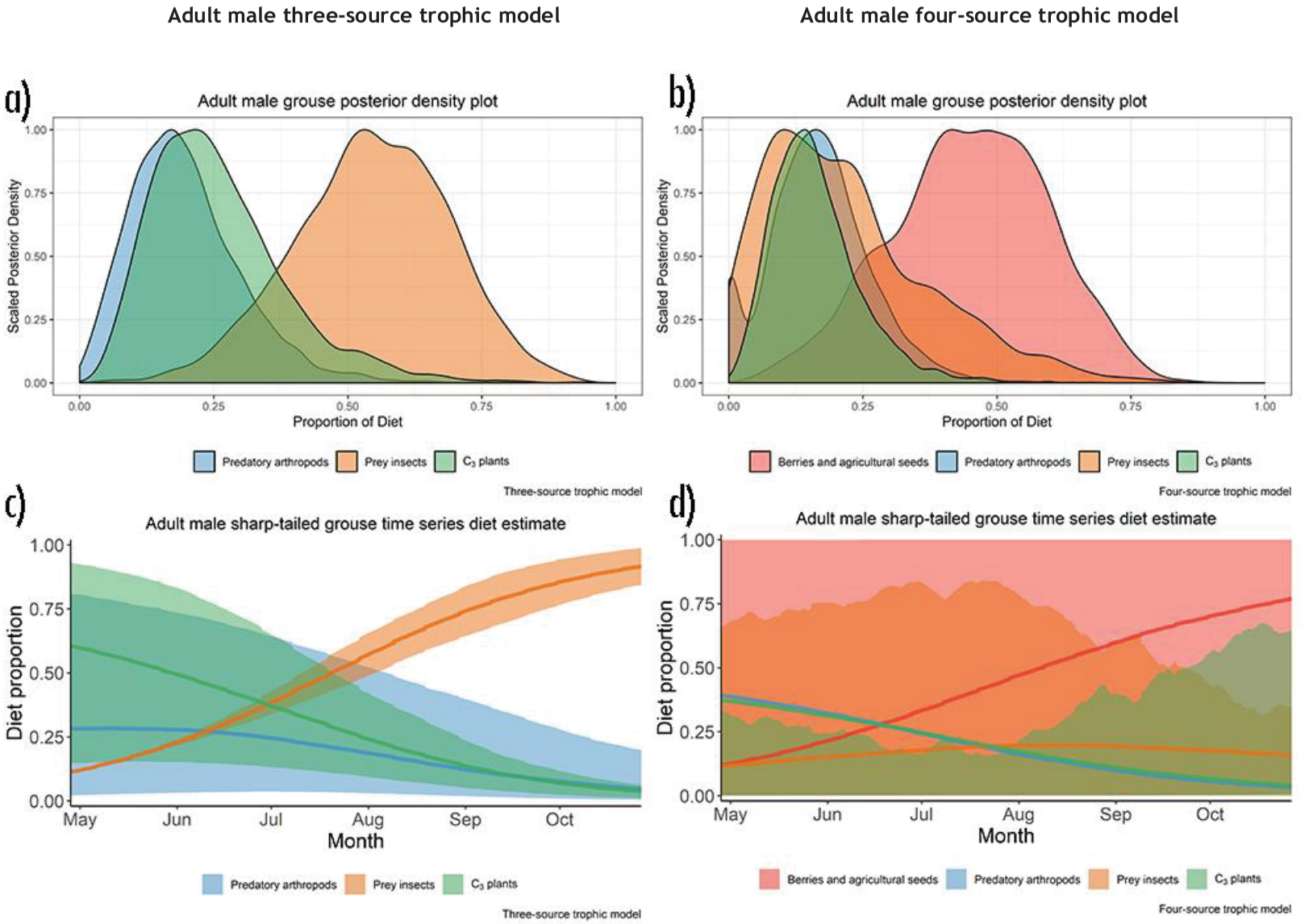

Figure 12 - Comparison of posterior density plot and time series estimate for adult male grouse models. The posterior density plot is a probability distribution for the proportions of each diet source. Time series estimates are given via the median estimated value (line) and the 95% credible interval (ribbon)

Table 13 - Summary of model estimates for adult male grouse corresponding to Figure 12 with standard deviation (SD) and Bayesian credible intervals (CI)

Three-source Trophic model overall average diet proportions

Source	Median	SD	95% CI
"Predatory" arthropods	0.18	0.10	0.04 - 0.43
"Prey" arthropods	0.55	0.14	0.25 - 0.81
C_3 Plants	0.24	0.13	0.08 - 0.56

Four-source Trophic model overall average diet proportions

Source	Median	SD	95% CI
Berries and ag. seeds	0.46	0.15	0.15 - 0.71
"Predatory" arthropods	0.16	0.09	0.00 - 0.37
"Prey" arthropods	0.19	0.15	0.00 - 0.60
C_3 Plants	0.15	0.08	0.04 - 0.37

Time series diet proportions

Month	Source	Median	95% CI
May	"Predatory" arthropods	0.28	0.02 - 0.81
	"Prey" arthropods	0.11	0.04 - 0.05
	C_3 Plants	0.61	0.15 - 0.93
August	"Predatory" arthropods	0.20	0.03 - 0.54
	"Prey" arthropods	0.54	0.36 - 0.52
	C_3 Plants	0.26	0.10 - 0.45
October	"Predatory" arthropods	0.05	0.00 - 0.20
	"Prey" arthropods	0.92	0.79 - 0.93
	C_3 Plants	0.04	0.01 - 0.06

Time series diet proportions

Month	Source	Median	95% CI
May	Berries and ag. seeds	0.12	0.00 - 1.00
	"Predatory" arthropods	0.39	0.00 - 0.37
	"Prey" arthropods	0.12	0.00 - 0.66
	C_3 Plants	0.37	0.00 - 0.34
August	Berries and ag. seeds	0.45	0.00 - 1.00
	"Predatory" arthropods	0.17	0.00 - 0.01
	"Prey" arthropods	0.19	0.00 - 0.81
	C_3 Plants	0.18	0.00 - 0.18
October	Berries and ag. seeds	0.77	0.01 - 1.00
	"Predatory" arthropods	0.03	0.00 - 0.16
	"Prey" arthropods	0.16	0.00 - 0.35
	C_3 Plants	0.04	0.00 - 0.64

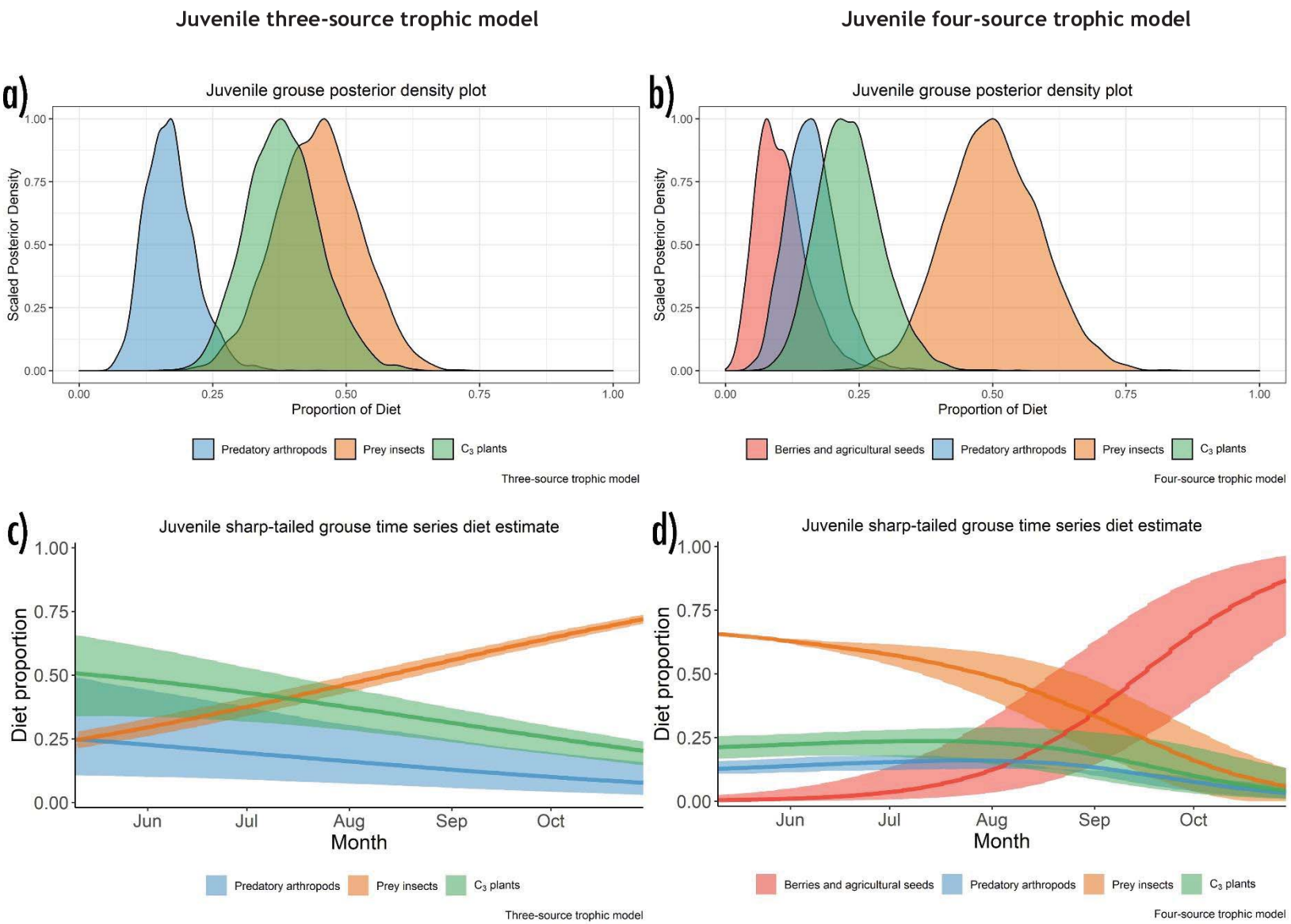

Figure 13 - Comparison of posterior density plot and time series estimate for juvenile grouse models. The posterior density plot is a probability distribution for the proportions of each diet source. Time series estimates are given via the median estimated value (line) and the 95% credible interval (ribbon)

Table 14 - Summary of model estimates for juvenile grouse corresponding to Figure 13 with standard deviation (SD) and Bayesian credible intervals (CI)

Three-source Trophic model overall average diet proportions

Source	Median	SD	95% CI
"Predatory" arthropods	0.17	0.05	0.09 - 0.27
"Prey" arthropods	0.45	0.08	0.29 - 0.60
C_3 Plants	0.38	0.07	0.26 - 0.52

Four-source Trophic model overall average diet proportions

Source	Median	SD	95% CI
Berries and ag. seeds	0.10	0.05	0.03 - 0.21
"Predatory" arthropods	0.16	0.05	0.08 - 0.26
"Prey" arthropods	0.50	0.09	0.34 - 0.67
C_3 Plants	0.23	0.06	0.13 - 0.36

Time series diet proportions

Month	Source	Median	95% CI
May	"Predatory" arthropods	0.25	0.11 - 0.49
	"Prey" arthropods	0.24	0.17 - 0.24
	C_3 Plants	0.51	0.34 - 0.66
August	"Predatory" arthropods	0.16	0.07 - 0.30
	"Prey" arthropods	0.47	0.42 - 0.49
	C_3 Plants	0.37	0.28 - 0.44
October	"Predatory" arthropods	0.08	0.03 - 0.16
	"Prey" arthropods	0.72	0.69 - 0.73
	C_3 Plants	0.20	0.15 - 0.24

Time series diet proportions

Month	Source	Median	95% CI
May	Berries and ag. seeds	0.00	0.00 - 0.02
	"Predatory" arthropods	0.13	0.11 - 0.16
	"Prey" arthropods	0.66	0.64 - 0.65
	C_3 Plants	0.21	0.17 - 0.25
August	Berries and ag. seeds	0.14	0.04 - 0.35
	"Predatory" arthropods	0.16	0.13 - 0.16
	"Prey" arthropods	0.48	0.35 - 0.54
	C_3 Plants	0.23	0.14 - 0.29
October	Berries and ag. seeds	0.87	0.65 - 0.96
	"Predatory" arthropods	0.03	0.01 - 0.06
	"Prey" arthropods	0.06	0.02 - 0.16
	C_3 Plants	0.04	0.01 - 0.13

Other model iterations – Model iterations using different source grouping methods showed a high level of sensitivity to the inclusion of C_4 grasses as a separate source, as well sensitivity to oversimplifying the mixing system (i.e. the *two-source* model).

Two-source model – This model estimated almost exclusive utilization of C_3 plant foods for adult female grouse (92%), a very high utilization of arthropods by adult male grouse (72%), and a high utilization of arthropods by juvenile grouse (63%). Seasonal trends in diet change were similar for adult male and juvenile grouse (increasing utilization of arthropods), and opposite for adult female grouse (Appendix 11.1).

Three-source C_4 model – This model, which was identical to the *two-source* model except for the inclusion of C_4 grasses as an additional source, estimated a similar seasonal diet trend in adult female grouse, with a slightly high estimate of overall arthropod utilization (15%). Estimates for adult male diet proportions were similar, but with more uncertainty. The time-series trend estimate for juvenile grouse was opposite to the *two-source* model, estimating a higher overall utilization of C_3 plants (69%) and a decreasing seasonal trend of arthropod utilization. C_4 grasses were not estimated to contribute more than 2% of diet proportion for either class (Appendix 11.2).

Four-source trophic C_4 model – This model, which was identical to the *three-source trophic* model used in the main analysis except for the inclusion of C_4 grasses, estimated a moderate use of arthropods (34%) and C_3 plant foods (60%) in adult female grouse while arthropod utilization estimates were high for adult male grouse (64%) and juvenile grouse (47%). No major seasonal trends were observed for adult female or juvenile grouse, however, estimation of adult male grouse arthropod utilization rose to 94% in the late season (Appendix 11.3).

Six-source model – This model showed extremely high levels of uncertainty in all of its estimates and did not meet MCMC convergence criteria (Appendix 11.4 and 13).

Sensitivity analysis – Changing the parameters of the *three-source trophic* model had no significant effects on diet proportion estimates, however, generally resulted in higher estimates of arthropod utilization (Table 15) (Appendix 14.1 and 14.5).

Table 15 - Effects of parameter changes in sensitivity analysis with three-source trophic model using adult female grouse dataset

Model alteration	Effect	Significance of effect
Without informative prior	1% higher estimate of "predatory" arthropod utilization 1% higher estimate of "prey" arthropod utilization 2% lower estimate of C_3 plant utilization	Not significant
Without lipid correction	2% lower estimate of "predatory" arthropod utilization 10% higher estimate of "prey" arthropod utilization 8% lower estimate of C_3 plant utilization	Not significant
Using Torres-posche TDF	1% lower estimate of "predatory" arthropod utilization 10% higher estimate of "prey" arthropod utilization 9% lower estimate of C_3 plant utilization	Not significant
Using SIDER TDF	10% higher estimate of "predatory" arthropod utilization 3% lower estimate of "prey" arthropod utilization 7% lower estimate of C_3 plant utilization	Not significant

Layman metrics – Bayesian ellipses calculated using SIBER (Jackson et al. 2011) showed that relative resource use in isotopic niche space was similar for adult female grouse and juvenile grouse (probability of a difference in ellipse size = 25%), and larger for adult male grouse (probability of a difference in ellipse size between adult female and adult male grouse = 99%) (Figure 14). Seasonal niche estimates show small changes to ellipse areas over the study period. Changes are mostly non-significant (within 95% credible intervals), except for juvenile grouse that show a significantly larger ellipse area during the September - October period (posterior probability of a difference = 100%) (Figures 14b – 14d). Trophic position estimates based on $\delta^{15}N$ values showed an overall decrease in trophic position through the study period. Adult male grouse were on average estimated to be feeding at a higher trophic level than other classes, and adult female grouse were lowest. The range of variation was highest for adult male grouse, and lowest for juvenile grouse (Table 16).

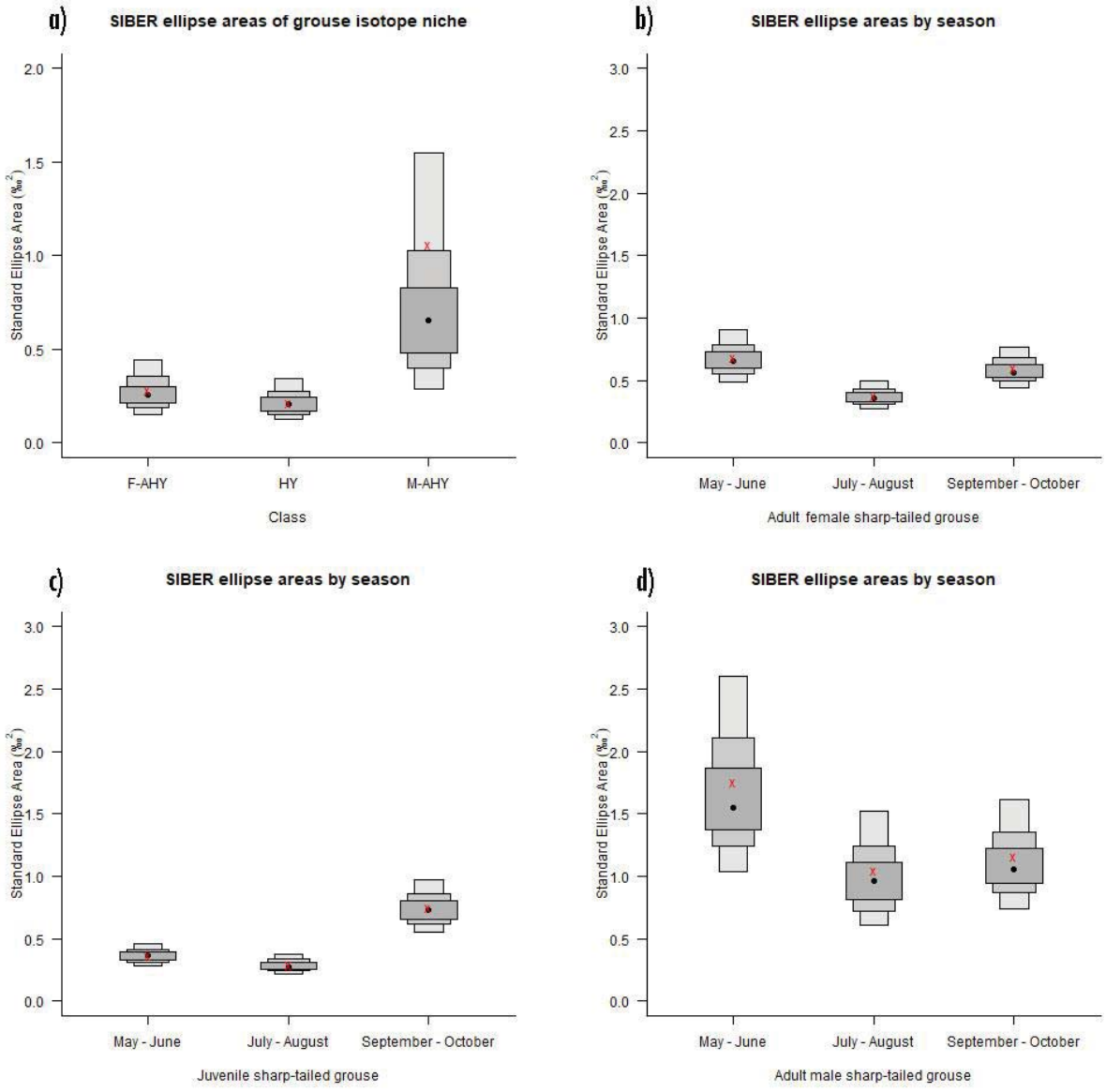

Figure 14 - SIBER isotope ellipse area estimates. Higher values indicate a larger ellipse and wider isotopic niche. The red x's represent the ellipse value calculated using a conventiaonl convex hull. The rectangles represent 50%, 75%, and 95% credible intervals

Table 16 - Seasonal trophic position estimates for all grouse classes

Class	Spring	Summer	Fall	Change	Mean	n
Adult female	3.04	2.92	2.81	-0.23	2.92	15
Adult male	3.20	3.11	2.90	-0.30	3.07	8
Juvenile	3.04	3.03	2.91	-0.13	2.99	17
Mean	3.09	3.02	2.87	-0.22		

Protein factor - Average protein content of plant and arthropod samples estimated from nitrogen-to-protein conversion factors are presented in Table 17.

Table 17 - Summary of estimated protein content of potential food items of sharp-tailed grouse

Food type	Protein (%)
Agricultural seed	16.8
Berry	6.7
Forb	12.3
Sprouting grass (C_3)	15.0
Grass (C_4)	7.0
Grass seed (C_3)	9.2
Grasslike	11.6
Shrub bud	9.5
Plant average	**11.02**
Araneae (Spiders)	58.3
Lithobiomorpha (Centipedes)	53.4
Coleoptera (Beetles)	47.2
Diptera (Flies)	56.2
Hemiptera (True bugs)	49.6
Hymenoptera (Ants and wasps)	53.4
Lepidoptera (Moths and butterflies)	47.9
Odonata (Damselflies)	58.8
Opiliones (Harvestmen)	58.4
Orthoptera (Grasshoppers and crickets)	56.4
Arthropod average	**54.0**

3.5 DISCUSSION

Model outcomes were sensitive to the inclusion of additional sources. A limitation of these models was that they did not account for seasonal change in available plant food, i.e. the availability of ripened berries in the fall. However, the *three-source trophic* model provided an appropriate diet estimate during early- and mid-season, while the *four-source trophic* model was better suited for estimating diet proportions of grouse later in the season. From the sequential plotting of primary feathers on an isotope biplot (Figure 9) it is apparent that a diet shift occurred for all classes of grouse, and that they gravitated toward the same food source in the late season: ripened berries and agricultural seeds. Of interest as well, from the time series estimates, was the trend consistent across all grouse classes of early season use of "predatory" arthropods. The progression of resource use from "predatory" arthropods in the early season to "prey" arthropods in the middle and late season is consistent with arthropod prey availability for grouse and is ecologically relevant.

The results from this study simultaneously demonstrate the power of isotopes as a biotracer for investigating feeding relationships as well as the limitations involved. The isotope values obtained from grouse feathers in this study show a clear trend over the season for each class. Several interesting observations were made regarding differences between classes of sharp-tailed grouse with regards to feeding ecology and potential nutrient allocation. The sensitivity analysis did not point to any major influence from the choice of TDF, priors, or lipid correction. However, a two-tracer isotope mixing model approach may not be the ideal tool for estimating feeding relationships in sharp-tailed grouse given the isotopic similarity of some of the important food sources and their omnivorous feeding habits. This research points to a need for additional methods to be employed if stable isotopes are to be used to disentangle mixing systems involving omnivorous grouse.

The additional model iterations that tested different source grouping methods demonstrated that an oversimplified model (i.e. *two-source* model) was not able to estimate diet proportions in a way that reflected previously known grouse foraging behaviour (Jones 1966; Renhowe 1968). Adding C_4 grasses as a source affected the oversimplified model slightly, however, as C_4 grasses likely contributed very little to grouse diets in the study area, the model outcomes still did not reflect expected diet proportions or

trends. Including C_4 grasses in the model that separated arthropods by trophic separation (i.e. *three-source trophic* C_4) produced estimates closer to known foraging habits and further confirmed that C_4 sources were unlikely to contribute to grouse diets in the study area. This improved estimate may have been due to the C_4 source acting as a proxy in isospace for where berries and agricultural seeds would be, were they included. The drastic difference in $\delta^{13}C$ between C_4 grass and berries and agricultural seeds, however, still rendered this model unreliable. Early season results from the *four-source trophic* model also suggested that including a source that was not ecologically coherent, i.e. ripened berries in the spring, distorted model estimates. The *six-source* model approach, which most accurately represented different potential food sources in isotopic space, demonstrated the limitations of a two-tracer model as the number of possible combinations of sources becomes too great for a reliable estimate.

The *three-source trophic* model sources were isotopically different enough to allow for a confident estimate (Appendix 9.3) and likely represented an appropriate mixing system for grouse during early- to mid- summer. The high utilization of arthropods that was estimated was expected during this time. In addition, the switch from utilization of both "predatory" and "prey" arthropods towards more "prey" arthropods agrees with previously known foraging habits and coincides with the type of arthropods available as prey in the study area (Table 18; Appendix 4). It is noteworthy that despite the relatively poor resolution in diet proportion estimates for some grouse classes (i.e. adult males) that stable isotope analysis was able to distinguish this ecologically important switch of resource use for all classes. However, the degree to which arthropods were estimated to be utilized was much higher than expected (66% for adult females, 39% for adult males, and 49% for juveniles). This estimate was unlikely to be representative of the actual proportion of biomass intake of these food sources, however, it may be accurate in the context of isotopic routing.

An inherent assumption in SIMMs is that nutrients from consumed foods are evenly distributed throughout the consumers tissues. This is not a realistic assumption, and it is up to the researcher to be mindful of the type of consumer tissue that is being sampled and the metabolic process that is involved in its synthesis. The foundations of isotope ecology are indeed found in the nutritional physiology of the

Table 18 - Relative abundance and relative biomass of arthropod orders estimated from sweep netting

Order	May - June		July - August		September - October	
	Relative abundance (%)	Relative biomass (%)	Relative abundance (%)	Relative biomass (%)	Relative abundance (%)	Relative biomass (%)
Araneae	12.3	14.2	9.6	2.9	9.4	2.9
Coleoptera	21.4	37.4	3.7	2.4	11.2	4.6
Diptera	24.4	6.4	12.2	2.3	30.9	5.4
Hemiptera	15.6	11.0	62.6	47.7	33.4	16.9
Hymenoptera	19.1	9.7	4.1	0.8	3.6	0.8
Ixodidae	0.1	<0.1	-	-	-	-
Lepidoptera	5.7	11.6	2.1	3.8	1.3	1.1
Odonata	0.1	0.3	0.2	0.4	-	-
Opiliones	-	-	<0.1	0.1	-	-
Orthoptera	1.1	9.4	5.3	39.5	10.2	68.3
Total	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**

organism (Martinez Del Rio et al. 2009). In cases where isotopic routing occurs, the isotope value of a consumer tissue does not reflect that of the bulk diet but rather the portion of dietary nutrients that went into producing that tissue. This effect has been found most prevalent in omnivores, and may vary with diet quality (Gannes et al. 1997; Layman et al. 2012). Podlesak and McWilliams (2006) reported that the routing of $\delta^{15}N$ and $\delta^{13}C$ differed depending on diet composition, and that when yellow-rumped warblers (*Dendroica coronata*) were fed a high protein diet (such as one that included arthropods) the $\delta^{15}N$ values of their proteinaceous tissues reflected those of dietary protein very closely. They concluded that wild birds consuming arthropods opportunistically may have tissue $\delta^{15}N$ values that disproportionately reflect the protein obtained from arthropods. Therefore, it is possible that protein assimilated by sharp-tailed grouse from ingested arthropods were preferentially allocated to the synthesis of their feathers. Indeed, cystine and methionine are amino acids important to the production of feathers in gallinaceous birds (Bearhop et al. 2002; Blair 2008) and are found in much higher concentrations in the proteins of arthropods than in plant foods (Savory 1989). Lipids, carbohydrates, and energy stores are thought to have a minimal contribution to the production of feathers, further suggesting that isotope signals of feathers should be expected to reflect dietary protein rather than bulk diet (Murphy 1996; Bearhop et al. 2002). Thus, the isotope signals found in

grouse feathers may be more reflective of the proteinaceous component of their diet, i.e. arthropods (Table 17), than other diet constituents.

Early season diet proportion estimates were similar for juvenile grouse and adult female grouse. Given that grouse chicks are known to consume arthropods almost exclusively during the first few weeks of life (Blomberg et al. 2013; Johnsgard 2016) it was expected that this would be reflected in the isotope signal of the first primary feathers (P9 and P10) in juvenile grouse. While estimated arthropod utilization was high in the *three-source trophic* model for the early season for juvenile grouse (49%), it was not significantly higher than of adult females (66%). The estimate was significantly higher for juveniles in the *four-source trophic* model (79%), however the inappropriate inclusion of berries in the early season likely distorted this estimate. This discrepancy between known foraging habits and model estimates may also be explained by isotopic routing. Grouse chicks require adequate nutrients for rapid production of flight muscles, feathers, and internal organs. This may affect isotopic routing to feathers in two ways. First, nutrients obtained from arthropods may not be preferentially routed to the production of feathers, as in adult grouse, but towards the production of other proteinaceous tissues like muscle, as well as internal organs and feathers. The first pennaceous feathers produced by grouse chicks during that time are indeed of poor quality, and most of them (P1 – P8) are replaced that same summer (Pyle 2008). Second, digestion in juvenile grouse does not occur in the same way as in an adult grouse due to the time it takes for their cecae to develop. Once developed, the cecae allow grouse to extract more nutrients from poor quality foods (Leopold 1953; Remington 1989). The absence of fully developed cecae in juvenile grouse could lead to differential isotope fractionation compared to adult grouse. The need for juvenile grouse to allocate nutrients to full body growth, coupled with differential digestive efficiency may explain why the isotope values obtained from the first primary feathers (P9 and P10) do not reflect diet in the same manner as in adult grouse. This hypothesis is further supported by evidence from other studies, including one using Japanese quail (*Coturnix japonica*) (Hobson et al. 1993), that indicated lower $\delta^{15}N$ values in organisms that were growing (Martinez Del Rio et al. 2009).

The *three-source trophic* model provided insights into the feeding ecology of sharp-tailed grouse during the spring and early summer. However, given what is known about late summer and fall grouse feeding

ecology, i.e. high utilization of berries, the *three-source trophic* model is unlikely to provide an accurate estimate of late season diet. Esophageal crop analysis from grouse harvested in the study area during October estimated that berries (snowberry, rose hips, chokecherry, and saskatoon) made up 55% of grouse diets by dry weight, and occurred in 88% of crops (Chapter 2). It is therefore not surprising that the *four-source trophic* model that included berries and agricultural seeds as a separate source estimated high utilization of that source during the late season (between 75-87%), albeit with high uncertainty for adult grouse (Figure 12d; Table 13). Due to their isotopic similarity, agricultural seeds were necessarily combined with berries for modeling purposes. However, although agricultural seeds are known to be consumed by grouse in October (35% by dry weight), the frequency of occurrence of agricultural seeds (18%) was much lower than berries (88%), and only found in the crop of one juvenile grouse out of 69 (Chapter 2). Therefore, diet proportions estimated for this source were assumed to consist mostly of berries.

The early and middle season estimates using the *four-source trophic* model were not significantly different from the *three-source trophic* model for adult grouse (95% CI's overlapped), however, uncertainty of the *four-source trophic* model estimates given the range of credible limits was high, except in the juvenile grouse model. The *four-source trophic* model also estimated higher than expected combined arthropod utilization during October (9-19%), relative to what was observed from esophageal crop analysis (3.4% by dry weight) (Chapter 2). The discrepancy between the model estimate and esophageal crop analysis further agrees with the isotopic routing hypothesis that nutrients gained from high protein food sources may be preferentially allocated towards feather synthesis.

Viewed from the perspective of the trophic position (TP) estimates (Table 16), which were derived solely from $\delta^{15}N$ values, the slight decrease in TP throughout the study period can be attributed to known foraging habits. Initially high TP (3.09) may have been due to higher utilization of "predatory" arthropods that were available as food in the spring (i.e. Araneae and Coleoptera), followed by a shift towards more "prey" arthropods (i.e. Orthoptera and Lepidoptera) that were more available during mid-summer causing a slight decrease in TP (3.02) (Table 18). Finally, a further decrease in TP (2.87) in

the late season may be attributed to the increased intake of berries and reduced availability of arthropod prey.

The ellipses produced using the SIBER package (Jackson et al. 2011) reflected the range of isotope values measured in grouse feathers. Small ellipse areas suggested a narrow feeding niche, and a large ellipse suggested more variation in food selection. It should be noted that isotopic niche, although related to trophic niche, is not directly representative (Jackson et al. 2011; Layman et al. 2012). This is likely due to many of the same issues previously discussed surrounding the interpretation of isotope values relative to the tissue being sampled, the spatial and temporal scale, and metabolic factors. Nevertheless, these metrics give an impression of the similarities and differences among grouse classes, as well as temporal variation. Adult male grouse appeared to have the most diverse diet between classes (Figures 9 and 14a), but changes observed throughout the season were not significant (Figure 14d). This observation made sense in the context of grouse hens and chicks foraging in closer proximity to each other while male grouse would not be expected to have the same spatial constraints on their foraging habits. As might be expected from juvenile grouse, either as a product of actual diet change or of differential isotopic routing, a significant change in ellipse size was observed between May – August and September – October (probability of a difference = 1.0) (Figure 14c) In the context of brood rearing behaviour this made sense. Grouse broods break up in September (Bergerud and Gratson 1988; Roersma 2001), which coincides approximately with the measured change in isotopic niche, i.e. the larger ellipse, which can be attributed to a greater diversity in food selection among juvenile grouse after leaving their brood.

3.5.1 Conclusion

The *three-source trophic* model likely represented the model structure that most accurately reflected the mixing space from which sharp-tailed grouse were feeding in the early and middle season, while the *four-source trophic* model was more representative of late season food availability. However, due to the similarity in $\delta^{13}C$ of berries and "prey" arthropods, model estimation precision was poor for the *four-source trophic* model. Given the occurrence of berries as a food source only later in the season, it was possible to obtain reliable estimates of early- to mid-season feeding relationships using the *three-*

source trophic model that excluded berries as a potential food source. High estimates of arthropod utilization were reasonable in the context of isotopic routing, which was hypothesized to be causing nutrients from protein rich arthropod foods to be preferentially allocated to the synthesis of primary feathers. Time-series TP estimates agreed with model estimates as well as previously documented foraging habits of grouse, i.e. utilization of arthropods when they were abundant, higher utilization of "predatory" arthropods in the early season, and a subsequent drop in TP as grouse fed on ripening berries in the fall. Isotopic niche, i.e. ellipse area in isospace, was also found to reflect known feeding behaviour and differences among male, female, and juvenile grouse.

These results indicate that stable isotope measurements of sharp-tailed grouse primary feathers can elucidate information about feeding ecology, relative resource use, and nutrient allocation. Isotopic routing of nutrients gained from arthropod prey indicate that their nutritional importance to grouse is disproportionate to the actual amount consumed. In other words, despite consuming mostly plant foods, as indicated by conventional diets studies, arthropod prey may be critical for grouse during molt due to their high protein content. Grasshoppers represented the most abundant arthropod prey by relative biomass, and "prey" arthropods (grasshoppers being the main constituent) were estimated to contribute a large amount of nutrients towards feather growth in this study. Their prevalence in the summer diets of grouse is also reflected in conventional diet study literature. As such, grasshoppers are likely the main source of nutrients used for feather synthesis in plains sharp-tailed grouse.

3.5.2 Recommendations for further Study

Given the results of this study a two-tracer isotope mixing model approach is not recommended for future investigations into the feeding relationships of sharp-tailed grouse, or other omnivorous birds. The use of compound-specific isotope analysis may be a more appropriate tool as it is able to utilize the isotope signals of specific amino acids and provide a mixing model with many more tracers specifically relevant to nutrient allocation (Larsen et al. 2009). However, extensive background research should be undertaken before allocating funds to this method. Analysing feathers as well as other tissues simultaneously, while taking into account differential turnover rates, may also yield greater insight in nutrient and isotopic routing in grouse. Grouse cecae are unique adaptations to

coping with nutrient-poor foods, and insight into their role in nutrient extraction and allocation may be of interest. Finally, the allocation of ingested lipids was not addressed in this study. Lipids are likely an important energy source for sharp-tailed grouse, and arthropods (grasshoppers in particular) are rich in lipid content (Appendix 6). Further research into the energy balance of sharp-tailed grouse and the role of lipids may be warranted.

CHAPTER 4: SHARP-TAILED GROUSE FOOD WEB DYNAMICS AND CLIMATE CHANGE

Abstract

The study of food webs is important for understanding ecosystem function and stability. Modern food web theory suggests that interaction strength between species in a food web, temporal and spatial variation, and indirect effects on food webs are of major significance for system stability. A diversity of species with varying phenologies within a system promotes stability through redundancy in ecosystem functions. Climate change and human development are affecting ecosystems across the globe by altering connectivity, diversity, and environmental conditions (i.e. thermal and hydrologic). Direct effects from these changes have consequences for species survival and extinction risk, however, indirect effects that alter nutrient flow, species interactions, and food web dynamics are far more influential. Higher order consumers are more sensitive to these changes, and fragmentation of habitat is a major contributor of ecosystem instability, reducing the potential for integration of resources across food webs, and further exacerbating the effects of climate change. Predicting the effects of climate change on multitrophic food webs is notoriously difficult. Increasing our knowledge of species interactions and interaction strength within food webs is key to improving our ability to make reliable predictions. The phenology of grassland arthropods and timing with grassland bird fledgling nutrient demands is an important interaction that warrants attention. Arthropods are sensitive to changes in seasonal thermal and hydrologic cycles and act as an important nutrient rich food source for sharp-tailed grouse and other grassland birds, worthy of attention with respect to conservation efforts. A key limitation in predicting the effects of ecological changes is a lack of observational data, i.e. ecological monitoring.

4.1 FOOD WEB THEORY

The study of food webs is fundamental to understanding ecological function, nutrient flow, and ecosystem dynamics. Food web research has had implications for many disciplines of ecology including population dynamics, community structure, ecosystem function, and evolutionary biology (Layman et al. 2015). Raymond Lindeman was among the first to posit that food web structure affects not only community level dynamics, but also total ecosystem function (Lindeman 1942) by viewing ecosystem interactions through the lens of energy and nutrient flow, a precursor to the idea of trophic cascades (Layman et al. 2015). Advances in food web theory have largely outpaced experimental and empirical quantification of food webs (Winemiller and Layman 2005), and a great deal of debate has been focused on the theoretical relationship between biodiversity and ecosystem stability (MacArthur 1955; May 1972; Lehman and Tilman 2000). Stability can be defined in many ways, but generally refers to the ability of a given ecosystem to maintain a natural state of equilibrium in the face of perturbation, i.e. environmental stochasticity, disturbance, etc. Equilibrium may also be variously defined and is largely dependant on the chosen spatial and temporal scale, i.e. many ecosystems undergo cyclical disturbance regimes that may be considered within their equilibrium (Leverkus et al. 2017). Loss of biodiversity can have a profound influence on ecosystem function and can affect important ecological services (Loreau and Thebault 2005). It was argued by some that diversity is directly related to stability (MacArthur 1955) while others argued that once a critical level of diversity and connectivity in a system is reached it becomes unstable (Gardner and Ashby 1970; May 1972).

Today, that debate has evolved into the recognition that the nature of species interactions (i.e. interaction strength, species traits, and foraging strategies), the role of time and space, abiotic factors, and indirect effects are of greater importance than diversity alone in determining the stability of a system. Some have argued that the disagreements surrounding the stability-diversity debate were due to models that attributed generalized relationships within ecosystems to measures of stability that necessarily relied on species numbers, like biomass or productivity (Doak et al. 1998), or by ignoring interactions between biotic and abiotic processes during experimental manipulations (Huston 1997). However, it has since been demonstrated through the application of robust theoretical models that not

only are interaction strength and indirect effects highly influential on system stability, but that variation of food web dynamics over time and space are the basis for stability (Moore 2005). Generalist consumers that are able to integrate resource use over time and space by switching from one resource to another when availability changes mediate the effects of lower-level variability. This creates complex consumer-resource interactions that are resistant to perturbation as long as habitat connectivity is maintained (Kondoh 2003; McCann et al. 2005). The integration of resources in this way can also be thought of in terms of trophic niche width. The idea of trophic niche (Elton 1927) has been used in ecology for a long time to quantify a species' position within a food web or ecosystem. A collapse in niche width, or width of resource use, characterized by a "homogenization of energy flow pathways to top predators" is likely to result from habitat fragmentation, or a significant reduction of diversity, and thus render a system less resilient to perturbation (Layman et al. 2007).

Following this logic, it has also been argued that diversity indirectly promotes stability through the proliferation of species that perform similar functional roles within a system but that possess various phenological traits that respond differently to environmental fluctuations. An ecosystem containing phenologically diverse species that perform similar ecological roles is more likely to maintain its functional state, i.e. remain stable, in the event of a temporary reduction of biodiversity (resulting from perturbation) due to the functional redundancy in the system. The asynchronicity of the different species' response to adverse conditions creates a "buffering" effect where ecosystem function is maintained despite the inhibition of some species' functional role. This has been referred to as the "insurance hypothesis" (Naeem 1998; Yachi and Loreau 1999). Analysis by Montoya et al. (2005) also demonstrated that species with many food web connections may act as buffers in a system, as the net effect of each species on the system is less than for species with fewer connections. The differential responses of species creates a complex dynamic and emphasises the importance of understanding the indirect effects of perturbation on food web stability, which have long been recognized (Darwin 1859), but are challenging to predict (Montoya et al. 2005). Equally important to the temporal variability in species' functional roles is the spatial variation associated with heterogeneous disturbance patterns on landscapes. These patterns have been largely disrupted by large monoculture agricultural

developments and fire suppression strategies. Varying frequency of occurrence and intensity of natural fires creates a mosaic of landscape features, habitat types, and vegetation suitable for many species (Leverkus et al. 2017).

A clear and widespread example of a human-caused indirect effect on food webs is the use of agricultural insecticides to control pest-insect outbreak events, and the indirect effects on grassland birds. Many newly hatched birds require nutrient rich food for rapid body development, which they obtain in the form of arthropod prey. In grassland environments, these prey often consist of grasshoppers (Orthoptera: Acrididae) and insect larvae (Maher 1979; Knapton 1980). A study by Johnson et al. (1996) examined the indirect effects of insecticides that remove grassland arthropods used as food for nestling songbirds. Birds in unsprayed areas showed a clear preference for grasshoppers (more than 80% of prey items were grasshoppers) as food for their nestlings, which has also been shown in similar studies (Maher 1979). One species of grasshopper, the brown-spotted range grasshopper (*Psoloessa delicatula*), was found to make up 20% of the grasshoppers found in the diets of nestling Chestnut-collared longspurs (*Calcarius ornatus*). In sprayed areas where grasshopper numbers were reduced by more than 90%, parent birds switched to feeding their nestlings other arthropods while still utilizing the remaining and newly hatching grasshoppers (Johnson et al. 1996). In this example the food web link between nestling birds and grasshoppers was significantly affected, and functional redundancy (other arthropod prey) in the system allowed the parent birds to continue feeding their young by switching to another food resource. In addition, the selection of newly hatching grasshoppers demonstrated ecological resilience resulting from varying grasshopper phenology: the grasshopper species that were already hatched at the time of spraying were killed and no longer available as prey, however, their functional role as prey for songbird nestlings was soon filled again by other species with later hatching times, which were present in this case.

Importantly, however, the diet switch from key species of grasshoppers to other arthropod prey may not have been without consequence to the nestling birds, or adults, as diet quality was likely altered. Arthropod utilization by insectivorous birds is known to be selective, favouring more nutritious prey (Razeng and Watson 2015). Given the clear preference for grasshoppers in several grassland songbird

diet studies (Maher 1979; Knapton 1980; Petersen and Best 1986), it is possible that they are more nutritionally beneficial than alternate arthropod prey chosen in their absence.

On the other hand, a study done by Imlay et al. (2017) showed no effect of insect abundance on nestling mass and survival of three insectivorous bird species. Their study aimed to test the implication that insect declines are responsible for population declines in insectivorous birds. Although nests from two of the three study species were found to hatch earlier in areas with higher insect abundance, no relationship was found between insect abundance near the nests and nestling survival and mass. This result was inconsistent with several other studies, and Imlay and her colleagues offered potential explanations for this inconsistency: a possible mismatch between sampled insects and prey insects; not taking into account nutritional quality of potential prey insects; periods of low insect abundance may not have been sufficient to affect nestling survival and mass; or that low insect availability was offset by increased foraging efforts by the parents. The latter possibility may have been the result of a trade-off of parental survival to ensure the survival of their offspring by reducing their own arthropod consumption (Saino et al. 1999). This example demonstrates the complexity of food web dynamics and the difficulty in measuring the impact of indirect effects, like the reduction of certain arthropod prey types, when behavioural traits (e.g. parental trade-off), interaction strength (e.g. prey selection), and other indirect effects (e.g. weather events) can obscure the measured effect.

Grazing management has also been identified as a contributing factor to rangeland habitat suitability for grassland birds including sharp-tailed grouse (Mcnew et al. 2017), as well as general range health (Fleischner 1994). In a Montana study that examined the effects of rangeland management on sharp-tailed grouse nest site selection and nest survival, no strong relationships could be identified with the use of rest-rotation grazing intended to mimic historic disturbance regimes (Milligan et al. 2019). While other studies point to a relationship between grazing management and grassland bird health (Derner et al. 2009), as well as other wildlife (Holechek et al. 1982), results are rarely definitive (Dettenmaier et al. 2017). However, changes to microhabitat caused by cattle grazing have been shown to have a significant influence on arthropod species composition and abundance. Grasshoppers may be variously affected by increased stocking rates, causing a decrease in the abundance of some species like the

lesser migratory grasshopper (*Melanoplus sanguinipes*) and an increase in others like Dawson's grasshopper (*Melanoplus dawsoni*) (Holmes et al. 1979). Ecologically appropriate grazing practices (i.e. mimicking historic disturbance regimes) have also been attributed to a general increase in arthropod food availability for grassland birds (Sullins et al. 2018; Goosey et al. 2019), and incorporation of fire in addition to cattle grazing has been shown to promote habitat heterogeneity beneficial to grassland birds, including prairie grouse (Fuhlendorf et al. 2006; Winder et al. 2016).

4.2 CLIMATE CHANGE AND TROPHIC DYNAMICS

The effects of climate change on plant and animal populations worldwide are evident (Walther et al. 2002; Root et al. 2003; Booth et al. 2012) and are increasingly altering species distributions, abundances, and increasing the risk of extinctions (Thomas et al. 2004). Predicting ecological responses to climate change is complicated by many of the factors already discussed, and it is clear that making predictions based on the direct influence of climate change (i.e. thermal) to a species' population is not sufficient (Zhang et al. 2017). A species may be well within the limits of the thermal niche, while interactions with other species populations, food availability, and predation effects may be altered directly, or indirectly, by changes to weather and climate. In fact, the indirect effects of climate change on species populations has been shown to be more significant than direct effects (Zhang et al. 2017).

One such effect of climate change, which has already been discussed in the above examples and is the focus of this thesis, is the indirect effect of changes to arthropod food availability to grassland birds like sharp-tailed grouse. Arthropods are a major component of most ecosystems, and grasslands are no exception. They provide many ecosystem services, including constituting an important food source for many animals, and are highly sensitive to changes in weather and climate (Prather et al. 2013). Significant declines in arthropod abundance worldwide have been noted (Nebel et al. 2010; Hallmann et al. 2017) and threaten seasonally available food resources for grouse and other birds, as well as a

multitude of ecological services that have ecosystem-wide repercussions (i.e. seed dispersal, pollination, decomposition, nutrient cycling, pest control, water quality, etc.) (Prather et al. 2013). Indirectly, decreases in arthropod abundance coupled with potential changes to their phenology and timing of emergence creates a complicated and unpredictable series of changes to food web and ecological dynamics across time and space. In addition, habitat fragmentation is increasingly added as a stressor to food web stability. Buffering effects like the insurance hypothesis, are unlikely to compensate for the compounding destabilizing effects of both climate change and habitat fragmentation.

In the context of sharp-tailed grouse ecology, adverse effects caused by changes to weather and climate may not limit the ability of grouse to meet thermal requirements (direct effect) if appropriate habitat heterogeneity is available (Raynor et al. 2018). However, indirect effects like alterations to prey arthropod diversity, phenology, and abundance (Laws and Joern 2013; Prather et al. 2013) may threaten the availability of nutrient rich arthropod foods during times of high energy demand, i.e. during early development and molt (Moss and Hanssen 1980; Connelly et al. 1998). A factor that may compound the adverse affect of weather on the grouse success is foraging time, especially in chicks. Grouse chicks do not posses the same insulative capabilities as adults and so are sensitive to inclement weather, i.e. prolonged wet conditions or excessive heat (Hart et al. 1950; Raynor et al. 2018). As such, weather events that reduce arthropod abundance and thus prey availability, like excessive rain or prolonged low temperatures in the spring (Bale et al. 2002; Prather et al. 2013), also affect the amount of time a grouse chick can spend foraging before risking hypothermia (Spidsø 1980). The same compounding effect has been noted in other galliforms with similar brood rearing strategies, like grey partridge (*Perdix perdix*) that have been studied extensively in England (Cross 1969; Potts 2012).

Ecological stability is strongly related to food web structure and dynamics which are affected directly and indirectly by climate change and anthropogenic influences. The study of food webs can be used as an indicator of ecosystem condition and health and help to gauge species' susceptibility to extirpation or extinction, especially for higher trophic level species (Voigt et al. 2003). The complexity of interactions and challenges in making accurate predictions in food web and ecological research are

best met by approaching important research questions from several different angles and using several different methodologies (Winemiller and Layman 2005). For sharp-tailed grouse, grasshoppers and other grassland insects and spiders constitute an important seasonal food source that may be significantly altered by climate change, agricultural pest management practices, and fire suppression in the future. Seasonal arthropod prey availability should be considered as an important aspect of grouse ecology and special food web relationships (i.e. Dawson's grasshopper and plains sharp-tailed grouse in southern and central Alberta described in Chapter 2) warrant consideration with respect to conservation efforts. In order to improve our ability to predict and avert adverse effects on natural ecological systems there is a need for increased monitoring and surveillance of ecosystem metrics including species composition (particularly in reference to arthropods), effects of disturbance (i.e. grazing and fire) on species composition and species interactions, and empirical observations regarding food web dynamics and how their temporal and spatial adaptability.

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APPENDIX 1: VEGETATION SURVEYS

Species composition: The proportion of a plant species relative to others in a plant community.

Canopy cover: The area of ground covered by the vertical projection of the outer perimeter of the plant. Openings within the canopy were included.

Frequency: The average frequency of occurrence of a plant species in sampling plots.

Wild Rose conservation site spring vegetation survey (May 2018) (n = 100 plots)

Common name	Scientific name	Species composition (%)	Canopy cover (%)	Frequency (%)
	Forbs			
Three-flowered avens	*Geum triflorum*	4.0	2.4	27
Yellow prairie violet	*Viola nuttallii*	2.6	1.4	40
Prairie goldenbean	*Thermopsis rhombifolia*	2.4	1.5	26
Woolly groundsel	*Senecio canus*	2.2	1.3	18
Northern bedstraw	*Galium boreale*	1.8	1.0	31
Prairie Crocus	*Anemone patens*	1.6	0.9	22
Silky lupine	*Lupinus sericeus*	1.4	0.8	20
Wild strawberry	*Fragaria virginiana*	1.4	0.8	24
Goldenrod	*Solidago*	1.2	0.7	13
Western yarrow	*Achillea millefolium*	1.1	0.6	26
Sulfur cinquefoil	*Potentilla recta*	1.0	0.5	14
Groundsel	*Senecio*	0.9	0.7	4
Yellow puccoon	*Lithospermum ruderale*	0.9	0.5	12
Bastard Toadflax	*Comandra umbellata*	0.7	0.5	13
Fringed sagewort	*Artemisia frigida*	0.7	0.5	7
Unidentified forb		0.6	0.3	12
Prairie sage	*Artemisia ludoviciana*	0.5	0.3	13
Sticky purple geranium	*Geranium viscosissimum*	0.5	0.3	12
Moss phlox	*Phlox hoodii*	0.5	0.4	6
False Solomon's seal	*Maianthemum stellatum*	0.5	0.3	8
Death Camas	*Zigadenus elegans*	0.4	0.2	10
Meadowrue	*Thalictrum*	0.4	0.2	6
Common dandelion	*Taraxacum officinale*	0.4	0.2	13
Darkthroat shootingstar	*Dodecatheon radicatum*	0.4	0.2	6
Unidentified forb		0.3	0.2	7

Prairie spikemoss	*Selaginella densa*	0.1	0.1	1
Unidentified forb		0.1	0.1	4
Nodding onion	*Allium cernuum*	0.1	0.1	4
Goatsbeard	*Tragopogon dubius*	0.1	<0.1	2
Alumroot	*Heuchera cylindrica*	0.1	<0.1	2
Vetch	*Vicia*	0.1	<0.1	4
Hairy rockcress	*Arabis hirsuta*	0.1	<0.1	3
Early cinquefoil	*Potentilla concinna*	<0.1	<0.1	1
Forget-me-not	*Myosotis*	<0.1	<0.1	1
Anemone	*Anemone*	<0.1	<0.1	1
Mustard	Brassicaceae	<0.1	<0.1	1
Cushion milk-vetch	*Astragalus gilviflorus*	<0.1	<0.1	1
Unidentified forb		<0.1	<0.1	1
Unidentified forb		<0.1	<0.1	1
	Shrubs			
Western snowberry	*Symphoricarpos occidentalis*	13.5	8.3	65
Prickly rose / Woods' rose	*Rosa acicularis / R. woodsii*	7.9	4.7	70
Chokecherry	*Prunus virginiana*	3.7	2.5	8
Saskatoon	*Amelanchier alnifolia*	2.8	1.8	9
Shrubby cinquefoil	*Potentilla fruticosa*	0.8	0.5	4
Northern gooseberry	*Ribes oxyacanthoides*	0.7	0.6	3
	Grasses and grass-likes			
Grass	Poaceae	37.8	22.8	100
Spike rush	*Eleocharis*	0.3	0.3	1
Low Sedge	*Carex stenophylla*	0.2	0.1	2
Bare ground		3.2	2.2	17
Total		100		
Average vegetation height (cm)	17.4			
Average litter depth (cm)	5.4			

Twin River Heritage Rangeland Natural Area spring vegetation survey (May 2018) (n = 100 plots)

Common name	Scientific name	Species composition (%)	Canopy cover (%)	Frequency (%)
	Forbs			
Prairie goldenbean	*Thermopsis rhombifolia*	5.5	4.0	53
Prairie crocus	*Anemone patens*	3.5	2.6	32
Silky lupine	*Lupinus sericeus*	3.4	2.5	28
Goldenrod	*Solidago*	2.4	1.6	23
Fringed sagewort	*Artemisia frigida*	2.2	1.5	23
Northern bedstraw	*Galium boreale*	2.0	1.5	26
Unidentified forb		1.8	1.2	13
Prairie sage	*Artemisia ludoviciana*	1.6	1.1	17
Western yarrow	*Achillea millefolium*	1.2	1.0	16
Aster	Asteraceae	1.0	0.7	9
Sticky purple geranium	*Geranium viscosissimum*	0.8	0.6	9
Bastard toadflax	*Comandra umbellata*	0.7	0.5	17
Unidentified forb		0.6	0.4	10
Yellow puccoon	*Lithospermum ruderale*	0.6	0.4	5
Common dandelion	*Taraxacum officinale*	0.5	0.4	12
Three-flowered avens	*Geum triflorum*	0.5	0.4	3
Creeping thistle	*Cirsium arvense*	0.3	0.3	11
Milk vetch	*Astragalus*	0.3	0.2	8
Goatsbeard	*Tragopogon dubius*	0.2	0.2	8
Moss phlox	*Phlox hoodii*	0.1	0.1	4
Wavy-leaf thistle	*Cirsium undulatum*	0.1	0.1	4
Pussytoes	*Antennaria*	0.1	0.1	1
Meadowrue	*Thalictrum*	0.1	0.1	1
Showy locoweed	*Oxytropis splendens*	0.1	0.1	1
Unidentified forb		0.1	0.1	2
Vetch	*Vicia*	0.1	0.1	4
Prairie onion	*Allium textile*	0.1	0.1	4
Unidentified forb		0.1	0.1	3
Unidentified forb		0.1	0.1	2
Unidentified forb		0.1	0.1	1
Unidentified forb		0.1	0.1	1
False Solomon's seal	*Maianthemum stellatum*	0.1	0.1	1
Prairie spikemoss	*Selaginella densa*	<0.1	<0.1	1
Alumroot	*Heuchera richardsonii*	<0.1	<0.1	1
Unidentified forb		<0.1	<0.1	1
Sulfur cinquefoil	*Potentilla recta*	<0.1	<0.1	1
Unidentified forb		<0.1	<0.1	1
Groundsel	*Senecio*	<0.1	<0.1	2

Violet	*Viola*	<0.1	<0.1	2
Yellow prairie violet	*Viola nuttallii*	<0.1	<0.1	2
Unidentified forb		<0.1	<0.1	1
Early cinquefoil	*Potentilla concinna*	<0.1	<0.1	1
Narrow leaf vetch	*Vicia americana*	<0.1	<0.1	1
Unidentified forb		<0.1	<0.1	1
Field chickweed	*Cerastium arvense*	<0.1	<0.1	1
	Shrubs			
Western snowberry	*Symphoricarpos occidentalis*	11.1	8.3	46
Prickly rose / Woods' rose	*Rosa acicularis / R. woodsii*	7.1	5.3	54
Sagebrush	*Artemisia cana*	0.6	0.5	2
Chokecherry	*Prunus virginiana*	0.2	0.2	1
	Grasses and grass-likes			
Grass	Poaceae	49.6	36.3	100
Sedge	*Carex*	0.1	0.1	2
Rush	*Juncus*	<0.1	0.0	1
Bare ground		0.5	0.4	13
Total		100		
Average vegetation height (cm)	16.7			
Average litter depth (cm)	3.8			

Wild Rose conservation site summer vegetation survey (July-August 2018) (n = 100 plots)

Common name	Scientific name	Species composition (%)	Canopy cover (%)	Frequency (%)
		Forbs		
Yellow puccoon	*Lithospermum ruderale*	3.6	3.2	18
Prairie goldenbean	*Thermopsis rhombifolia*	2.4	2.1	35
Silky lupine	*Lupinus sericeus*	2.1	1.9	20
Three-flowered avens	*Geum triflorum*	1.9	1.6	24
Northern bedstraw	*Galium boreale*	1.8	1.7	31
Penstemon	*Penstemon*	1.7	1.7	22
Prairie sage	*Artemisia ludoviciana*	1.3	1.2	27
Western yarrow	*Achillea millefolium*	1.1	1.1	30
Wild bergamont	*Monarda fistulosa*	1.0	1.1	12
Smooth fleabane	*Erigeron glabellus*	1.0	0.9	14
Canada goldenrod	*Solidago canadensis*	0.9	0.9	12
Bastard toadflax	*Comandra umbellata*	0.9	0.8	17
Wild licorice	*Glycyrrhiza lepidota*	0.7	0.7	4
Creeping thistle	*Cirsium arvense*	0.7	0.8	9
Smoot blue aster	*Aster laevis*	0.7	0.6	7
Tufted fleabane	*Erigeron caespitosus*	0.7	0.7	13
Meadowrue	*Thalictrum*	0.6	0.9	8
Wild strawberry	*Fragaria virginiana*	0.6	0.7	13
Prairie crocus	*Anemone patens*	0.5	0.5	25
Golden aster	*Heterotheca villosa*	0.5	0.4	12
Sticky purple geranium	*Geranium viscosissimum*	0.5	0.5	18
Smooth aster	*Symphyotrichum laeve*	0.4	0.4	5
Fringed sagewort	*Artemisia frigida*	0.4	0.4	11
Milk vetch	*Astragalus*	0.4	0.3	7
Graceful cinquefoil	*Potentilla gracilis*	0.2	0.3	7
Aster	Asteraceae	0.2	0.2	5
Prairie spikemoss	*Selaginella densa*	0.2	0.2	1
False Solomon's seal	*Maianthemum stellatum*	0.2	0.2	3
Moss phlox	*Phlox hoodii*	0.1	0.1	2
Dotted blazing-star	*Liatris punctata*	0.1	0.1	5
Field chickweed	*Cerastium arvense*	0.1	0.1	1
False Solomon's seal	*Maianthemum stellatum*	0.1	0.1	2
Cut-leaved anemone	*Anemone multifida*	0.1	<0.1	2
Unidentified forb		0.1	<0.1	2
Wavy-leaf thistle	*Cirsium undulatum*	0.1	0.1	1
Horsetail	*Equisetum arvense*	0.1	0.1	1
Wild mint	*Mentha arvensis*	0.1	0.1	1
Unidentified forb		<0.1	<0.1	1
Scarlet gaura	*Gaura coccinea*	<0.1	<0.1	1

Unidentified forb		<0.1	<0.1	1
Goatsbeard	*Tragopogon dubius*	<0.1	<0.1	2
Lacy tansyaster	*Xanthisma spinulosum*	<0.1	<0.1	2
Common dandelion	*Taraxacum officinale*	<0.1	<0.1	2
Woolly groundsel	*Senecio canus*	<0.1	<0.1	1
Gumweed	*Grindelia squarrosa*	<0.1	<0.1	1
Harebell	*Campanula rotundifolia*	<0.1	<0.1	1
	Shrubs			
Western snowberry	*Symphoricarpos occidentalis*	14.7	14.7	71
Prickly rose / Woods' rose	*Rosa acicularis / R. woodsii*	8.7	8.2	69
Saskatoon	*Amelanchier alnifolia*	1.3	1.2	8
Shrubby cinquefoil	*Potentilla fruticosa*	0.7	0.5	4
Northern gooseberry	*Ribes oxyacanthoides*	0.7	0.7	2
Skunkbrush	*Rhus trilobata*	0.5	0.5	1
Chokecherry	*Prunus virginiana*	0.2	0.2	2
	Grasses and grass-likes			
Grass	Poaceae	43.6	43.7	100
Baltic rush	*Juncus balticus*	0.1	0.1	1
Sedge	*Carex*	<0.1	<0.1	1
Bare ground		1.4	1.3	11
Total		100		
Average vegetation height (cm)	23.5			
Average litter depth (cm)	5.2			

Twin River Heritage Rangeland Natural Area summer vegetation survey (July-August 2018)
(n = 100 plots)

Common name	Scientific name	Species composition (%)	Canopy cover (%)	Frequency (%)
		Forbs		
Creeping thistle	*Cirsium arvense*	4.7	5.3	26
Tufted fleabane	*Erigeron caespitosus*	4.5	3.0	29
Prairie goldenbean	*Thermopsis rhombifolia*	4.2	3.1	39
Prairie spikemoss	*Selaginella densa*	4.1	3.3	9
Silky lupine	*Lupinus sericeus*	2.8	2.2	10
Northern bedstraw	*Galium boreale*	2.6	2.8	33
Smoot blue aster	*Aster laevis*	2.0	1.4	10
Western yarrow	*Achillea millefolium*	1.9	1.5	18
Prairie sage	*Artemisia ludoviciana*	1.8	1.4	18
Sticky purple geranium	*Geranium viscosissimum*	1.7	2.0	20
Milk vetch	*Astragalus*	1.1	1.2	12
Golden aster	*Heterotheca villosa*	0.9	0.6	6
Fringed sagewort	*Artemisia frigida*	0.8	0.6	12
Bastard toadflax	*Comandra umbellata*	0.5	0.3	6
Wild licorice	*Glycyrrhiza lepidota*	0.4	0.3	4
Common dandelion	*Taraxacum officinale*	0.4	0.5	7
Pussytoes	*Antennaria*	0.4	0.2	1
Broomweed	*Gutierrezia sarothrae*	0.4	0.3	2
Goldenrod	*Solidago*	0.3	0.3	3
Penstemon	*Penstemon*	0.3	0.3	4
Smooth fleabane	*Erigeron glabellus*	0.3	0.3	3
Aster	Asteraceae	0.3	0.2	4
Three-flowered avens	*Geum triflorum*	0.3	0.2	3
Wild blue flax	*Linum lewisii*	0.2	0.2	1
Blanketflower	*Gaillardia aristata*	0.2	0.2	1
Wavy-leaf thistle	*Cirsium undulatum*	0.2	0.2	3
Prairie crocus	*Anemone patens*	0.1	0.1	3
Nodding onion	*Allium cernuum*	0.1	0.1	2
Death Camas	*Zigadenus elegans*	0.1	0.1	1
Moss phlox	*Phlox hoodii*	0.1	0.1	5
Graceful cinquefoil	*Potentilla gracilis*	0.1	0.1	2
Stinging nettle	*Urtica dioica*	0.1	0.1	1
Yellow prairie violet	*Viola nuttallii*	0.1	0.1	2
Yellow puccoon	*Lithospermum ruderale*	0.1	0.1	1
Vetch	*Vicia*	0.1	0.1	1
Water parsnip	*Sium suave*	0.1	0.1	2
Cut-leaved anemone	*Anemone multifida*	<0.1	0.1	1
Skelton-weed	*Lygodesmia juncea*	<0.1	<0.1	1

Meadowrue	*Thalictrum*	<0.1	<0.1	1
Goatsbeard	*Tragopogon dubius*	<0.1	<0.1	2
	Shrubs			
Western snowberry	*Symphoricarpos occidentalis*	9.9	9.3	46
Prickly rose / Woods' rose	*Rosa acicularis / R. woodsii*	6.4	6.1	47
Chokecherry	*Prunus virginiana*	0.2	0.3	1
	Grasses and grass-likes			
Grass	Poaceae	41.1	36.6	100
Sedge	*Carex*	0.6	0.4	3
Rush	*Juncus*	0.5	0.6	7
Bare ground		2.3	1.5	12
Total		100		
Average vegetation height (cm)	21.7			
Average litter depth (cm)	4.4			

APPENDIX 2: PRIMARY FEATHER MEASUREMENTS

Measurements taken following methods from Caldwell (1980). All measurements given in mm (n = 119).

ID	Site	Year	P10 calamus diameter	P9 calamus diameter	P8 calamus diameter	P7 calamus diameter	P9/P8 calamus ratio	P10 rachis length	P9 rachis length	P8 rachis length	P7 rachis length	Estimated age	Estimated Sex	Known age (bursa)	Known sex (testes/ovaries)	Tail feather length
166	TR	2018	2.68	3.09	3.51	3.55	0.88	122	138	142	143	HY	M	HY	M	-
169	WR	2018	2.7	3.12	BQ	3.63	-	120	135	BQ	141	HY	F	HY	F	-
176	TR	2018	2.85	3.32	3.72	3.76	0.89	123	142	146	145	HY	M	HY	M	-
179	TR	2018	2.7	3.18	BQ	3.49	-	126	142	BQ	141	HY	F	HY	F	-
180	TR	2018	2.74	3.23	BQ	BQ	-	121	139	BQ	BQ	HY	F	HY	F	-
186	TR	2018	2.85	3.31	BQ	3.7	-	122	141	BQ	144	HY	F	HY	F	-
200	TR	2018	2.71	3.22	3.65	3.63	0.88	124	144	149	147	HY	U	HY	M	-
165	TR	2018	BQ	3.46	3.61	3.68	0.96	BQ	140	143	141	AHY	F	AHY	F	-
167	WR	2018	BQ	BQ	3.53	3.64	-	BQ	BQ	147	146	AHY	F	AHY	F	-
168	WR	2018	BQ	BQ	3.45	3.5	-	BQ	BQ	148	146	AHY	F	AHY	F	-
170	TR	2018	BQ	3.61	3.67	3.81	0.98	BQ	14.4	14.6	14.8	AHY	M	AHY	M	-
171	WR	2018	2.7	3.32	3.51	3.69	0.95	118	140	146	146	AHY	F	AHY	F	-
172	TR	2018	BQ	3.48	3.7	3.81	0.94	BQ	150	150	150	AHY	M	AHY	M	-
173	WR	2018	BQ	3.32	3.59	3.68	0.92	BQ	140	144	144	AHY	F	AHY	F	-
174	WR	2018	2.81	3.35	3.55	3.71	0.94	121	144	147	145	AHY	F	AHY	F	-
175	TR	2018	BQ	BQ	3.55	3.6	-	BQ	BQ	144	142	AHY	F	AHY	F	-
177	TR	2018	BQ	3.51	3.85	3.92	0.91	BQ	148	152	152	AHY	M	AHY	M	-
178	TR	2018	BQ	BQ	3.51	3.65	-	BQ	BQ	148	146	AHY	F	AHY	F	-
181	TR	2018	BQ	BQ	3.5	3.57	-	BQ	BQ	144	143	AHY	F	AHY	F	-
182	TR	2018	2.96	3.46	3.69	3.78	0.94	119	143	145	145	AHY	M	AHY	M	-
183	TR	2018	BQ	3.3	3.51	3.62	0.94	BQ	135	140	139	AHY	F	AHY	F	-
184	TR	2018	2.86	3.33	3.58	3.71	0.93	121	144	149	149	AHY	U	AHY	M	-

185	TR	2018	BQ	BQ	3.71	3.71	-	BQ	BQ	-	142	AHY	F	AHY	F	-
187	TR	2018	BQ	BQ	3.5	3.56	-	BQ	BQ	147	145	AHY	F	AHY	F	-
1	WR	2017	BQ	BQ	3.94	3.99	-	BQ	BQ	148	148	AHY	F	-	-	110.5
2	WR	2017	BQ	BQ	3.47	3.51	-	BQ	BQ	139	140	AHY	M	-	-	98
3	WR	2017	BQ	BQ	3.47	3.5	-	BQ	BQ	146	148	AHY	U	-	-	-
4	WR	2017	BQ	BQ	3.52	3.63	-	BQ	BQ	141	14.3	AHY	U	-	-	94
5	WR	2017	-	3.08	3.46	-	0.89	-	138	136	-	HY	F	-	-	120
6	WR	2017	BQ	BQ	3.38	3.46	-	BQ	BQ	124	145	AHY	F	-	-	116.5
7	WR	2017	BQ	BQ	BQ	3.61	-	BQ	BQ	BQ	148	AHY	F	-	-	108
8	WR	2017	BQ	BQ	3.53	3.56	-	BQ	BQ	-	-	AHY	F	-	-	127.5
9	WR	2017	2.88	3.31	3.73	3.74	0.89	123	138	141	142	HY	F	-	-	122
10	WR	2017	2.79	3.34	3.63	3.77	0.92	132	148	149	148	HY	F	-	-	128.5
11	WR	2017	2.89	3.48	3.61	3.74	0.96	118	145	148	148	AHY	M	-	-	136
12	WR	2017	2.74	3.2	3.64	3.73	0.88	121	137	141	-	HY	F	-	-	129
13	WR	2017	2.82	3.35	3.56	3.63	0.94	120	-	149	149	AHY	F	-	-	124
14	TR	2017	2.89	3.33	3.71	3.8	0.90	122	138	145	142	HY	U	-	-	-
15	WR	2017	2.74	3.27	3.7	3.75	0.88	120	136	144	146	HY	M	-	-	128.5
16	TR	2017	2.83	3.26	3.59	3.54	0.91	125	139	143	143	HY	U	-	-	-
18	TR	2017	2.79	3.19	3.46	3.63	0.92	115	133	140	143	HY	U	-	-	-
20	TR	2017	BQ	BQ	3.44	3.57	-	BQ	BQ	146	145	AHY	U	-	-	-
21	TR	2017	2.83	3.15	3.57	3.71	0.88	127	143	148	147	HY	U	-	-	-
22	TR	2017	2.87	3.36	3.52	3.66	0.95	123	145	147	149	AHY	U	-	-	-
23	TR	2017	2.8	3.14	BQ	3.54	-	119	136	BQ	140	HY	U	-	-	-
24	TR	2017	BQ	3.49	3.69	3.83	0.95	BQ	142	146	146	AHY	U	-	-	-
25	WR	2017	2.78	3.3	3.6	3.68	0.92	127	143	148	148	HY	M	-	-	122
26	TR	2017	2.86	3.37	3.7	3.84	0.91	-	141	145	-	HY	U	-	-	-
27	WR	2017	BQ	BQ	3.45	3.58	-	BQ	BQ	143	140	AHY	F	-	-	115.5
28	WR	2017	BQ	BQ	3.41	3.66	-	BQ	BQ	147	146	AHY	F	-	-	128
29	TR	2017	2.8	3.39	3.51	3.6	0.97	115	140	148	147	AHY	U	-	-	-
30	TR	2017	2.75	3.35	3.57	3.7	0.94	112	149	151	154	AHY	U	-	-	-

31	TR	2017	2.88	3.31	3.50	3.69	0.95	114	134	136	139	AHY	U	-	-	-
32	TR	2017	2.7	3.18	3.53	3.55	0.90	118	134	138	138	HY	U	-	-	-
35	TR	2017	2.8	3.10	3.45	3.6	0.90	119	136	139	140	HY	U	-	-	-
36	WR	2017	2.96	3.55	3.82	3.86	0.93	123	148	151	150	AHY	M	-	-	131
37	WR	2017	BQ	3.26	3.48	3.52	0.94	BQ	145	148	14.8	AHY	M	-	-	122.5
38	WR	2017	2.72	3.14	3.55	3.63	0.88	119	140	141	142	HY	F	-	-	120
39	WR	2017	2.87	3.32	3.73	3.82	0.89	119	143	138	148	HY	M	-	-	125.5
40	WR	2017	BQ	3.47	3.54	3.73	0.98	BQ	145	148	149	AHY	F	-	-	134
41	WR	2017	BQ	BQ	3.58	3.65	-	BQ	BQ	142	142	AHY	F	-	-	108.5
42	WR	2017	BQ	BQ	3.6	3.7	-	BQ	BQ	-	145	AHY	F	-	-	131
43	WR	2017	BQ	BQ	3.72	3.86	-	BQ	BQ	149	149	AHY	M	-	-	129.5
44	WR	2017	2.93	3.42	3.71	3.79	0.92	129	143	149	150	HY	U	-	-	-
45	WR	2017	BQ	3.5	3.71	3.85	0.94	BQ	143	147	147	AHY	M	-	-	132.5
46	WR	2017	BQ	BQ	3.66	3.65	-	BQ	BQ	146	144	AHY	U	-	-	-
47	WR	2017	BQ	BQ	3.52	3.55	-	BQ	BQ	142	143	AHY	U	-	-	-
48	WR	2017	BQ	BQ	3.63	3.67	-	BQ	BQ	142	142	AHY	M	-	-	120
49	WR	2017	2.77	3.24	3.6	3.7	0.90	117	147	151	-	HY	F	-	-	107.5
50	WR	2017	2.85	3.3	3.64	3.66	0.91	124	-	142	146	HY	M	-	-	125
51	WR	2017	2.94	3.35	3.88	3.91	0.86	123	139	141	141	HY	M	-	-	112.5
52	WR	2017	2.91	3.4	3.7	3.9	0.92	124	148	149	146	AHY	M	-	-	128.5
53	WR	2017	2.76	3.19	3.51	3.52	0.91	124	137	142	-	HY	F	-	-	129
54	WR	2017	BQ	3.55	3.71	3.8	0.96	BQ	151	148	-	AHY	M	-	-	138.5
55	WR	2017	2.9	3.32	3.7	3.69	0.90	120	136	141	-	HY	M	-	-	-
56	WR	2017	2.78	3.26	3.55	3.65	0.92	121	136	141	140	HY	F	-	-	124.5
58	WR	2017	2.88	-	3.76	3.76	-	123	-	141	143	U	M	-	-	132
59	WR	2017	BQ	BQ	3.5	3.59	-	BQ	BQ	145	143	AHY	F	-	-	126
60	WR	2017	2.76	3.07	3.46	3.53	0.89	123	138	140	139	HY	F	-	-	123
61	WR	2017	BQ	3.46	3.69	3.67	0.94	BQ	143	146	145	AHY	F	-	-	129.5
62	WR	2017	2.68	3.1	3.4	3.5	0.91	124	-	141	144	HY	F	-	-	128.5
63	WR	2017	2.79	3.3	3.62	3.73	0.91	125	138	142	143	HY	F	-	-	118

64	WR	2017	2.87	3.37	3.65	3.69	0.92	127	141	148	147	HY	M	-	-	125.5
65	WR	2017	-	3.49	3.66	-	0.95	-	141	146	-	AHY	M	-	-	126.5
66	WR	2017	2.96	3.4	3.9	3.89	0.87	122	138	144	144	HY	M	-	-	133.5
67	WR	2017	BQ	BQ	3.53	3.67	-	BQ	BQ	142	142	AHY	F	-	-	128.5
68	TR	2017	2.8	3.45	3.75	3.83	0.92	122	149	150	148	AHY	U	-	-	-
69	TR	2017	2.61	3.32	3.61	3.69	0.92	114	142	144	145	AHY	U	-	-	-
70	TR	2017	2.88	3.27	3.65	3.71	0.90	124	137	144	142	HY	U	-	-	-
71	TR	2017	BQ	-	3.36	3.62	-	BQ	135	148	-	AHY	U	-	-	-
72	TR	2017	BQ	3.25	3.43	3.47	0.95	BQ	-	143	-	AHY	U	-	-	-
96	TR	2017	2.82	3.27	3.52	3.69	0.93	114	139	144	145	AHY	U	-	-	-
97	TR	2017	2.9	3.27	3.43	3.58	0.95	120	147	150	150	AHY	U	-	-	-
98	TR	2017	2.84	3.24	3.71	3.72	0.87	128	144	147	149	HY	U	-	-	-
99	WR	2017	2.7	3.2	BQ	3.59	-	116	136	BQ	143	HY	F	-	-	128
100	WR	2017	3	3.37	3.81	3.81	0.88	133	151	152	151	HY	M	-	-	134
101	WR	2017	2.87	3.33	3.66	3.57	0.91	125	141	146	147	HY	M	-	-	130.5
102	WR	2017	BQ	BQ	3.76	3.65	-	BQ	BQ	146	149	AHY	M	-	-	126
103	WR	2017	2.9	3.4	3.51	3.71	0.97	123	145	147	146	AHY	U	-	-	131
104	WR	2017	2.61	3.16	3.47	3.5	0.91	120	135	142	142	HY	U	-	-	-
105	WR	2017	BQ	3.56	3.77	3.86	0.94	BQ	141	145	145	AHY	M	-	-	128.5
152	TR	2018	BQ	BQ	3.77	3.88	-	BQ	BQ	146	146	AHY	U	-	-	-
153	TR	2018	BQ	BQ	3.75	3.96	-	BQ	BQ	148	148	AHY	U	-	-	-
154	TR	2018	BQ	BQ	3.7	3.74	-	BQ	BQ	147	145	AHY	U	-	-	-
155	TR	2018	BQ	BQ	3.88	3.91	-	BQ	BQ	145	144	AHY	U	-	-	-
156	TR	2018	2.79	3.37	BQ	3.88	-	121	141	BQ	146	HY	U	-	-	-
159	TR	2018	BQ	BQ	3.57	3.74	-	BQ	BQ	151	151	AHY	U	-	-	-
160	TR	2018	2.72	3.17	3.52	3.52	0.90	127	144	147	147	HY	U	-	-	-
16	TR	2018	BQ	BQ	3.69	3.8	-	BQ	BQ	148	146	AHY	U	-	-	-
164	TR	2018	2.94	3.29	3.76	-	0.88	126	144	149	-	U	U	-	-	-
201	TR	2018	BQ	BQ	3.77	3.89	-	BQ	BQ	147	149	AHY	U	-	-	-
202	TR	2018	2.71	3.16	BQ	3.63	-	122	141	BQ	141	HY	U	-	-	-

203	TR	2018	BQ	BQ	3.7	3.82	-	BQ	BQ	146	147	AHY	U	-	-	-
204	TR	2018	BQ	BQ	3.49	3.51	-	BQ	BQ	142	142	AHY	U	-	-	-
205	TR	2018	2.66	3.1	3.5	3.53	0.89	119	135	142	139	HY	U	-	-	-
206	TR	2018	2.81	3.37	BQ	BQ	-	129	147	BQ	BQ	HY	U	-	-	-
207	TR	2018	BQ	BQ	BQ	3.7	-	BQ	BQ	BQ	147	AHY	U	-	-	-
208	TR	2018	BQ	BQ	3.61	3.73	-	BQ	BQ	143	144	AHY	U	-	-	-
209	TR	2018	BQ	BQ	3.8	3.8	-	BQ	BQ	149	147	AHY	U	-	-	-

Missing data were the result of broken or missing feathers. Feathers in blood quill were not measured.

BQ = Feather in blood quill, i.e. still growing

AHY = After-hatching-year (adult)

HY = Hatching-year (juvenile)

U = Unknown

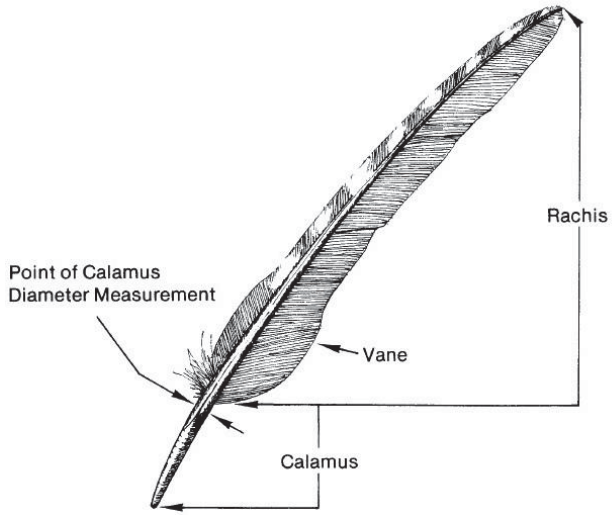
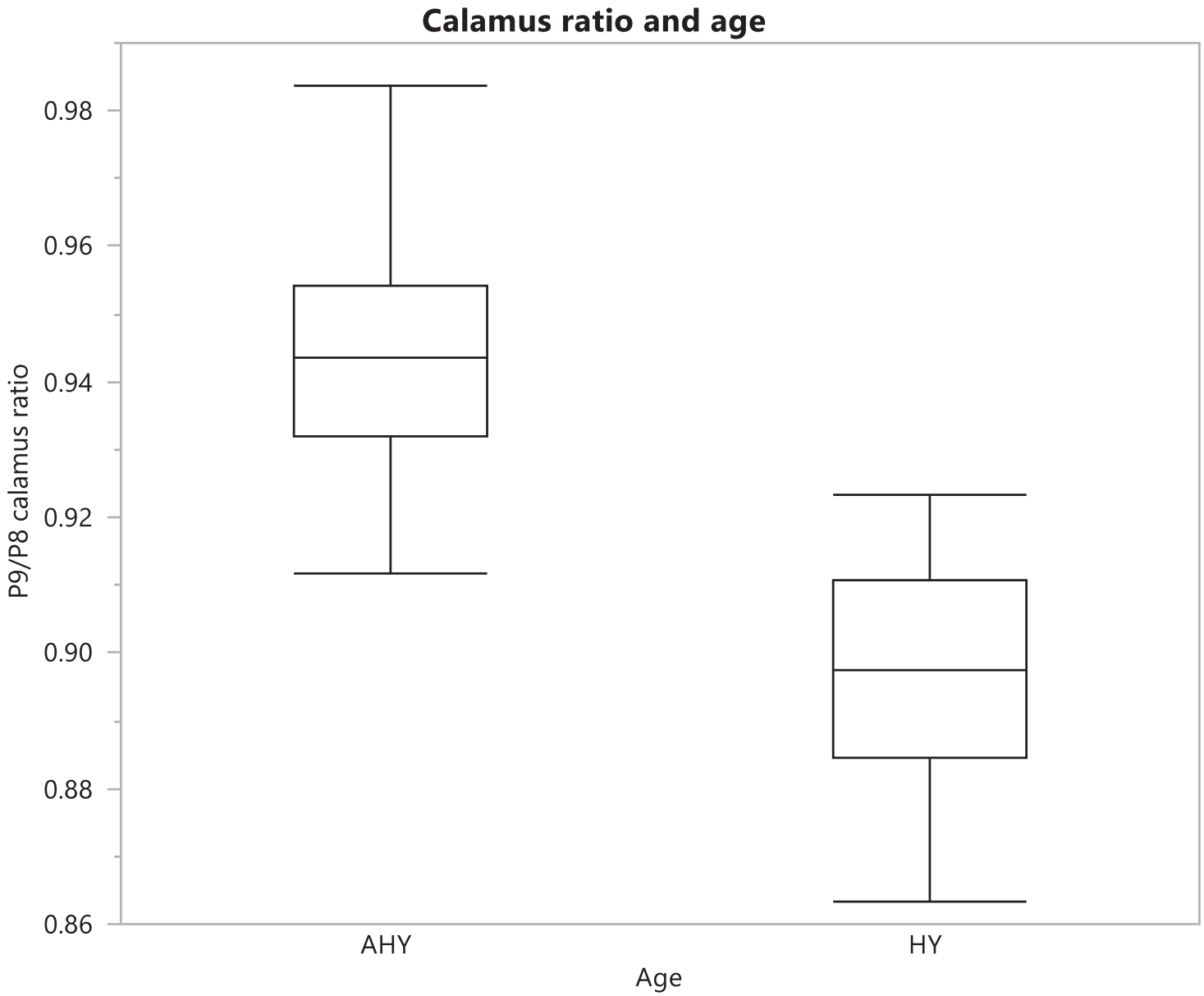


Diagram of feather measurement points, from Caldwell (1980)


Calamus ratio and age
P9/P8 calamus ratio
0.98
0.96
0.94
0.92
0.90
0.88
0.86
AHY
HY
Age

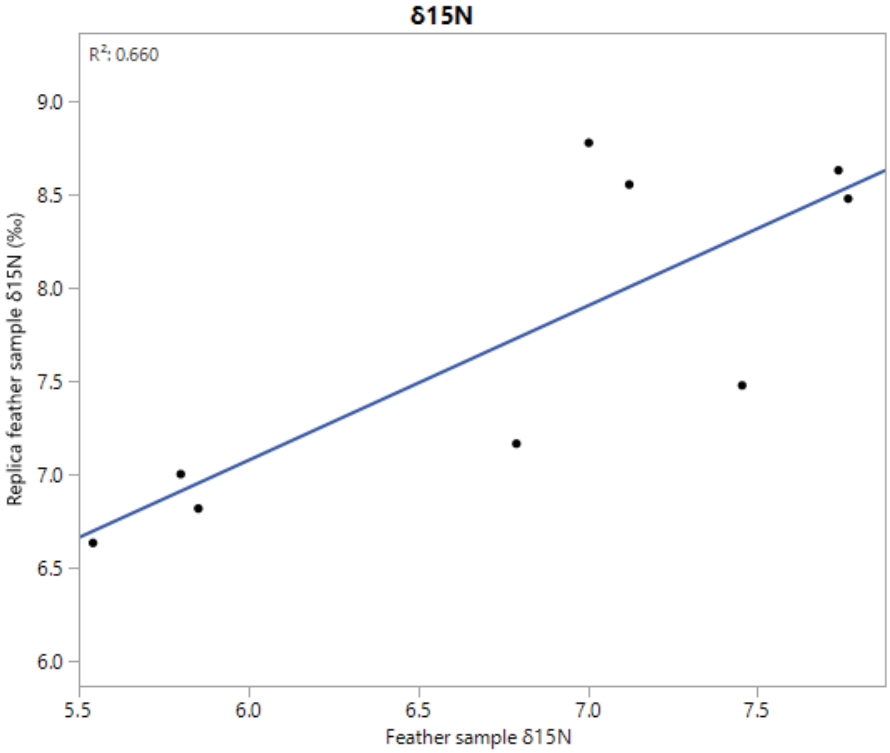
APPENDIX 3.1: RESAMPLING REPLICATE FEATHER SAMPLES

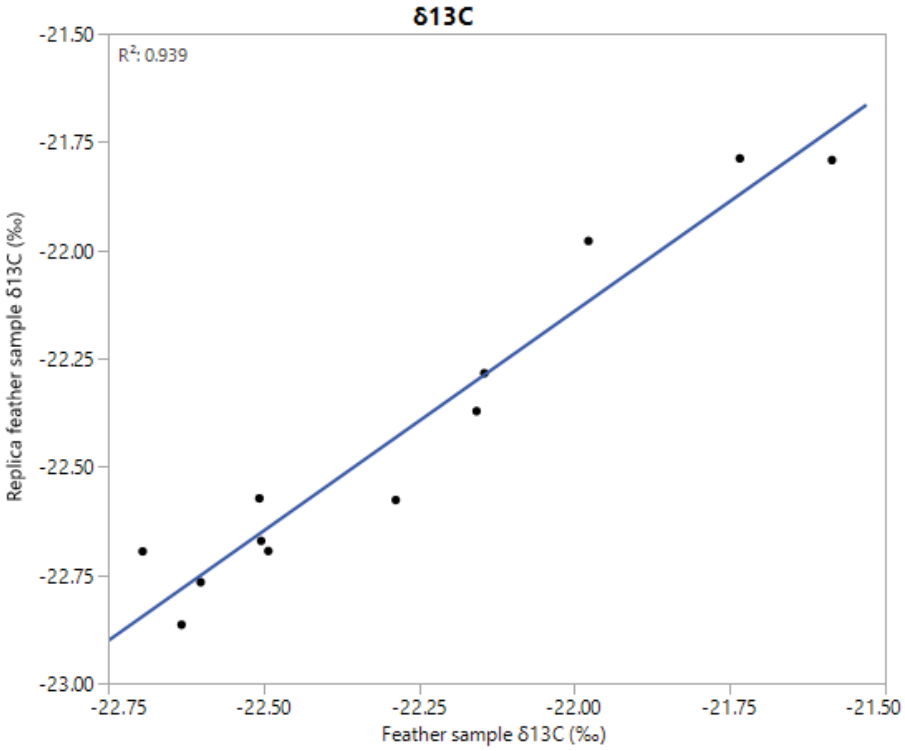
Taken from three adult female grouse.

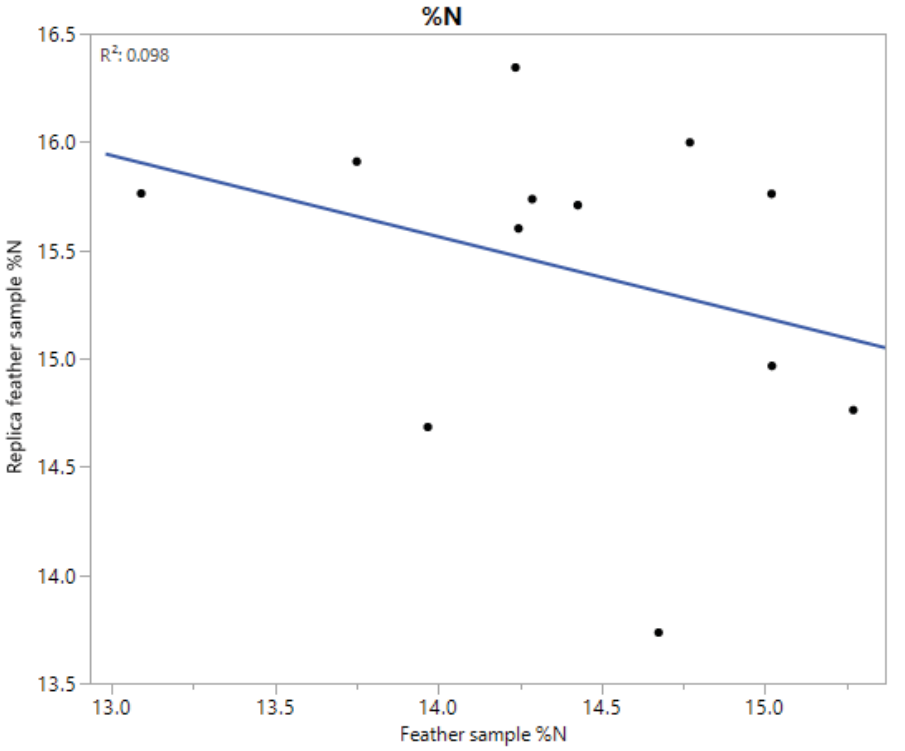
Average difference		R^2
$\delta^{15}N$	0.94 ‰	0.660
$\delta^{13}C$	0.14 ‰	0.939
%N	1.27 %	0.098
%C	2.78 %	0.013

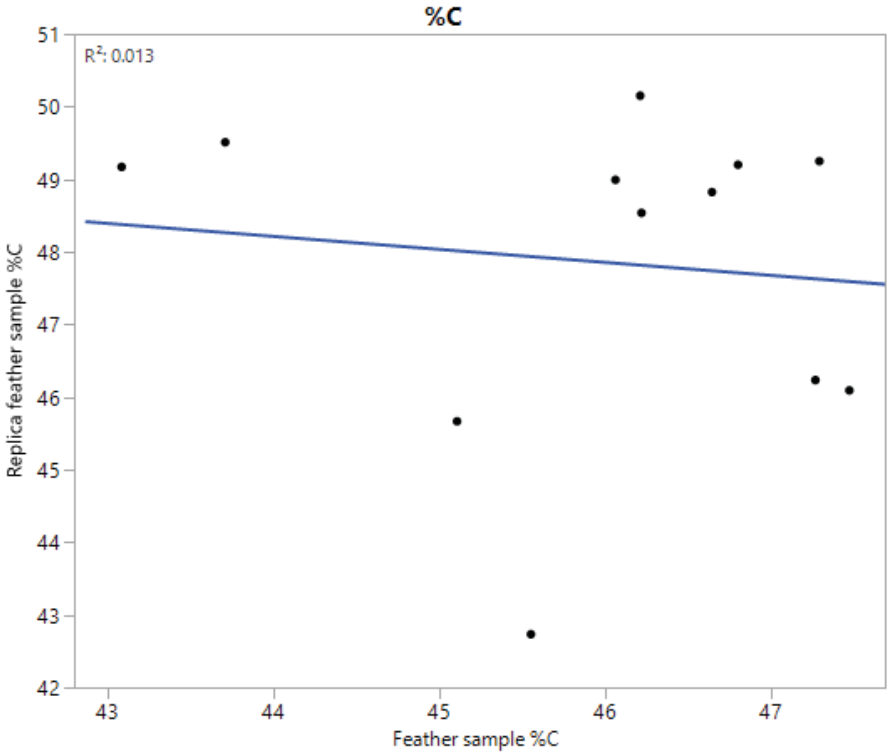
Isotope measurements plotted against replica sample values (n = 12*):

*3 sample were missing $\delta^{15}N$ measurements




δ13C
R²: 0.939
Replica feather sample δ13C (‰)
Feather sample δ13C (‰)
-21.50
-21.75
-22.00
-22.25
-22.50
-22.75
-23.00
-22.75
-22.50
-22.25
-22.00
-21.75
-21.50

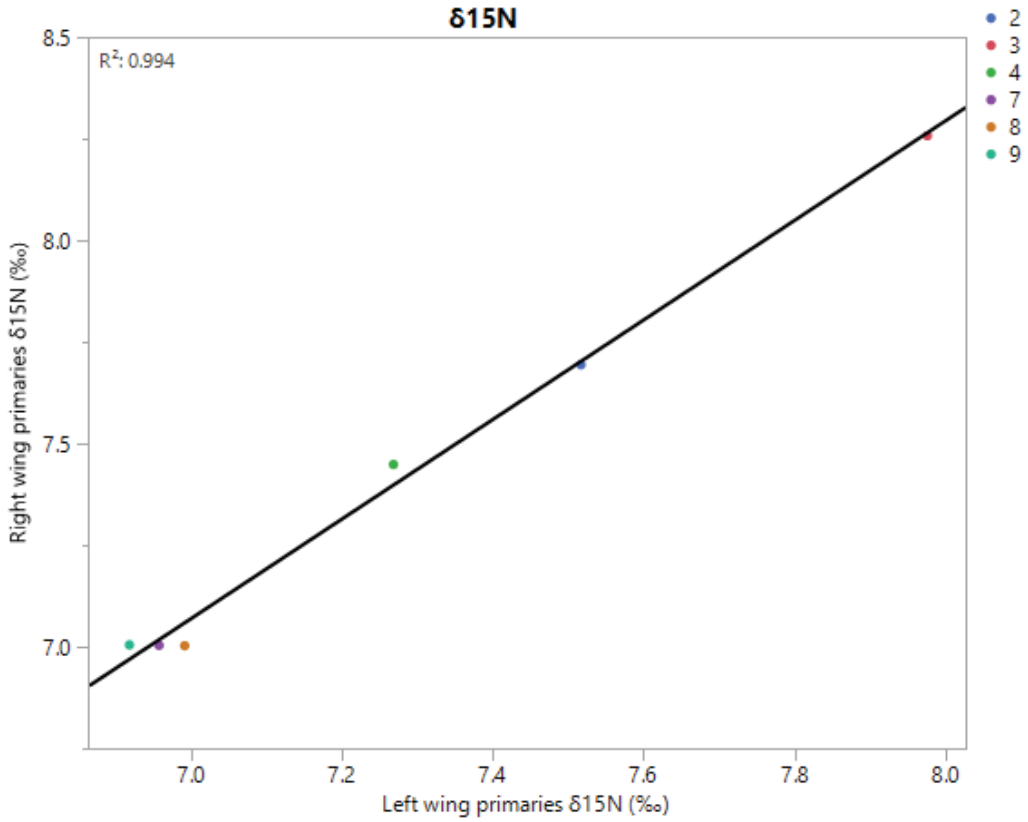

%N
R²: 0.098
Replica feather sample %N
Feather sample %N
16.5
16.0
15.5
15.0
14.5
14.0
13.5
13.0
13.5
14.0
14.5
15.0

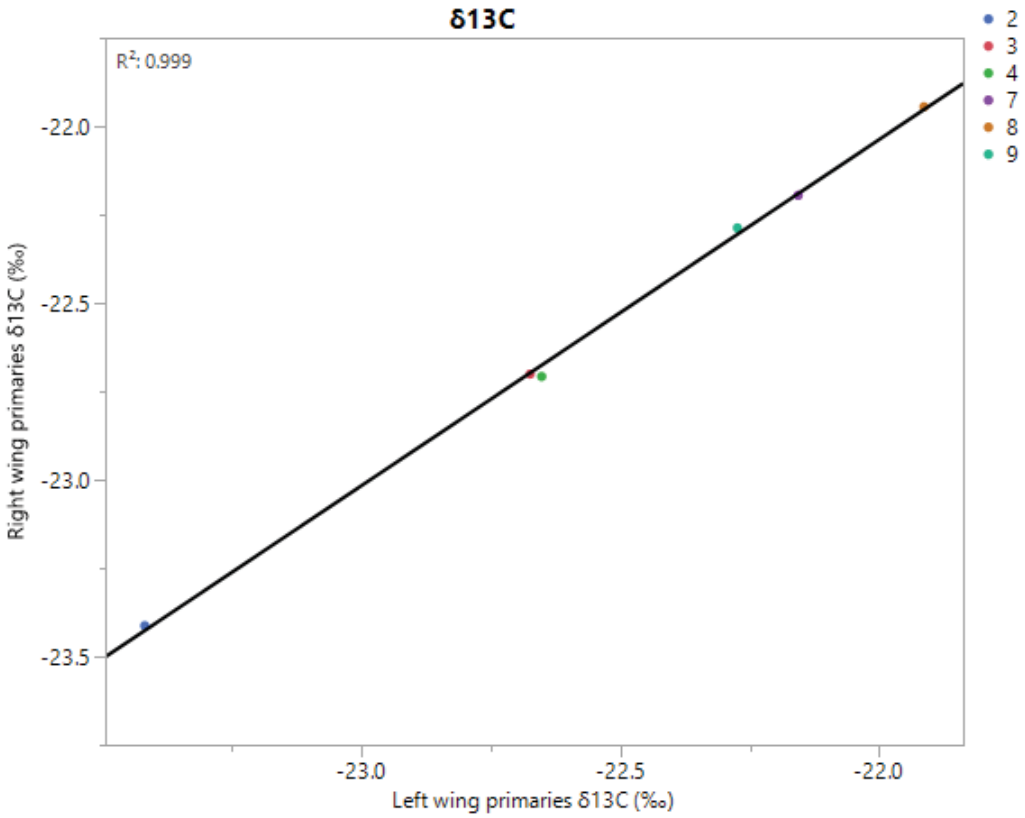

%C
R²: 0.013
Replica feather sample %C
Feather sample %C
51
50
49
48
47
46
45
44
43
42
43
44
45
46
47

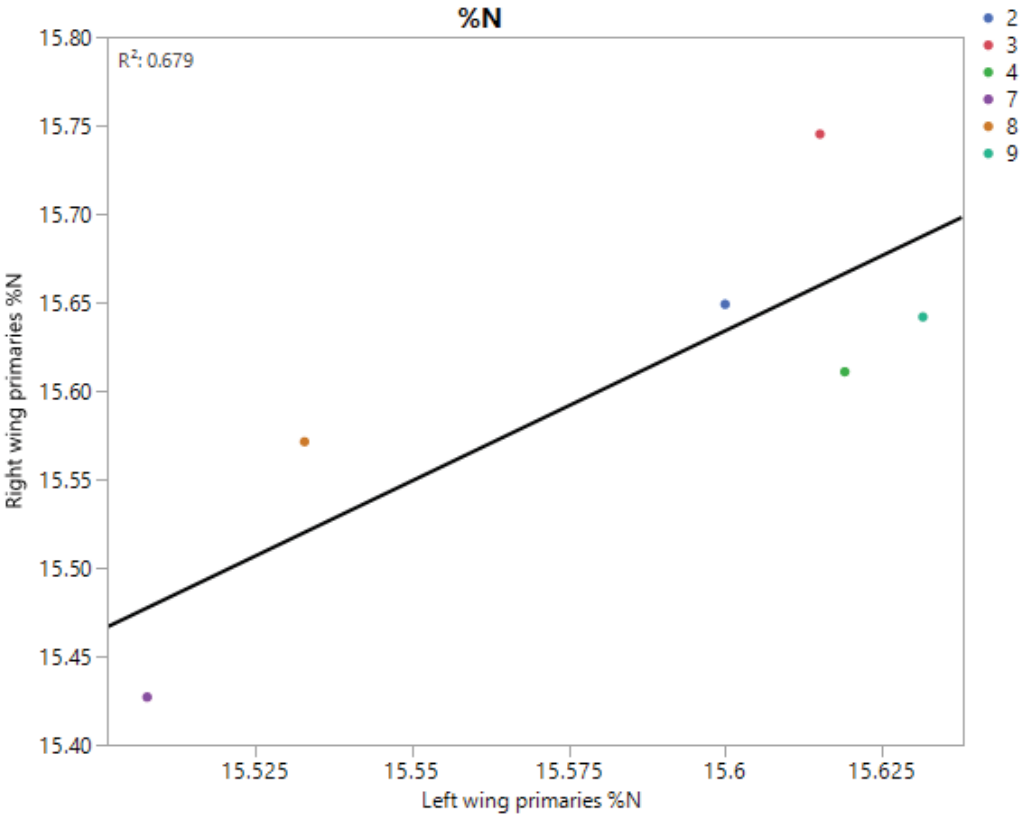
APPENDIX 3.2: OPPOSITE WING REPLICATE FEATHER SAMPLES

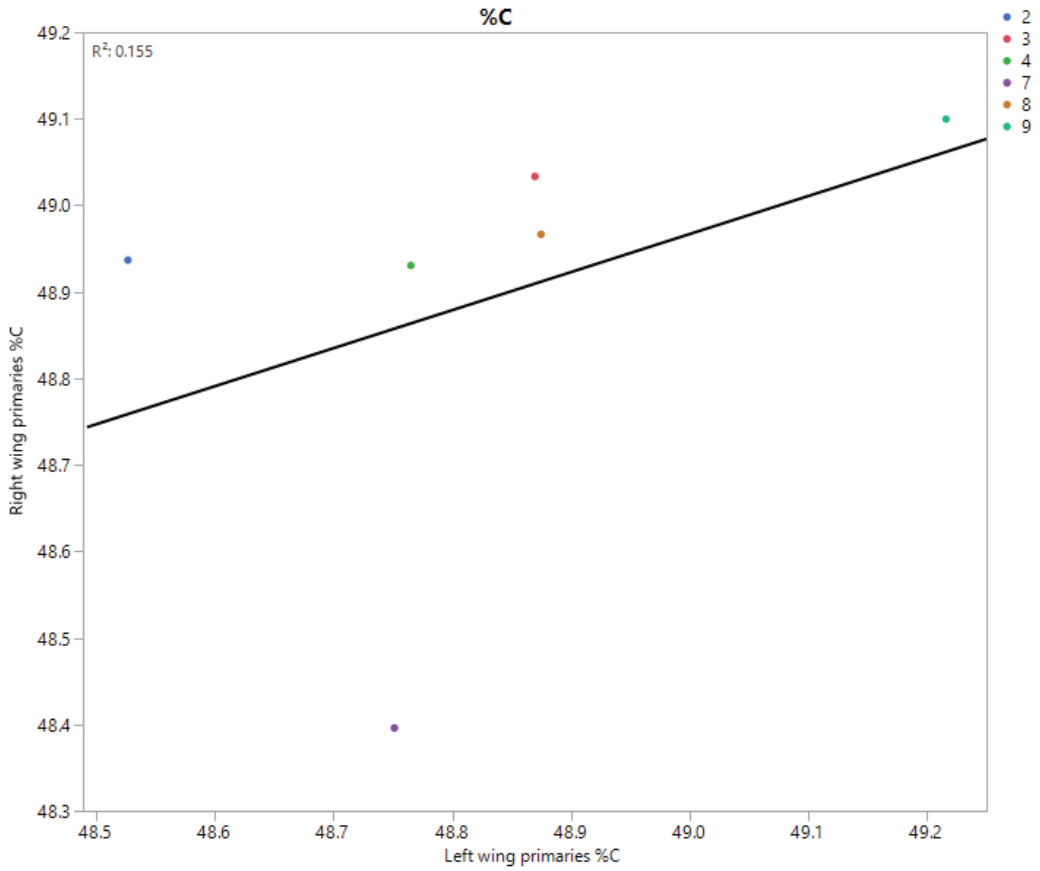
	Average difference	R^2
$\delta^{15}N$	0.13 ‰	0.994
$\delta^{13}C$	0.03 ‰	0.999
%N	5.28 %	0.679
%C	21.72 %	0.155

Isotope measurements plotted against values from same primary of opposite wing:




δ13C
R²: 0.999
-22.0
-22.5
-23.0
-23.5
Right wing primaries δ13C (‰)
-23.0
-22.5
-22.0
Left wing primaries δ13C (‰)
2
3
4
7
8
9

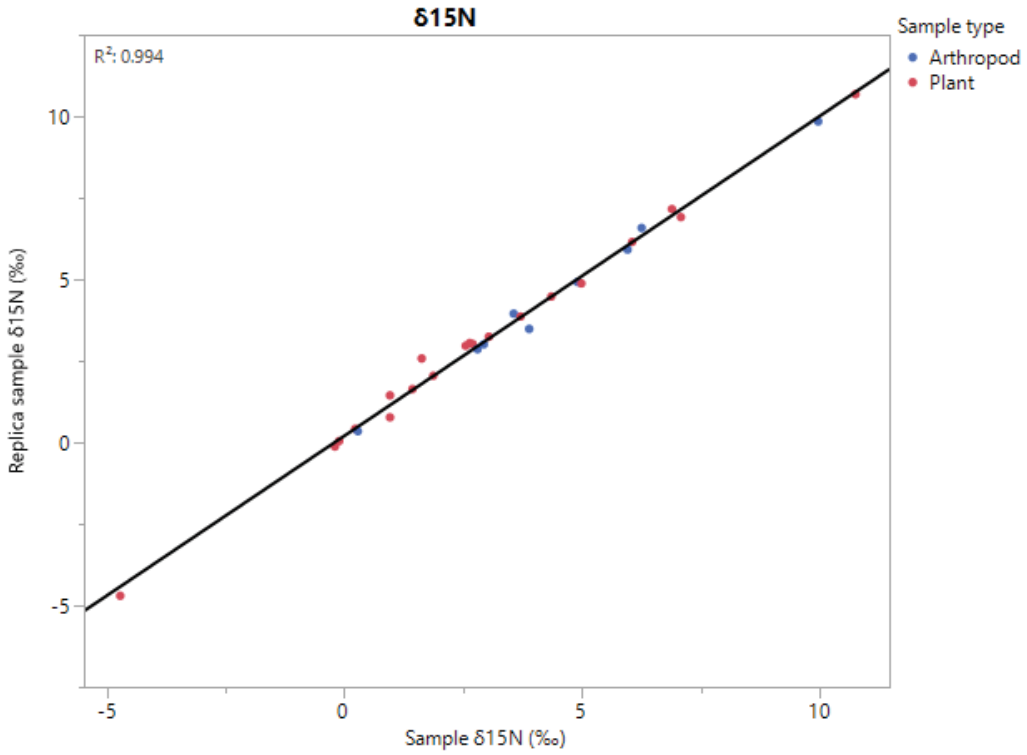

%N
R²: 0.679
15.80
15.75
15.70
15.65
15.60
15.55
15.50
15.45
15.40
Right wing primaries %N
15.525
15.55
15.575
15.6
15.625
Left wing primaries %N
2
3
4
7
8
9

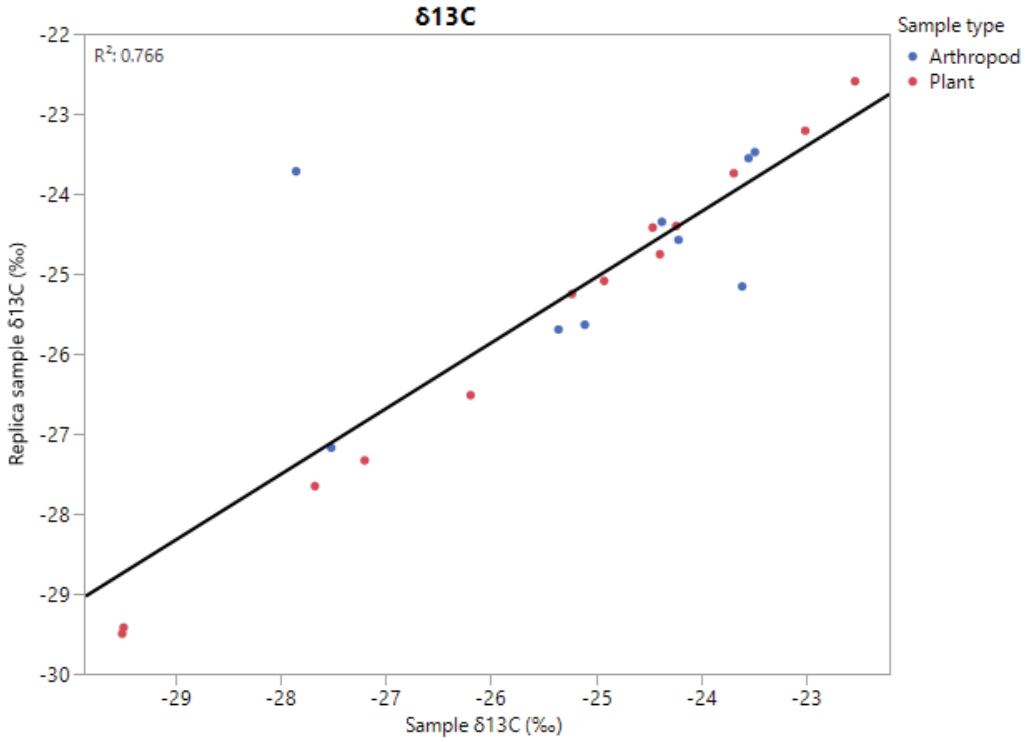

%C
R²: 0.155
Right wing primaries %C
Left wing primaries %C
49.2
49.1
49.0
48.9
48.8
48.7
48.6
48.5
48.4
48.3
48.5
48.6
48.7
48.8
48.9
49.0
49.1
49.2
2
3
4
7
8
9

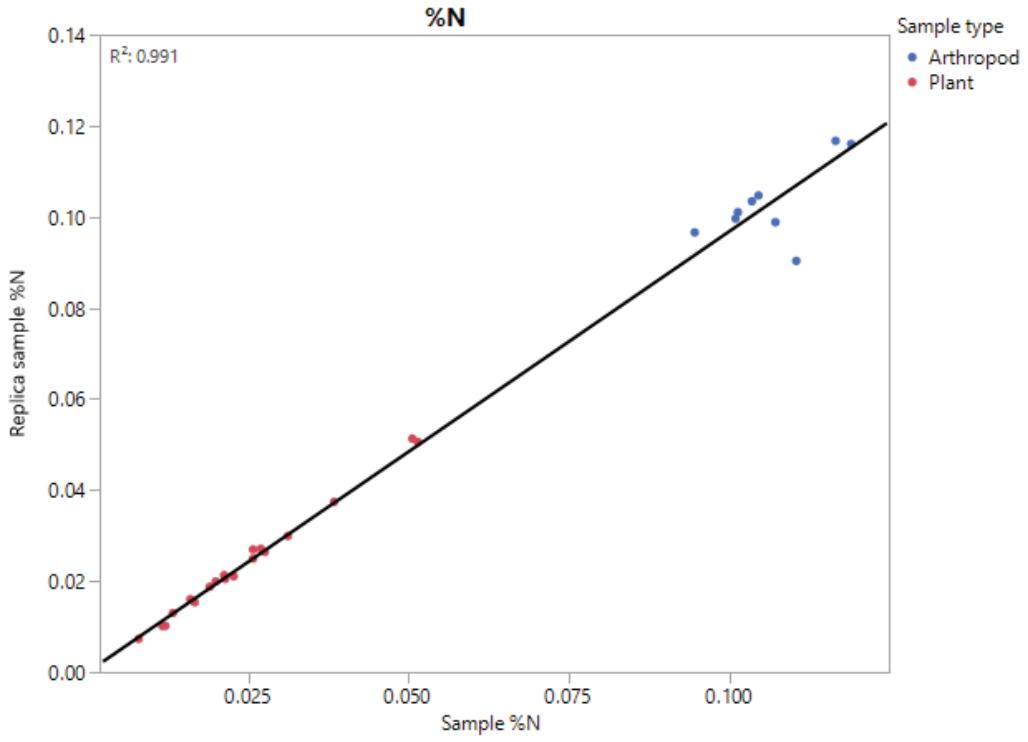
APPENDIX 3.3: RESAMPLING REPLICATE PLANT AND ARTHROPOD SAMPLES

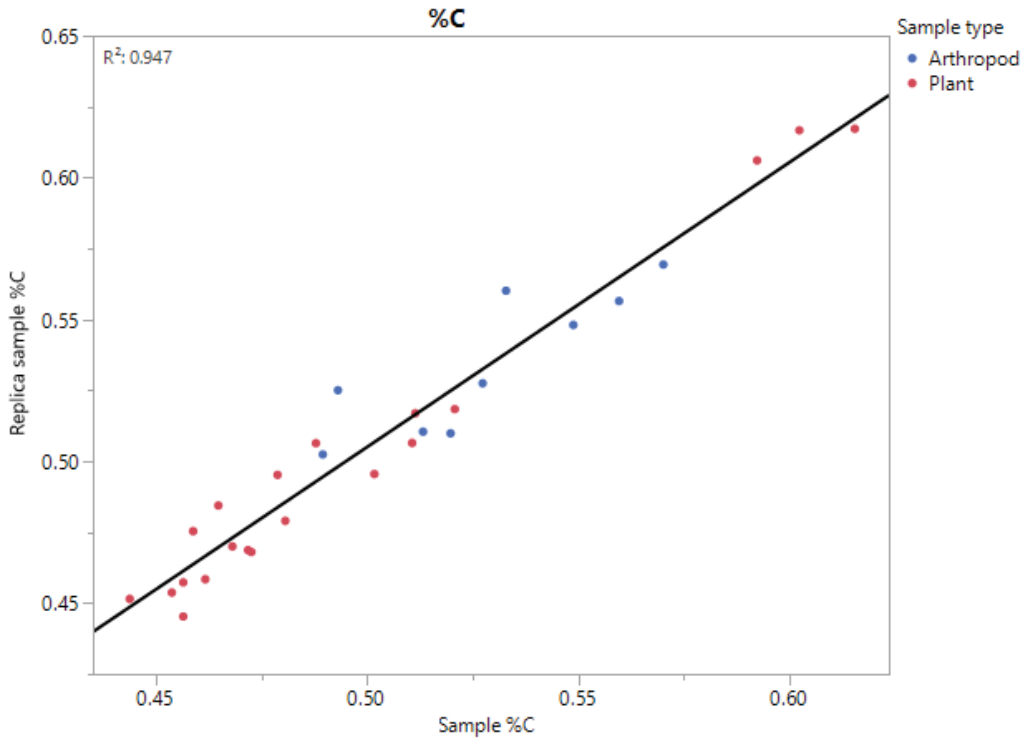
Average difference

	Arthropods	Plants	R^2 (combined)
$\delta^{15}N$	0.17 ‰	0.24 ‰	0.994
$\delta^{13}C$	0.81 ‰	0.12 ‰	0.766
%N	0.38 %	0.09 %	0.991
%C	1.00 %	0.81 %	0.947




δ13C
R²: 0.766
Sample type
Arthropod
Plant
Replica sample δ13C (‰)
Sample δ13C (‰)
-22
-23
-24
-25
-26
-27
-28
-29
-30
-29
-28
-27
-26
-25
-24
-23


%N
R²: 0.991
Sample type
Arthropod
Plant
Replica sample %N
Sample %N
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0.025
0.050
0.075
0.100


%C
R²: 0.947
Sample type
Arthropod
Plant
Replica sample %C
Sample %C
0.65
0.60
0.55
0.50
0.45
0.45
0.50
0.55
0.60

APPENDIX 4: ARTHROPOD RELATIVE ABUNDANCE AND RELATIVE BIOMASS

Twin River	May - June (n = 45 transects)				July - August (n = 30 transects)				September - October (n = 21 transects)			
	Number per transect	Biomass per transect (mg)	Rel. ab.	Rel. biomass	Number per transect	Biomass per transect (mg)	Rel. ab.	Rel. biomass	Number per transect	Biomass per transect (mg)	Rel. ab.	Rel. biomass
Araneae	3.0	15	5.7%	3.9%	7.0	34	8.0%	3.7%	3.1	19	12.2%	3.3%
Coleoptera	13.2	234	25.2%	59.7%	5.1	41	5.8%	4.4%	5.2	43	20.1%	7.6%
Coccinellidae	0.3	2	0.6%	0.6%	<0.1	1	<0.1	0.1%	0.3	10	1.3%	1.8%
Curculionidae	1.0	11	2.0%	2.8%	1.1	6	1.3%	0.6%	0.7	2	2.6%	0.3%
Elateridae	0.1	<1	0.1%	0.1%	-	-	-	-	-	-	-	-
Other Coleoptera	11.7	221	22.4%	56.2%	3.9	34	4.5%	3.7%	4.2	31	16.3%	5.5%
Diptera	15.0	23	28.8%	5.9%	12.5	23	14.2%	2.5%	5.1	25	20.0%	4.3%
Ephemeroptera	-	-	-	-	0.1	1	0.1%	0.1%	-	-	-	-
Hemiptera	8.1	39	15.5%	10.0%	51.8	211	58.8%	23.2%	8.5	83	32.9%	14.6%
Auchenorrhyncha	7.8	29	14.9%	7.5%	30.8	85	35.0%	9.4%	3.3	12	12.9%	2.1%
Sternorrhyncha					0.1	<1	0.2%	<0.1%	0.0	0	0.2%	<0.1%
Heteroptera	0.3	9	0.6%	2.5%	20.9	126	23.7%	13.8%	5.1	71	19.8%	12.5%
Hymenoptera	8.9	17	17.0%	4.3%	3.4	9	3.9%	0.9%	1.1	5	4.4%	0.8%

Formicidae	3.0	3	5.7%	0.8%	0.7	1	0.8%	0.1%	0.5	1	1.8%	0.1%
Other Hymenoptera	5.9	14	11.3%	3.5%	2.8	7	3.1%	0.8%	0.7	4	2.6%	0.7%
Ixodidae	<0.1	<1	<0.1%	<0.1%	-	-	-	-	-	-	-	-
Lepidoptera	3.1	16	6.0%	4.0%	2.3	53	2.7%	5.8%	0.4	4	1.5%	0.8%
Lepidoptera adults	2.7	8	5.1%	2.1%	1.9	20	2.1%	2.2%	0.3	3	1.1%	0.6%
Lepidoptera larvae <2cm	0.4	6	0.9%	1.4%	0.4	10	0.5%	1.1%	0.1	1	0.4%	0.2%
Lepidoptera larvae >2cm	<0.1	2	<0.1%	0.4%	0.1	23	0.1%	2.5%	-	-	-	-
Neuroptera total	-	-	-	-	<0.1	1	<0.1%	0.1%	-	-	-	-
Odonata	0.1	1	0.1%	0.4%	0.2	6	0.3%	0.6%	-	-	-	-
Opiliones	-	-	-	-	<0.1	<1	<0.1%	<0.1%	-	-	-	-
Orthoptera	0.9	46	1.7%	11.7%	5.5	535	6.2%	58.6%	2.3	392	8.9%	68.5%
Acrididae	0.9	46	1.7%	11.7%	3.5	503	4.0%	55.1%	2.0	379	7.8%	66.2%
Gryllidae	-	-	-	-	1.9	32	2.2%	3.5%	0.2	10	0.9%	1.8%
Tettigoniidae	-	-	-	-	-	-	-	-	0.0	3	0.2%	0.5%
Total	**52.3**	**392**	**100%**	**100%**	**88.0**	**912**	**100%**	**100%**	**25.8**	**572**	**100%**	**100%**

Wild Rose	May - June (n = 51 transects)				July - August (n = 35 transects)				September - October (n = 40 transects)			
	Number per transect	Biomass per transect (mg)	Rel. ab.	Rel. biomass	Number per transect	Biomass per transect (mg)	Rel. ab.	Rel. biomass	Number per transect	Biomass per transect (mg)	Rel. ab.	Rel. biomass
Araneae	5.9	37	19.0%	24.4%	9.4	27	11.2%	2.2%	0.8	6	6.6%	2.6%
Coleoptera	5.5	23	17.7%	15.1%	1.3	3	1.5%	0.3%	0.3	4	2.3%	1.5%
Chrysomelidae	<0.1	<1	0.1%	0.1%	-	-	-	-	0.1	3	0.9%	1.3%
Coccinellidae	0.6	9	2.0%	5.8%	<0.1	<1	<0.1%	<0.1%	0.1	0	0.5%	0.1%
Curculionidae	2.7	4	8.5%	2.7%	0.7	2	0.8%	0.2%	-	-	-	-
Elateridae	0.4	3	1.3%	1.9%	-	-	-	-	-	-	-	-
Other Coleoptera	1.8	7	5.8%	4.6%	0.6	1	0.7%	0.1%	0.1	<1	0.9%	0.2%
Diptera	6.3	10	20.1%	6.8%	8.6	25	10.3%	2.1%	5.1	16	41.8%	6.5%
Hemiptera	4.9	18	15.6%	11.9%	55.5	883	66.4%	72.3%	4.1	48	33.9%	19.2%
Auchenorrhyncha	4.4	3	14.0%	2.3%	46.0	132	55.0%	10.8%	1.2	24	10.2%	9.7%
Sternorrhyncha					0.9	1	1.0%	0.1%	2.8	24	23.0%	9.5%
Heteroptera	0.5	14	1.6%	9.6%	8.7	750	10.4%	61.4%	0.1	<1	0.7%	0.0%
Hymenoptera	6.6	23	21.2%	15.1%	3.7	7	4.4%	0.6%	0.3	2	2.9%	0.7%
Formicidae	2.4	3	7.5%	1.9%	1.0	1	1.2%	0.0%	<0.1	<1	0.4%	<0.1%
Other Hymenoptera	4.3	20	13.7%	13.2%	2.6	7	3.1%	0.6%	0.3	2	2.5%	0.7%

Ixodidae	<0.1	<1	0.1%	<0.1%	-	-	-	-	-	-	-	-
Lepidoptera	1.7	29	5.5%	19.3%	1.3	23	1.6%	1.8%	0.1	3	1.1%	1.4%
Lepidoptera adults	0.5	6	1.6%	4.2%	0.7	9	0.9%	0.7%	0.1	1	0.5%	0.5%
Lepidoptera larvae <2cm	1.2	23	3.8%	15.1%	0.5	11	0.6%	0.9%	0.1	2	0.5%	0.9%
Lepidoptera larvae >2cm	-	-	-	-	<0.1	3	0.0%	0.2%	-	-	-	-
Odonata	<0.1	<1	0.1%	0.3%	0.1	3	0.2%	0.2%	-	-	-	-
Opiliones	-	-	-	-	<0.1	1	<0.1%	0.1%	-	-	-	-
Orthoptera	0.2	11	0.6%	7.1%	3.7	249	4.4%	20.4%	1.4	170	11.5%	68.1%
Acrididae	0.2	11	0.6%	7.1%	1.2	195	1.5%	15.9%	1.2	161	9.9%	64.4%
Gryllidae	-	-	-	-	2.5	55	3.0%	4.5%	0.2	9	1.6%	3.7%
Tettigoniidae	-	-	-	-	-	-	-	-	-	-	-	-
Total	**31.2**	**150**	**100%**	**100%**	**83.5**	**1221**	**100%**	**100%**	**12.2**	**250**	**100%**	**100%**

APPENDIX 5.1: ISOTOPE VALUES AND ELEMENTAL CONCENTRATIONS FOR SAMPLED ARTHROPODS

n = 136

[1] Sites: WR = Wild Rose; TR = Twin River Heritage Rangeland Natural Area. Seasons defined as spring (Spr) = May - June; summer (Sum) = July - August; Fall = September - October

[2] Lipid correction calculated from experimentally derived formula (Appendix F)

[3] Protein content calculated using *k*p: 4.76 from Janssen et al. (2017)

Scientific name	Common name	Order	Site/Season[1]	n	%N	%C	C:N	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{13}C$ corrected[2] (‰)	Protein (%)[3]
Philodromidae	Running crab spider	Araneae	TR Fall	8	11.91	52.28	4.39	7.40	-24.63	-23.76	56.7
Thomisidae	Crab spider	Araneae	TR Fall	15	11.78	53.49	4.54	8.10	-24.50	-23.58	56.1
Thomisidae	Crab spider	Araneae	TR Spr	5	13.48	50.71	3.76	8.15	-24.73	-24.09	64.2
Salticidae	Jumping spider	Araneae	TR Spr	1	12.87	47.68	3.71	6.92	-24.24	-23.62	61.2
Philodromidae	Running crab spider	Araneae	TR Spr	1	12.76	49.82	3.91	6.95	-24.92	-24.22	60.7
Araneidae	Orb weaver	Araneae	TR Spr	1	12.72	49.53	3.89	6.22	-23.94	-23.25	60.6
Pisauridae	Nursery web spider	Araneae	TR Spr	4	12.31	47.88	3.89	7.60	-24.80	-24.12	58.6
Salticidae	Jumping spider	Araneae	TR Sum	4	12.59	49.82	3.96	6.34	-24.96	-24.25	59.9
Thomisidae	Crab spider	Araneae	TR Sum	27	12.35	52.97	4.29	6.78	-24.57	-23.74	58.8
Philodromidae	Running crab spider	Araneae	TR Sum	4	11.66	51.18	4.39	6.41	-24.40	-23.53	55.5
Araneidae	Orb weaver	Araneae	TR Sum	1	11.00	52.93	4.81	6.00	-26.04	-25.02	52.4
Pisauridae	Nursery web spider	Araneae	TR Sum	2	10.93	53.10	4.86	7.49	-24.77	-23.73	52.0
Araneidae	Orb weaver	Araneae	WR Fall	1	12.84	44.93	3.50	7.04	-26.11	-25.56	61.1
Salticidae	Jumping spider	Araneae	WR Fall	1	12.55	49.99	3.98	6.55	-24.12	-23.40	59.7
Pisauridae	Nursery web spider	Araneae	WR Fall	2	12.49	50.42	4.04	6.49	-24.84	-24.10	59.5
Thomisidae	Crab spider	Araneae	WR Fall	9	11.08	52.98	4.78	7.60	-24.65	-23.64	52.7

Philodromidae	Running crab spider	Araneae	WR Fall	3	10.51	55.62	5.29	7.75	-24.78	-23.58	50.0
Thomisidae	Crab spider	Araneae	WR Spr	30	13.65	49.96	3.66	7.55	-24.40	-23.80	65.0
Gnaphosidae	Ground spider	Araneae	WR Spr	3	12.31	48.53	3.94	7.75	-24.52	-23.82	58.6
Tetragnathidae	Long-jawed orb weaver	Araneae	WR Spr	8	12.26	47.74	3.90	6.52	-25.03	-24.34	58.3
Philodromidae	Running crab spider	Araneae	WR Spr	3	12.18	47.96	3.94	7.65	-24.06	-23.36	58.0
Araneidae	Orb weaver	Araneae	WR Spr	3	12.18	44.96	3.69	5.82	-25.11	-24.49	58.0
Salticidae	Jumping spider	Araneae	WR Spr	10	12.09	50.68	4.19	6.78	-24.89	-24.09	57.6
Tetragnathidae	Long-jawed orb weaver	Araneae	WR Sum	1	13.40	44.99	3.36	8.12	-24.32	-23.83	63.8
Thomisidae	Crab spider	Araneae	WR Sum	29	12.51	51.06	4.08	6.36	-24.50	-23.74	59.5
Pisauridae	Nursery web spider	Araneae	WR Sum	6	12.38	51.21	4.14	6.52	-25.31	-24.53	58.9
Araneidae	Orb weaver	Araneae	WR Sum	7	12.37	50.50	4.08	7.06	-25.02	-24.26	58.9
Gnaphosidae	Ground spider	Araneae	WR Sum	1	12.09	39.57	3.27	9.63	-25.10	-24.63	57.5
Salticidae	Jumping spider	Araneae	WR Sum	20	11.96	52.19	4.36	6.08	-24.77	-23.91	56.9
Chrysomelidae	Leaf beetle	Coleoptera	TR Fall	62	8.95	54.92	6.14	5.72	-27.86	-26.35	42.6
Coccinella septempunctata	Seven-spot ladybird	Coleoptera	TR Fall	5	8.35	60.87	7.29	11.25	-25.65	-23.73	39.7
Elateridae	Click beetle	Coleoptera	TR Spr	1	11.86	50.38	4.25	6.83	-26.08	-25.27	56.5
Dichelonyx backi	Green rose chafer	Coleoptera	TR Spr	50	11.75	51.48	4.38	5.93	-25.37	-24.50	55.9
Coleoptera herbivores	Herbivorous beetles	Coleoptera	TR Spr	18	11.14	51.67	4.64	5.93	-26.02	-25.06	53.0
Curculionoidea	Weevil	Coleoptera	TR Spr	18	10.72	53.20	4.96	5.89	-25.80	-24.72	51.0
Trirhabda canadensis	Goldenrod leaf beetle	Coleoptera	TR Sum	12	10.22	52.84	5.17	2.19	-27.32	-26.17	48.6
Necrophorus	Burying beetle	Coleoptera	TR Sum	1	10.03	55.81	5.57	9.90	-27.34	-26.05	47.7
Chrysomelidae	Leaf beetle	Coleoptera	TR Sum	48	9.16	48.31	5.27	7.98	-27.03	-25.84	43.6
Curculionoidea	Weevil	Coleoptera	TR Sum	1	8.43	58.70	6.96	4.82	-28.13	-26.32	40.1
Coccinella septempunctata	Seven-spot ladybird	Coleoptera	WR Fall	4	7.39	62.71	8.49	7.25	-26.32	-23.96	35.2
Elateridae	Click beetle	Coleoptera	WR Spr	14	11.09	52.60	4.74	5.63	-25.64	-24.65	52.8
Curculionoidea	Weevil	Coleoptera	WR Spr	23	10.85	52.93	4.88	5.81	-25.50	-24.45	51.7
Blapstinus	Darkling beetle	Coleoptera	WR Spr	1	9.56	49.59	5.19	3.76	-25.53	-24.37	45.5
Meloidae	Blister beetle	Coleoptera	WR Spr	1	9.00	52.92	5.88	3.31	-23.36	-21.95	42.8
Curculionoidea	Weevil	Coleoptera	WR Sum	5	10.39	53.06	5.11	7.27	-25.60	-24.47	49.5
Blapstinus	Darkling beetle	Coleoptera	WR Sum	1	10.34	51.28	4.96	3.88	-26.12	-25.05	49.2

Meloidae	Blister beetle	Coleoptera	WR Sum	1	10.03	50.91	5.07	3.68	-25.78	-24.67	47.8
Chrysomelidae	Leaf beetle	Coleoptera	WR Sum	11	9.52	49.53	5.20	4.75	-25.14	-23.98	45.3
Coccinella septempunctata	Seven-spot ladybird	Coleoptera	WR/TR Spr	11	9.74	57.94	5.95	6.61	-25.74	-24.31	46.4
Asilidae	Robber fly	Diptera	TR Spr	1	12.20	51.31	4.21	9.00	-24.85	-24.05	58.1
Culicidae	Mosquito	Diptera	TR Spr	4	11.40	49.22	4.32	3.90	-28.80	-27.96	54.3
Asilidae	Robber fly	Diptera	WR Sum	5	12.57	51.11	4.07	7.87	-24.39	-23.64	59.8
Tabanidae	Deer fly	Diptera	WR Sum	14	11.07	46.88	4.24	6.50	-30.07	-29.26	52.7
Auchenorrhyncha	Spittlebug and leafhopper	Hemiptera	TR Fall	12	11.18	53.40	4.78	3.37	-24.59	-23.58	53.2
Pentatomidae	Stink bug	Hemiptera	TR Fall	5	9.09	56.59	6.23	4.52	-24.29	-22.76	43.3
Miridae	Plant bug	Hemiptera	TR Fall	30	8.65	59.03	6.83	7.61	-24.86	-23.11	41.2
Membracidae	Treehopper	Hemiptera	TR Fall	7	5.84	29.58	5.07	1.08	-25.06	-23.94	27.8
Nabidae	Damsel bug	Hemiptera	TR Spr	5	11.76	51.67	4.39	6.50	-24.43	-23.56	56.0
Auchenorrhyncha	Spittlebug and leafhopper	Hemiptera	TR Spr	23	10.94	48.37	4.42	3.35	-23.61	-22.73	52.1
Miridae	Plant bug	Hemiptera	TR Spr	11	10.61	48.32	4.56	4.91	-24.83	-23.90	50.5
Pentatomidae	Stink bug	Hemiptera	TR Spr	7	10.12	55.53	5.49	2.89	-25.34	-24.08	48.2
Stenopodainae	Assassin bug	Hemiptera	TR Sum	9	12.01	52.22	4.35	6.04	-24.92	-24.07	57.2
Phymatina	Ambush bug	Hemiptera	TR Sum	12	11.84	50.72	4.28	6.59	-24.25	-23.42	56.3
Miridae	Plant bug	Hemiptera	TR Sum	16	10.76	53.76	5.00	4.70	-23.72	-22.63	51.2
Auchenorrhyncha	Spittlebug and leafhopper	Hemiptera	TR Sum	46	10.56	54.99	5.21	4.10	-23.33	-22.16	50.2
Membracidae	Treehopper	Hemiptera	TR Sum	33	10.55	52.51	4.98	1.06	-23.57	-22.49	50.2
Nabidae	Damsel bug	Hemiptera	TR Sum	2	10.30	54.65	5.31	4.91	-24.38	-23.18	49.0
Pentatomidae	Stink bug	Hemiptera	TR Sum	24	10.07	55.63	5.52	3.33	-23.55	-22.27	47.9
Pentatomidae	Stink bug	Hemiptera	WR Fall	2	10.47	54.53	5.21	2.49	-25.82	-24.66	49.9
Auchenorrhyncha	Spittlebug and leafhopper	Hemiptera	WR Fall	37	10.46	56.98	5.45	2.83	-24.36	-23.11	49.8
Membracidae	Treehopper	Hemiptera	WR Fall	31	10.34	54.85	5.30	0.31	-23.55	-22.35	49.2
Pentatomidae	Stink bug	Hemiptera	WR Fall	10	10.30	54.87	5.33	3.23	-23.65	-22.44	49.0
Miridae	Plant bug	Hemiptera	WR Fall	19	8.68	57.63	6.64	7.08	-24.34	-22.65	41.3

Miridae	Plant bug	Hemiptera	WR Spr	11	11.58	49.85	4.31	4.43	-24.68	-23.84	55.1
Nabidae	Damsel bug	Hemiptera	WR Spr	3	11.01	53.09	4.82	4.96	-24.22	-23.19	52.4
Pentatomidae	Stink bug	Hemiptera	WR Spr	16	10.57	53.75	5.08	3.53	-24.96	-23.84	50.3
Nabidae	Damsel bug	Hemiptera	WR Sum	2	11.67	50.75	4.35	6.90	-25.39	-24.53	55.5
Phymatina	Ambush bug	Hemiptera	WR Sum	16	11.32	48.52	4.29	5.75	-24.16	-23.33	53.9
Stenopodainae	Assassin bug	Hemiptera	WR Sum	11	11.22	49.29	4.39	4.25	-24.97	-24.10	53.4
Auchenorrhyncha	Spittlebug and leafhopper	Hemiptera	WR Sum	137	10.85	55.66	5.13	3.20	-24.44	-23.31	51.7
Membracidae	Treehopper	Hemiptera	WR Sum	63	10.72	54.06	5.04	0.31	-23.30	-22.20	51.0
Pentatomidae	Stink bug	Hemiptera	WR Sum	55	10.18	55.44	5.45	3.14	-23.98	-22.73	48.5
Miridae	Plant bug	Hemiptera	WR Sum	40	9.16	47.41	5.18	4.13	-24.22	-23.06	43.6
Ichneumonidae/Braconidae	Ichneumon and braconid (parasitoid) wasp	Hymenoptera	TR Spr	8	11.71	51.78	4.42	5.69	-26.24	-25.36	55.7
Symphyta	Sawfly	Hymenoptera	TR Spr	2	11.62	47.79	4.11	4.40	-26.89	-26.12	55.3
Apoidea	Bee	Hymenoptera	TR Spr	2	10.43	48.81	4.68	1.23	-22.95	-21.98	49.7
Ichneumonidae/Braconidae	Ichneumon and braconid (parasitoid) wasp	Hymenoptera	WR Spr	6	12.05	52.88	4.39	7.68	-27.52	-26.65	57.4
Symphyta	Sawfly	Hymenoptera	WR Spr	4	11.33	49.40	4.36	3.46	-26.01	-25.15	53.9
Ichneumonidae/Braconidae	Ichneumon and braconid (parasitoid) wasp	Hymenoptera	WR Sum	6	11.33	50.04	4.42	5.85	-26.26	-25.38	53.9
Formicidae	Ant	Hymenoptera	WR/TR Fall	12				8.69	-24.88	-25.60	0.0
Formicidae	Ant	Hymenoptera	WR/TR Spr	93	10.06	48.65	4.84	5.67	-24.62	-23.59	47.9
Formicidae	Ant	Hymenoptera	WR/TR Sum	53	8.59	48.11	5.60	6.15	-24.28	-22.97	40.9
Lepidoptera adults	Moth and butterfly	Lepidoptera	WR/TR Fall	3	11.41	55.35	4.85	3.15	-26.36	-25.32	54.3
Lepidoptera adults	Moth and butterfly	Lepidoptera	WR/TR Spr	39	11.71	54.54	4.66	3.44	-26.46	-25.49	55.7
Lepidoptera adults	Moth and butterfly	Lepidoptera	WR/TR Sum	41	10.61	57.37	5.41	5.07	-26.60	-25.36	50.5
Lepidoptera larva	Moth and butterfly larva	Lepidoptera	WR/TR Fall	4	7.09	49.88	7.04	2.42	-24.58	-22.75	33.7

Lepidoptera larva	Moth and butterfly larva	Lepidoptera	WR/TR Spr	30	9.69	51.16	5.28	3.04	-26.42	-25.23	46.1
Lepidoptera larva	Moth and butterfly larva	Lepidoptera	WR/TR Sum	29	9.83	52.83	5.38	2.68	-25.72	-24.49	46.8
Lithobiomorpha	Stone centipede	Lithobiomorpha	WR Sum	4	11.21	47.48	4.24	5.48	-24.43	-23.61	53.4
Zygoptera	Damselflies	Odonata	WR Sum	4	12.36	50.01	4.05	5.72	-28.15	-27.41	58.8
Opiliones	Harvestmen	Opiliones	WR Sum	1	11.83	51.19	4.33	6.41	-25.23	-24.39	56.3
Opiliones	Harvestmen	Opiliones	WR Sum	1	12.72	48.89	3.84	5.18	-24.72	-24.05	60.5
Conocephalus saltans	Prairie meadow katydid	Orthoptera	TR Fall	1	11.10	48.50	4.37	5.82	-24.07	-23.21	52.8
Oecanthus quadripunctatus	Four-spotted tree cricket	Orthoptera	TR Fall	4	10.03	48.89	4.88	4.43	-24.19	-23.15	47.7
Conocephalus saltans	Prairie meadow katydid	Orthoptera	TR Sum	1	11.59	50.14	4.33	5.78	-23.33	-22.48	55.2
Oecanthus quadripunctatus	Four-spotted tree cricket	Orthoptera	TR Sum	20	10.07	51.81	5.14	3.54	-23.55	-22.41	48.0
Arphia conspersa	Speckle-winged rangeland grasshopper (male)	Orthoptera	WR Spr	1	12.27	49.93	4.07	2.77	-23.39	-22.64	58.4
Melanoplus dawsoni	Dawson's grasshopper (male)	Orthoptera	WR Fall	2	12.32	50.50	4.10	2.48	-22.06	-21.30	58.7
Pseudochorthippus curtipennis	Marsh meadow grasshopper (female)	Orthoptera	WR Fall	3	11.49	51.67	4.50	3.68	-22.91	-22.00	54.7
Melanoplus dawsoni	Dawson's grasshopper (female)	Orthoptera	WR Fall	1	11.24	49.67	4.42	2.39	-22.41	-21.53	53.5
Oecanthus quadripunctatus	Four-spotted tree cricket	Orthoptera	WR Fall	9	10.11	51.28	5.07	3.88	-23.71	-22.60	48.1
Melanoplus bivittatus	Two-striped grasshopper (female)	Orthoptera	WR Sum	1	11.54	50.05	4.34	5.67	-22.40	-21.55	54.9
Conocephalus saltans instar	Prairie meadow katydid (4th instar)	Orthoptera	WR Sum	1	11.07	50.34	4.55	5.63	-24.37	-23.44	52.7
Oecanthus quadripunctatus	Four-spotted tree cricket	Orthoptera	WR Sum	74	10.11	52.74	5.21	2.97	-23.48	-22.32	48.1
Camnula pellucida	Clear-winged grasshopper	Orthoptera	WR/TR Fall	5	12.87	52.60	4.09	4.90	-26.05	-25.29	61.2
Pseudochorthippus curtipennis	Marsh meadow grasshopper	Orthoptera	WR/TR Fall	19	12.70	53.07	4.18	2.84	-26.42	-25.63	60.4
Melanoplus dawsoni	Dawson's grasshopper	Orthoptera	WR/TR Fall	21	12.70	52.61	4.14	2.60	-25.32	-24.54	60.4
Amphitornus coloradus	Slant-faced grasshopper	Orthoptera	WR/TR Fall	3	12.58	50.57	4.02	4.82	-24.26	-23.52	59.9

Melanoplus bruneri	Bruner's spur throat grasshopper	Orthoptera	WR/TR Fall	7	12.57	52.67	4.19	3.45	-25.94	-25.15	59.8
Arphia conspersa	Speckle-winged rangeland grasshopper	Orthoptera	WR/TR Fall	4	12.44	52.24	4.20	4.32	-26.11	-25.31	59.2
Encoptolophus costalis	W. clouded grasshopper	Orthoptera	WR/TR Fall	3	11.91	50.31	4.22	4.95	-25.39	-24.58	56.7
Aeropedellus clavatus	Club-horned grasshopper	Orthoptera	WR/TR Spr	6	12.73	49.99	3.93	2.51	-27.10	-26.40	60.6
Arphia conspersa	Speckle-winged rangeland grasshopper	Orthoptera	WR/TR Spr	4	12.43	52.68	4.24	3.24	-26.71	-25.89	59.2
Melanoplus infantalis instars	Little spur throat grasshopper instars	Orthoptera	WR/TR Spr	6	11.95	48.95	4.10	1.51	-26.27	-25.51	56.9
Melanoplus bivittatus instars	Two-striped grasshopper instars	Orthoptera	WR/TR Spr	2	11.63	48.99	4.21	1.33	-25.92	-25.11	55.4
Pseudochorthippus curtipennis instars	Marsh meadow grasshopper instars	Orthoptera	WR/TR Spr	5	11.42	49.27	4.32	1.45	-25.88	-25.04	54.3
Amphitornus coloradus	Slant-faced grasshopper	Orthoptera	WR/TR Sum	1	12.67	48.39	3.82	2.84	-21.17	-20.51	60.3
Melanoplus infantalis	Little spur throat grasshopper	Orthoptera	WR/TR Sum	6	12.54	51.02	4.07	4.55	-24.08	-23.33	59.7
Melanoplus bruneri	Bruner's spur throat grasshopper	Orthoptera	WR/TR Sum	12	12.44	53.70	4.32	2.65	-26.13	-25.29	59.2
Aeropedellus clavatus	Club-horned grasshopper	Orthoptera	WR/TR Sum	4	12.35	49.69	4.02	2.99	-26.30	-25.56	58.8
Pseudochorthippus curtipennis	Marsh meadow grasshopper	Orthoptera	WR/TR Sum	14	12.25	51.76	4.23	2.52	-26.20	-25.39	58.3
Melanoplus packardii	Packard's grasshopper	Orthoptera	WR/TR Sum	1	12.23	50.93	4.16	1.66	-25.24	-24.45	58.2
Camnula pellucida	Clear-winged grasshopper	Orthoptera	WR/TR Sum	3	12.15	52.29	4.30	4.35	-26.76	-25.92	57.8
Melanoplus dawsoni	Dawson's grasshopper	Orthoptera	WR/TR Sum	31	12.06	51.67	4.28	2.24	-25.21	-24.38	57.4
Melanoplus bivittatus	Two-striped grasshopper	Orthoptera	WR/TR Sum	5	12.06	52.83	4.38	4.00	-25.91	-25.05	57.4
Encoptolophus costalis	W. clouded grasshopper	Orthoptera	WR/TR Sum	2	11.53	49.37	4.28	4.60	-23.76	-22.93	54.9
			Total	1834							

APPENDIX 5.2: NON-WEIGHTED AVERAGE ISOTOPE VALUES FOR ARTHROPOD ORDERS

Order	Common name	%N	%C	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{13}C$ (‰) corrected[2]
Araneae	Spiders	12.25	49.82	7.09	-24.76	-24.00
Lithobiomorpha	Centipedes	11.21	47.48	5.48	-24.43	-23.61
Coleoptera	Beetles	9.93	53.58	5.92	-26.07	-24.79
Diptera	Flies	11.81	49.63	6.82	-27.03	-26.23
Hemiptera	True bugs	10.43	52.46	4.05	-24.36	-23.24
Hymenoptera	Ants and wasps	11.22	49.91	5.33	-25.67	-24.89
Lepidoptera	Moths and butterflies	10.06	53.52	3.30	-26.02	-24.77
Odonata	Dragonflies and damselflies	12.36	50.01	5.72	-28.15	-27.41
Opiliones	Harvestmen	12.27	50.04	5.80	-24.98	-24.22
Orthoptera	Grasshoppers and crickets	11.86	50.92	3.51	-24.76	-23.92

APPENDIX 5.3: AVERAGE RELATIVE BIOMASS OF ARTHROPODS

Values derived from wet weight data gathered from 222 sweep net transects during May – October 2018 at Wild Rose conservation site and Twin River Natural Heritage Rangeland.

Species	Relative Biomass
Aeropedellus clavatus (club-horned grasshopper)	7.6%
Amphitornus coloradus (slant-faced grasshopper)	1.8%
Arphia conspersa (speckle-winged rangeland grasshopper)	4.2%
Pseudochorthippus curtipennis (marsh meadow grasshopper)	10.1%
Camnula pellucida (clear-winged grasshopper)	9.3%
Encoptolophus costalis (Western cloud grasshopper)	3.3%
Melanoplus bivittatus (two-striped grasshopper)	8.2%
Melanoplus bruneri (Bruner's spur throat grasshopper)	17.0%
Melanoplus dawsoni (Dawson's grasshopper)	16.8%
Melanoplus infantilis (little spur throat grasshopper)	9.8%
Melanoplus packardii (Packard's grasshopper)	4.0%
Gryllidae (crickets)	7.9%
	100.0%

Order	Relative Biomass
Araneae (spiders)	6.6%
Coleoptera (beetles)	13.2%
Diptera (flies)	5.6%
Hemiptera (true bugs)	65.1%
Hymenoptera (ants and wasps)	2.9%
Lepidoptera (moths and butterflies)	6.0%
Odonata (dragonflies and damselflies)	0.5%
Opiliones (harvestmen)	0.1%
	100.0%

APPENDIX 6: LIPID CORRECTION

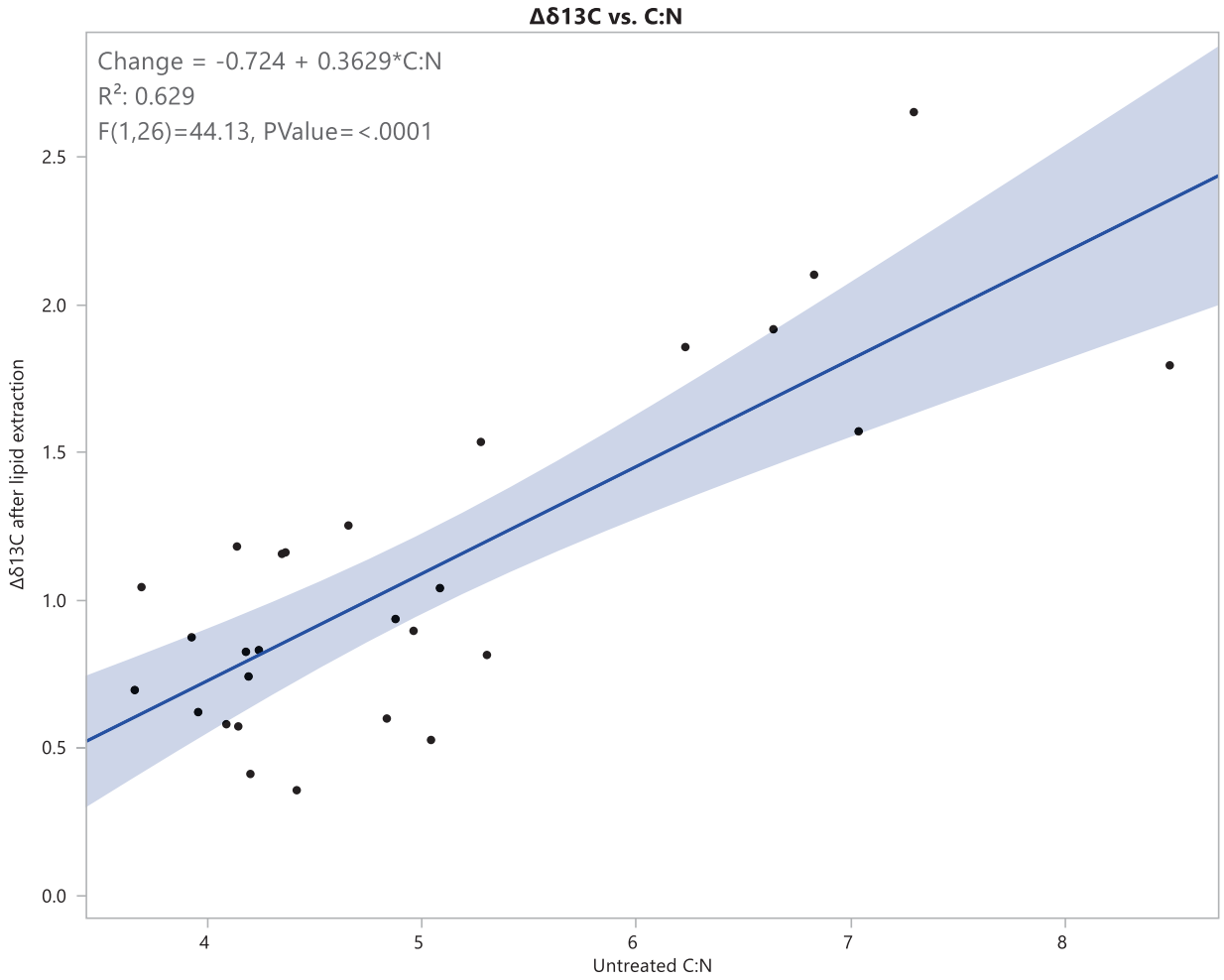
Lipid correction formula: $\Delta\delta^{13}C = -0.724 + 0.3692 * C:N$

$R^2 = 0.629$, $P = <0.001$

Subset of lipid extracted arthropod samples (n = 28)

Sample description	Order	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	C:N	$\delta^{15}N$ after lipid extraction (‰)	$\delta^{13}C$ after lipid extraction (‰)	Measured $\Delta\delta15N$ (‰)	Measured $\Delta\delta^{13}C$ (‰)	Corrected δ13C (‰)	Residual (‰)
Thomisidae (Crab spider)	Araneae	7.55	-24.40	3.66	7.78	-23.70	-0.23	0.70	-23.80	0.09
Salticidae (Jumping spider)	Araneae	6.34	-24.96	3.96	6.49	-24.34	-0.15	0.62	-24.25	0.09
Araneidae (Orb weaver)	Araneae	5.82	-25.11	3.69	6.14	-24.07	-0.32	1.04	-24.49	0.43
Pisauridae (Nursery web spider)	Araneae	6.52	-25.31	4.14	6.82	-24.13	-0.30	1.18	-24.53	0.40
Salticidae (Jumping spider)	Araneae	6.08	-24.77	4.36	6.21	-23.61	-0.13	1.16	-23.91	0.30
Coccinella septempunctata (Seven-spot ladybird)	Coleoptera	7.25	-26.32	8.49	7.04	-24.52	0.21	1.80	-23.96	0.56
Coccinella septempunctata (Seven-spot ladybird)	Coleoptera	11.25	-25.65	7.29	11.01	-23.00	0.24	2.65	-23.73	0.73
Chrysomelidae (Leaf beetle)	Coleoptera	7.98	-27.03	5.27	8.07	-25.49	-0.09	1.54	-25.84	0.35
Curculionoidea (Weevil)	Coleoptera	5.89	-25.80	4.96	5.91	-24.90	-0.02	0.90	-24.72	0.18
Pentatomidae (Stink bug)	Hemiptera	4.52	-24.29	6.23	4.63	-22.44	-0.12	1.86	-22.76	0.32
Membracidae (Treehopper)	Hemiptera	0.31	-23.55	5.30	0.32	-22.74	-0.01	0.81	-22.35	0.39
Membracidae (Treehopper)	Hemiptera	0.31	-23.30	5.04	0.26	-22.77	0.06	0.53	-22.20	0.58
Miridae (Plant bug)	Hemiptera	7.61	-24.86	6.83	7.69	-22.76	-0.07	2.10	-23.11	0.35
Miridae (Plant bug)	Hemiptera	7.08	-24.34	6.64	7.18	-22.42	-0.10	1.92	-22.65	0.23
Pentatomidae (Stink bug)	Hemiptera	3.53	-24.96	5.08	3.62	-23.92	-0.10	1.04	-23.84	0.08
Stenopodainae (Assassin bug)	Hemiptera	6.04	-24.92	4.35	6.14	-23.77	-0.10	1.16	-24.07	0.30
Formicidae (Ant)	Hymenoptera	5.67	-24.62	4.84	5.67	-24.02	0.00	0.60	-23.59	0.43

Ichneumon and braconid wasp	Hymenoptera	5.85	-26.26	4.42	5.89	-25.90	-0.04	0.36	-25.38	0.52
Lepidoptera adults (Moth and butterfly)	Lepidoptera	3.44	-26.46	4.66	3.52	-25.21	-0.08	1.25	-25.49	0.29
Lepidoptera larva (Moth and butterfly larva)	Lepidoptera	2.42	-24.58	7.04	2.30	-23.01	0.11	1.57	-22.75	0.26
Oecanthus quadripunctatus (Four-spotted tree cricket)	Orthoptera	4.43	-24.19	4.88	4.40	-23.26	0.04	0.94	-23.15	0.11
Melanoplus dawsoni (Dawson's grasshopper)	Orthoptera	2.60	-25.32	4.14	2.69	-24.75	-0.09	0.57	-24.54	0.21
Camnula pellucida (Clear-winged grasshopper)	Orthoptera	4.90	-26.05	4.09	4.98	-25.47	-0.08	0.58	-25.29	0.18
Melanoplus bivittatus (Two-striped grasshopper)	Orthoptera	4.32	-26.11	4.20	4.39	-25.70	-0.06	0.41	-25.31	0.39
Pseudochorthippus curtipennis (Marsh meadow grasshopper)	Orthoptera	2.84	-26.42	4.18	2.76	-25.60	0.08	0.83	-25.63	0.03
Melanoplus bruneri (Bruner's spur throat grasshopper)	Orthoptera	3.45	-25.94	4.19	3.58	-25.20	-0.13	0.74	-25.15	0.06
Arphia conspersa (Speckle-winged rangeland grasshopper)	Orthoptera	3.24	-26.71	4.24	3.36	-25.88	-0.12	0.83	-25.89	0.02
Aeropedellus clavatus (Club-horned grasshopper)	Orthoptera	2.51	-27.10	3.93	2.60	-26.22	-0.09	0.87	-26.40	0.17


Δδ13C vs. C:N
Change = -0.724 + 0.3629*C:N
R²: 0.629
F(1,26)=44.13, PValue=<.0001
Δδ13C after lipid extraction
Untreated C:N
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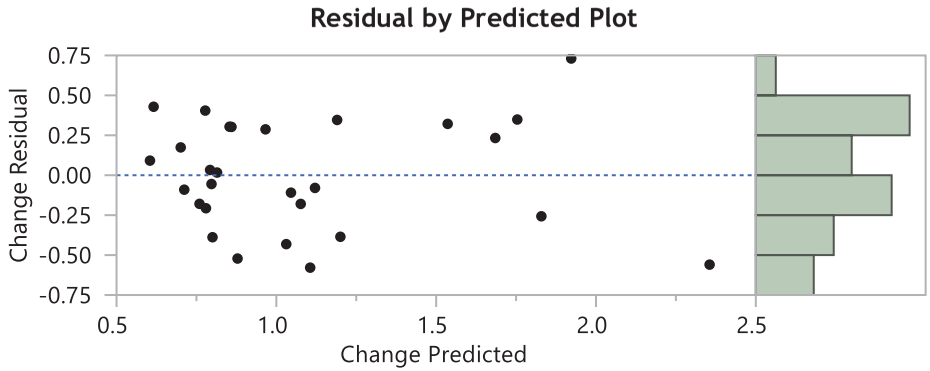
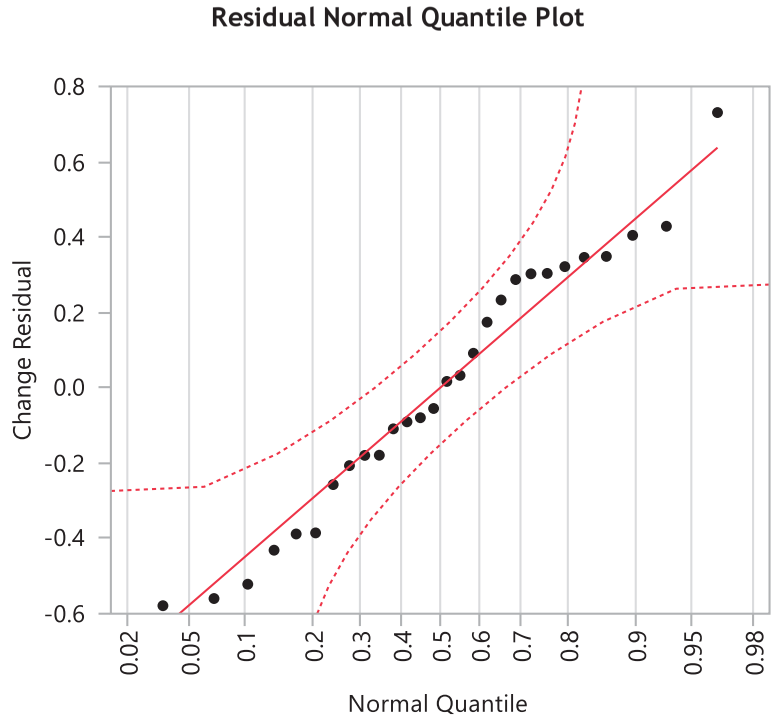
0.5
1.0
1.5
2.0
2.5
4
5
6
7
8


Residual by Predicted Plot
Change Residual
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
0.5
1.0
1.5
2.0
2.5
Change Predicted


Residual Normal Quantile Plot
Change Residual
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.02
0.05
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0.95
0.98
Normal Quantile

APPENDIX 7: STANDARDS USED TO CALIBRATE AND NORMALIZE ISOTOPE DATA

Standard	Name	Source	Mean %N from results	%N SD	Reference %N	Mean %C from results	%C SD	Reference %C	Mean $\delta^{15}N$ from results (‰)	$\delta^{15}N$ SD (‰)	Reference $\delta^{15}N$ (‰)	Mean $\delta^{13}C$ from results (‰)	$\delta^{13}C$ SD (‰)	Reference $\delta^{13}C$ (‰)
NIST 8414	Bovine Muscle	NIST	13.70 %	0.27	13.75 %	51.51 %	0.50	51.20 %	6.71	0.22	6.40	-25.47	0.49	-25.50
NIST 8574 / USGS 41	Glutamic acid	NIST/USGS	10.46 %	0.23	9.5 2%	44.79 %	1.00	40.82 %	47.58	0.21	47.57	37.62	0.14	37.63
NIST 8573 / USGS 40	Glutamic acid	NIST/USGS	10.08 %	0.27	9.52 %	43.23 %	0.80	40.82 %	-4.51	0.10	-4.52	-26.38	0.88	-26.39
BMO1	Wheat grain	In house	3.15 %	0.08	3.15 %	44.85 %	0.74	45.15 %	8.89	0.38	7.75	-23.83	0.33	-23.67
Cstv	Maize stover	In house	1.48 %	0.05	1.46 %	42.51 %	0.98	41.18 %	9.88	0.46	9.30	-12.49	0.10	-12.20
EDTA	$C_{10}H_{16}N_2O_{25}$		10.16 %	0.20	9.59 %	43.61 %	0.68	41.10 %	-0.03	0.18	-0.20	-43.16	0.70	-43.30

Average experimental error	
%N	0.38 %
%C	1.67 %
$\delta^{15}N$	0.40 ‰
$\delta^{13}C$	0.23 ‰

APPENDIX 8: ISOTOPE VALUES AND ELEMENTAL CONCENTRATIONS FOR SAMPLED PLANT MATERIAL

n = 103

[1] Sites: WR = Wild Rose; TR = Twin River Heritage Rangeland Natural Area. Seasons defined as spring (Spr) = May - June; summer (Sum) = July - August; Fall = September - October

[2] Lipid correction calculated from Post et al. (2007) Eq. 13, percent lipid estimated from Eq. 12.

[3] Protein content calculated using *k*p: 4.43 for dicots, 4.37 for monocots (Milton and Dintzis 1981; Yeoh and Wee 1994)

Sample Description	Plant type	Site/Season[1]	n	%N	%C	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{13}C$ corrected (‰)[2]	Lipid (%)[2]	Protein (%)[3]
Triticum (wheat)	Ag. seed	WR Spr	3	3.97	44.65	2.18	-26.18	-25.76	5.5	17.4
Medicago sativa (alfalfa)	Ag. seed	TR Spr	2	4.46	46.21	-0.13	-27.91	-27.27	7.9	19.7
Triticum (wheat)	Ag. seed	WR Sum	1	2.59	45.30	1.06	-23.11	-22.60	6.5	11.3
Triticum (wheat)	Ag. seed	WR Fall	1	2.98	45.56	1.74	-22.74	-22.19	6.9	13.0
Brassica (canola)	Ag. seed	TR Fall	4	4.34	56.95	4.30	-24.81	-22.67	24.7	19.2
Cicer (chickpeas)	Ag. seed	TR Fall	2	4.53	45.37	4.38	-22.00	-21.48	6.6	20.1
Rosa acicularis (prickly rose)	Berry	WR Spr	1	1.04	49.19	0.24	-24.41	-23.35	12.6	4.6
Prunus virginiana (chokecherry)	Berry	WR Spr	1	1.60	49.71	1.96	-26.93	-25.80	13.4	7.1
Symphoricarpos occidentalis (snowberry)	Berry	WR Spr	1	2.13	50.86	4.41	-25.24	-23.95	15.2	9.4
Symphoricarpos occidentalis (snowberry)	Berry	TR Spr	1	2.64	50.16	0.77	-24.32	-23.13	14.1	11.7
Rosa acicularis (prickly rose)	Berry	TR Spr	1	2.83	48.15	0.78	-25.79	-24.88	11.0	12.5
Amelanchier alnifolia (saskatoon)	Berry	WR Spr	2	2.95	49.16	1.12	-25.92	-24.87	12.5	13.0
Amelanchier alnifolia (saskatoon)	Berry	WR Sum	1	0.79	44.30	0.32	-25.20	-24.82	5.0	3.5
Prunus virginiana (chokecherry)	Berry	WR Sum	2	0.85	45.51	-1.14	-26.98	-26.44	6.8	3.8
Rosa acicularis (prickly rose)	Berry	WR Sum	4	1.21	48.38	0.03	-24.45	-23.51	11.3	5.4
Symphoricarpos occidentalis (snowberry)	Berry	WR Fall	1	0.76	46.90	-0.16	-24.44	-23.70	9.0	3.4

Prunus virginiana (chokecherry)	Berry	WR Fall	1	0.92	47.67	2.41	-25.23	-24.38	10.2	4.1
Rosa acicularis (prickly rose)	Berry	TR Fall	2	1.02	48.36	2.32	-25.21	-24.27	11.3	4.5
Symphoricarpos occidentalis (western snowberry)	Berry	TR Fall	1	1.11	47.46	2.76	-23.66	-22.85	9.9	4.9
Rosa acicularis (prickly rose)	Berry	WR Fall	2	1.27	50.00	2.13	-23.42	-22.25	13.8	5.6
Prunus virginiana (chokecherry)	Berry	WR Fall	1	1.44	49.81	1.74	-24.71	-23.57	13.5	6.4
Antennaria sp. (pussytoes)	Forb	WR Spr	2	1.46	45.68	-2.19	-28.56	-27.99	7.1	6.5
Antennaria sp. (pussytoes)	Forb	TR Spr	1	1.53	43.27	0.10	-28.41	-28.18	3.3	6.8
Phlox hoodii (moss phlox)	Forb	WR Spr	2	1.63	42.41	-0.94	-26.10	-25.99	2.0	7.2
Rumex crispus (curly dock)	Forb	TR Spr	1	1.88	49.68	11.68	-26.54	-25.42	13.3	8.3
Fragaria virginiana (strawberry)	Forb	WR Spr	1	1.98	47.24	-0.71	-27.05	-26.26	9.5	8.8
Heterotheca villosa (golden aster)	Forb	WR Spr	1	2.07	45.78	-0.40	-30.40	-29.82	7.3	9.2
Phacelia sp. (scorpionweed)	Forb	TR Spr	1	2.19	46.13	-1.90	-27.03	-26.40	7.8	9.7
Anemone patens (prairie crocus)	Forb	TR Spr	1	2.41	44.92	1.72	-24.92	-24.46	5.9	10.7
Comandra umbellata (bastard toadflax)	Forb	WR Spr	2	2.64	49.13	0.06	-26.21	-25.16	12.5	11.7
Anemone patens (prairie crocus)	Forb	WR Spr	1	2.65	46.43	0.62	-23.53	-22.86	8.3	11.7
Potentilla concinna (early cinquefoil)	Forb	WR Spr	2	2.65	46.39	-0.23	-26.00	-25.34	8.2	11.7
Cerastium arvense (field chickweed)	Forb	TR Spr	1	2.76	45.94	1.59	-28.72	-28.11	7.5	12.2
Penstemon nitidus (smooth blue beardtongue)	Forb	TR Spr	1	2.87	45.21	-1.37	-29.74	-29.24	6.4	12.7
Allium cernuum (nodding onion)	Forb	TR Spr	1	2.91	43.17	1.52	-27.45	-27.23	3.2	12.7
Dodecatheon pulchellum (darkthroat shooting star)	Forb	WR Spr	1	2.91	45.09	1.02	-30.12	-29.64	6.2	12.9
Sphaeralcea coccinea (globemallow)	Forb	WR Spr	1	2.94	43.44	5.95	-26.61	-26.35	3.6	13.0
Comandra umbellata (bastard toadflax)	Forb	TR Spr	1	2.95	51.53	1.39	-26.76	-25.37	16.2	13.1
Achillea millefolium (western yarrow)	Forb	WR Spr	2	3.02	46.57	2.76	-29.31	-28.62	8.5	13.4
Viola nuttallii (yellow prairie violet)	Forb	WR Spr	1	3.09	43.48	0.11	-28.51	-28.26	3.7	13.7
Anemone multifida (cut-leaf anemone)	Forb	WR Spr	1	3.09	48.34	0.92	-26.45	-25.51	11.3	13.7
Artemisia frigida (prairie sagewort)	Forb	WR Spr	1	3.09	46.29	1.21	-28.32	-27.67	8.1	13.7
Besseya wyomingensis (Wyoming kittentails)	Forb	WR Spr	1	3.10	47.20	-1.69	-26.97	-26.19	9.5	13.7
Taraxacum officinale (dandelion)	Forb	WR Spr	4	3.15	43.61	2.82	-29.46	-29.18	3.9	14.0
Brassicaceae (mustard)	Forb	WR Spr	1	3.16	43.60	-2.26	-28.71	-28.43	3.9	14.0
Musineon divaricatum (leafy wild parsley)	Forb	WR Spr	1	3.16	47.98	-1.63	-27.91	-27.03	10.7	14.0

Geum triflorum (three-flowered avens)	Forb	WR Spr	2	3.18	48.26	1.44	-28.33	-27.40	11.1	14.1
Lithospermum ruderale (puccoon)	Forb	WR Spr	2	3.21	43.84	1.06	-27.21	-26.91	4.2	14.2
Penstemon nitidus (smooth blue beardtongue)	Forb	WR Spr	1	3.36	47.51	-1.14	-28.31	-27.49	10.0	14.9
Heuchera sp. (alumroot)	Forb	WR Spr	1	3.49	48.56	-2.03	-29.91	-28.94	11.6	15.4
Melilotus officinalis (sweet clover)	Forb	WR Spr	1	3.50	45.96	-0.05	-27.72	-27.11	7.5	15.5
Geranium viscosissimum (sticky purple geranium)	Forb	WR Spr	1	3.58	49.21	2.80	-26.08	-25.02	12.6	15.9
Cirsium undulatum (wavyleaf thistle)	Forb	WR Spr	1	3.61	47.27	-0.31			9.6	16.0
Artemisia ludoviciana (prairie sage)	Forb	TR Spr	1	3.64	46.03	0.09	-28.75	-28.14	7.6	16.1
Thermopsis rhombifolia (goldenbean)	Forb	TR Spr	2	3.65	46.43	-0.74	-26.64	-25.97	8.3	16.2
Artemisia cana (silver sagebrush)	Forb	TR Spr	1	3.76	48.88	6.51	-26.73	-25.72	12.1	16.7
Viola nuttallii (yellow prairie violet)	Forb	TR Spr	1	3.78	44.51	3.79	-27.70	-27.30	5.3	16.8
Zigadenus venenosus (death camas)	Forb	WR Spr	1	3.98	48.47	4.20	-27.29	-26.33	11.5	17.4
Lupinus sericeus (silky lupine)	Forb	WR Spr	1	4.21	47.39	0.77	-26.89	-26.08	9.8	18.6
Thermopsis rhombifolia (goldenbean)	Forb	WR Spr	2	4.53	49.84	-1.10	-27.78	-26.63	13.6	20.1
Descurainia sophia (flixweed)	Forb	TR Spr	1	4.55	44.88	3.79	-27.34	-26.88	5.8	20.2
Galium boreale (northern bedstraw)	Forb	WR Spr	1	4.61	47.80	4.73	-26.58	-25.72	10.4	20.4
Astragalus sp. (milk vetch)	Forb	WR Spr	2	4.69	48.25	-1.05	-27.25	-26.33	11.1	20.8
Heracleum lanatum (cow parsnip)	Forb	TR Spr	1	5.26	47.04	0.78	-29.11	-28.35	9.2	23.3
Equisetum (horsetail)	Forb	WR Spr	1	9.91		4.48				
Rumex crispus (curly dock)	Forb	WR Sum	1	1.45	50.26	4.94	-25.51	-24.31	14.3	6.4
Cirsium arvense (creeping thistle)	Forb	TR Sum	1	1.46	47.78	1.45	-26.03	-25.17	10.4	6.5
Maianthemum sp. (solomon seal)	Forb	WR Sum	1	1.52	46.04	2.71	-25.48	-24.87	7.7	6.7
Erigeron caespitosus (tufted fleabane)	Forb	TR Sum	1	1.69	48.16	1.15	-27.37	-26.45	11.0	7.5
Solidago canadensis (Canada goldenrod)	Forb	TR Sum	1	1.78	50.14	2.58	-27.20	-26.01	14.1	7.8
Achillea millefolium (western yarrow)	Forb	TR Sum	1	1.79	49.07	0.54	-27.26	-26.23	12.4	7.9
Gaillardia aristata (blanketflower)	Forb	TR Sum	1	1.80	45.74	1.88	-28.63	-28.06	7.2	8.0
Aster laevis (smooth aster)	Forb	WR Sum	1	1.85	45.95	-0.94	-26.67	-26.07	7.5	8.2
Hymenoxys richardsonii (Richardson's bitterweed)	Forb	TR Sum	1	1.91	43.89	5.64	-28.22	-27.90	4.3	8.5
Heterotheca villosa (hairy golden aster)	Forb	TR Sum	1	1.96	46.78	1.91	-28.21	-27.49	8.8	8.7
Solidago canadensis (Canada goldenrod)	Forb	WR Sum	1	2.17	48.99	3.80	-26.04	-25.02	12.3	9.6

Galium boreale (northern bedstraw)	Forb	TR Sum	1	2.18	49.30	0.80	-25.86	-24.79	12.7	9.6
Selaginella densa (prairie spikemoss)	Forb	TR Sum	1	2.37	45.37	-0.77	-29.36	-28.84	6.6	
Geranium viscosissimum (sticky purple geranium)	Forb	TR Sum	1	2.47	49.12	3.91	-28.28	-27.23	12.5	11.0
Astragalus sp. (milk vetch)	Forb	TR Sum	1	2.60	44.62	-0.93	-27.04	-26.63	5.5	11.5
Lupinus sericeus (silky lupine)	Forb	TR Sum	1	3.16	47.55	1.74	-27.35	-26.52	10.0	14.0
Melilotus officinalis (sweet clover)	Forb	TR Sum	1	3.98	47.47	-0.03	-26.14	-25.32	9.9	17.6
Symphyotrichum falcatum (white prairie aster)	Forb	WR Fall	1	1.20	45.95	1.33	-27.23	-26.62	7.5	5.3
Rumex crispus (curly dock)	Forb	WR Fall	1	1.31	51.73	2.76	-28.10	-26.69	16.5	5.8
Artemisia ludoviciana (prairie sage)	Forb	WR Fall	1	1.56	46.14	4.38	-34.09	-33.46	7.8	6.9
Rumex crispus (curly dock)	Forb	TR Fall	1	1.99	49.86	10.71	-23.72	-22.57	13.6	8.8
Aster laevis (smooth aster)	Forb	WR Fall	1	2.63	45.15	1.41	-29.04	-28.55	6.3	11.6
Achillea millefolium (western yarrow)	Forb	WR Fall	1	2.70	44.76	1.53	-29.04	-28.60	5.7	12.0
Lithospermum ruderale (yellow puccoon)	Forb	WR Fall	1	2.87	36.22	1.40	-27.32	-28.08	-7.7	12.7
Poaceae (grass), emerging	Grass (C_3)	WR Spr	3	3.44	47.10	4.48	-26.75	-25.99	9.3	15.0
Bouteloua gracilis (blue grama)	Grass (C_4)	WR Sum	1	1.60	45.88	0.03	-13.70	-13.11	7.4	7.0
Poa pratensis (Kentucky bluegrass) seed	Grass seed (C_3)	WR Spr	1	1.94	48.18	0.00	-26.00	-25.08	11.0	8.5
Festuca sp. (fescue) seed	Grass seed (C_3)	WR Spr	1	2.70	48.32	1.56	-26.86	-25.93	11.2	11.8
Agropyron cristatum (crested wheatgrass) seed	Grass seed (C_3)	WR Spr	1	2.70	47.02	7.02	-24.32	-23.57	9.2	11.8
Bromus inermis (smooth brome) seed	Grass seed (C_3)	WR Spr	1	3.05	47.98	6.99	-22.56	-21.68	10.7	13.3
Bromus inermis (smooth brome) seed	Grass seed (C_3)	TR Sum	1	1.25	46.30	0.17	-25.71	-25.06	8.1	5.5
Hordeum jubatum (foxttail barley) seed	Grass seed (C_3)	WR Sum	1	1.35	46.49	5.31	-24.01	-23.33	8.4	6.0
Agropyron (wheatgrass) seed	Grass seed (C_3)	WR Sum	1	1.78	48.48	1.69	-26.24	-25.29	11.5	7.9
Juncus sp. (rush)	Grasslike	WR Spr	1	1.91	46.55	3.34	-25.50	-24.81	8.5	8.3
Carex stenophylla (sedge)	Grasslike	WR Spr	2	2.72	47.03	0.78	-28.07	-27.32	9.2	11.9
Juncus sp. (rush)	Grasslike	TR Spr	1	2.81	46.07	5.14	-28.81	-28.19	7.7	12.4
Carex (sedge)	Grasslike	TR Spr	1	3.18	42.72	5.63	-28.38	-28.23	2.5	13.9
Shrub buds	Shrub bud	TR Fall	1	2.14	51.69	2.85	-27.27	-25.87	16.5	9.5

APPENDIX 9.1: PLANT ISOTOPE AND ELEMENTAL CONCENTRATION COMPARISON

Wild plants vs. agricultural seeds

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sample Type	1	1	2.334081	0.3680	0.5456
Sample Type*Site	1	1	2.851046	0.4495	0.5042
Sample Type*Season	2	2	1.072059	0.0845	0.9190

ANOVA effect tests $\delta^{13}C$ (lipid corrected)

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sample Type	1	1	4.540062	0.9505	0.3322
Sample Type*Site	1	1	3.631429	0.7603	0.3855
Sample Type*Season	2	2	10.503790	1.0995	0.3374

ANOVA effect tests %N

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sample Type	1	1	10.844986	9.7056	0.0024*
Sample Type*Site	1	1	1.153544	1.0323	0.3122
Sample Type*Season	2	2	1.072857	0.4801	0.6203

ANOVA effect tests %C

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sample Type	1	1	0.378952	0.0129	0.9099
Sample Type*Site	1	1	3.836175	0.1304	0.7189
Sample Type*Season	2	2	1.864245	0.0317	0.9688

All plants compared by site and season

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Site	1	1	23.040831	3.7611	0.0554
Season	2	2	32.061398	2.6168	0.0782
Site*Season	2	2	19.524913	1.5936	0.2085

ANOVA effect tests $\delta^{13}C$ (lipid corrected)

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Site	1	1	0.534812	0.1110	0.7397
Season	2	2	58.709351	6.0926	0.0032*
Site*Season	2	2	82.709430	8.5832	0.0004*

Tukey's Least Squares mean differences $\delta^{13}C$ (season)

Level			Least Sq Mean
Fall	A		-24.73635
Sum	A		-25.06365
Spr		B	-26.53579

Tukey's Least Squares mean differences $\delta^{13}C$ (site*season)

Level			Least Sq Mean
TR,Fal	A		-23.28183
WR,Sum	A		-23.57760
WR,Fal	A	B	-26.19087
WR,Spr		B	-26.30940
TR,Sum		B	-26.54969
TR,Spr		B	-26.76218

ANOVA effect tests %N

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Site	1	1	3.810543	3.0838	0.0822
Season	2	2	32.004922	12.9505	<.0001*
Site*Season	2	2	2.356681	0.9536	0.3889

Tukey's Least Squares mean differences %N (season)

Level			Least Sq Mean
Spr	A		3.1489451
Fall		B	2.1547411
Sum		B	1.8651445

ANOVA effect tests %C

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Site	1	1	39.810257	1.4064	0.2385
Season	2	2	53.303302	0.9416	0.3936
Site*Season	2	2	31.992136	0.5651	0.5702

APPENDIX 9.2: ARTHROPOD ISOTOPE VALUE COMPARISON

All arthropods compared by order

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Order	11	11	283.12817	9.6799	<.0001*

ANOVA effect tests $\delta^{13}C$ (lipid corrected)

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Order	11	11	69.906814	4.5561	<.0001*

ANOVA effect tests %N

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Order	11	11	119.57621	10.9440	<.0001*

ANOVA effect tests %C

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Order	11	11	326.02383	2.4260	0.0091*

All arthropods compared by site*season

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Location	1	1	4.9283415	1.0981	0.2973
Season	2	2	0.7958230	0.0887	0.9152
Location*Season	2	2	6.1435893	0.6844	0.5068

ANOVA effect tests $\delta^{13}C$ (lipid corrected)

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Location	1	1	1.1836584	0.6832	0.4105
Season	2	2	8.9372072	2.5794	0.0810
Location*Season	2	2	3.1550625	0.9106	0.4057

ANOVA effect tests %N

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Location	1	1	5.860517	3.9281	0.0503
Season	2	2	25.258124	8.4649	0.0004*
Location*Season	2	2	6.363361	2.1326	0.1240

ANOVA effect tests %C

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Location	1	1	3.298818	0.2191	0.6408
Season	2	2	66.498068	2.2082	0.1153
Location*Season	2	2	79.464309	2.6387	0.0765

APPENDIX 9.3: GROUSE CLASS COMPARISON

Collection site effect

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sex*Primary*Location	9	9	2.648588	1.5343	0.1396
Primary*Location	9	9	2.936455	1.7011	0.0923

ANOVA effect tests $\delta^{13}C$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sex*Primary*Location	9	9	0.9168048	0.6466	0.7559
Primary*Location	9	9	1.1328463	0.7990	0.6177

Age effect (HY vs AHY):

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Age*Primary	9	9	7.711479	2.5621	0.0073*

ANOVA effect tests $\delta^{13}C$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Age*Primary	9	9	4.0776125	3.0938	0.0014*

Sex effect on AHY grouse

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sex*Primary	9	9	11.133851	3.6882	0.0003*

ANOVA effect tests $\delta^{13}C$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sex*Primary	9	9	1.6335789	0.9877	0.4517

Sex effect on HY grouse

ANOVA effect tests $\delta^{15}N$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sex*Primary	9	9	2.2024081	1.1834	0.3097

ANOVA effect tests $\delta^{13}C$

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Sex*Primary	9	9	0.4582143	0.4928	0.8777

APPENDIX 9.4: SOURCE T-TESTS

Welch's t-test's (assuming unequal variance)

	Model	Berries and ag. seeds	C_3 plants	C_4 plants[1]	C_3 and C_4 plants	Arthropods	"Predatory" arthropods	"Prey" arthropods	Hemiptera	n
$\delta^{15}N$ $\delta^{13}C$	Berries and ag. seeds									21
$\delta^{15}N$ $\delta^{13}C$	C_3 plants	t = 0.13, p = 0.127 t = 7.47, p = <0.001								102
$\delta^{15}N$ $\delta^{13}C$	C_4 plants[1]	t = 3.35, p = 0.003 t = 23.93, p = <0.001	t = 3.57, p = 0.001 t = 36.63, p = <0.001							10*
%N %C	C_3 and C_4 plants				**%N** **%C**	t = 50.13, p = <0.001 t = 11.54, p = <0.001				103
$\delta^{15}N$ $\delta^{13}C$	Arthropods				t = 8.76, p = <0.001 t = 7.20, p = <0.001					136
$\delta^{15}N$ $\delta^{13}C$	"Predatory" arthropods	t = 8.60, p = <0.001 t= 0.42, p = 0.680	t = 8.74, p = <0.001 t = 10.62, p = <0.001	t = 12.71, p = <0.001 t = 31.25, p = <0.001						96
$\delta^{15}N$ $\delta^{13}C$	"Prey" arthropods	t = 4.22, p = <0.001 t = 0.99, p = 0.329	t = 4.22, p = <0.001 t = 7.79, p = <0.001	t = 8.57, p = <0.001 t = 28.27, p = <0.001			t = 7.60, p = <0.001 t = 0.91, p = 0.365			40
$\delta^{15}N$ $\delta^{13}C$	Hemiptera	t = 5.07, p = <0.001 t = 2.12, p = 0.043	t = 5.07, p = <0.001 t = 15.07, p = <0.001	t = 8.50, p = <0.001 t = 29.68, p = <0.001			t = 2.74, p = 0.008 t = 4.42, p = <0.001	t = 2.03, p = 0.048 t= 4.17, p <0.001		30

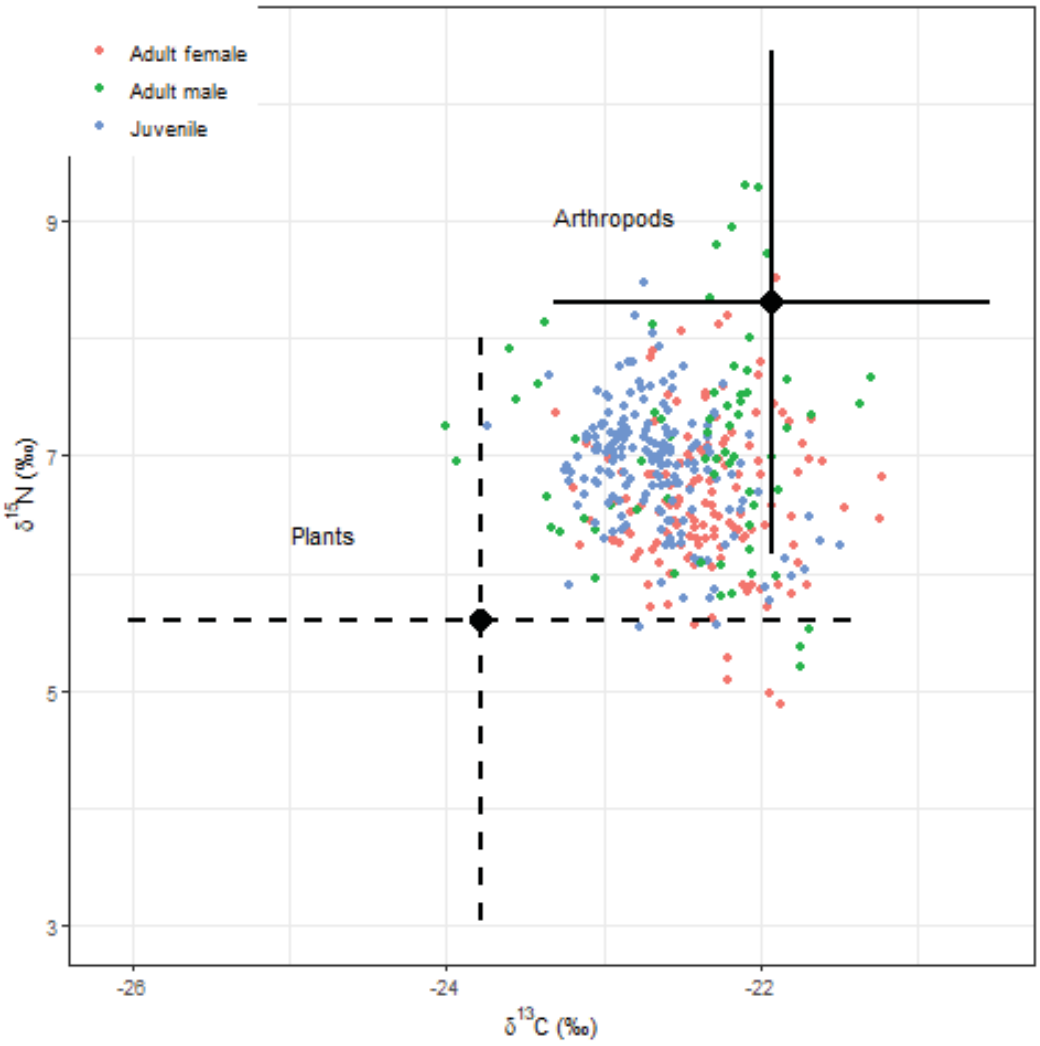
[1] Simulated dataset based on one measurement of blue grama grass (*Bouteloua gracilis*)

APPENDIX 10: SUMMARY STATISTICS USED IN MIXSIAR

Source	Mean δ15N	δ15N SD	Mean δ13C	δ13C SD	%N	%C	n
Berries and ag. seeds	1.58	1.54	-23.99	1.50	0.02	0.48	21
C_3 plants	1.77	2.54	-26.07	2.06	0.03	0.47	103
C_4 plants[1]	0.03	1.00	-13.11	1.00	0.02	0.46	10
C_3 and C_4 plants	1.75	2.54	-25.94	2.33	0.03	0.47	103
All arthropods	4.46	2.13	-24.09	1.34	0.11	0.52	136
"Predatory" arthropods	5.25	2.10	-24.14	1.27	0.11	0.52	96
"Prey" arthropods	3.23	1.25	-24.39	1.54	0.12	0.52	40
Hemiptera	4.05	1.92	-23.24	0.71	0.10	0.52	30

APPENDIX 11.1: TWO-SOURCE MODEL

Mixing space

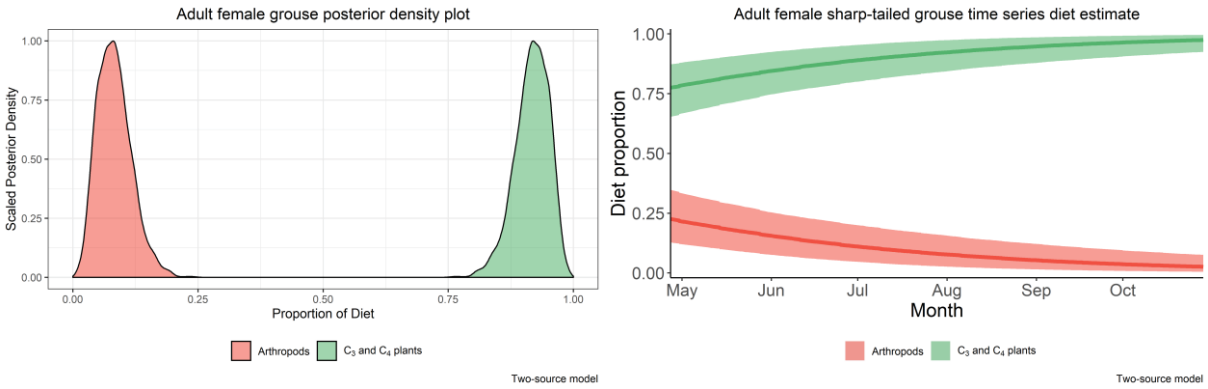


Sources corrected for trophic discrimination using TDF from Caut et al. (2009)

Model input summary statistics

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
Arthropods	4.464	2.131	-24.090	1.344	0.111	0.517	136
Plants	1.750	2.536	-25.938	2.326	0.027	0.465	103

Adult female



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

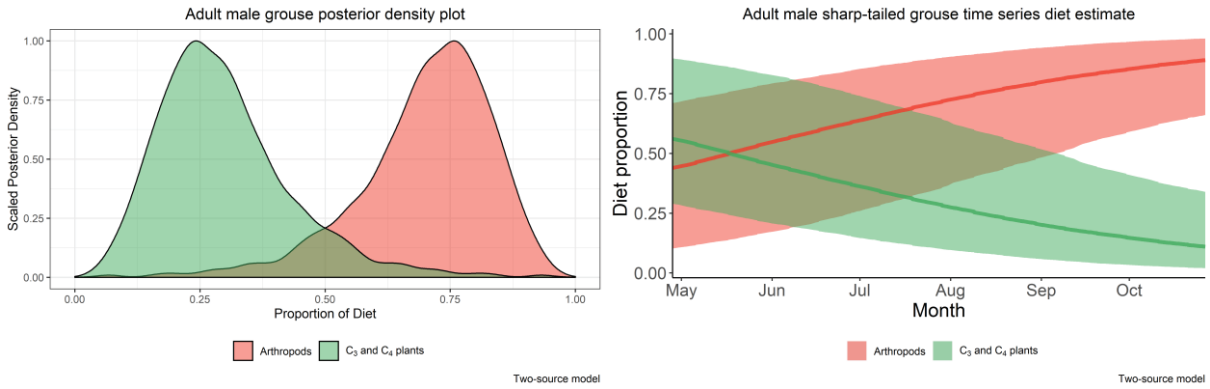
Adult female sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Arthropods	0.08	0.03	0.03 - 0.16
C_3 and C_4 plants	0.92	0.03	0.84 - 0.97

Adult female sharp-tailed grouse time series proportions

	Source	Median	95% CI
May	Arthropods	0.23	0.13 - 0.35
	C_3 and C_4 plants	0.77	0.65 - 0.87
August	Arthropods	0.08	0.03 - 0.16
	C_3 and C_4 plants	0.92	0.84 - 0.97
October	Arthropods	0.03	0.00 - 0.07
	C_3 and C_4 plants	0.97	0.93 - 1.00

Adult male



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

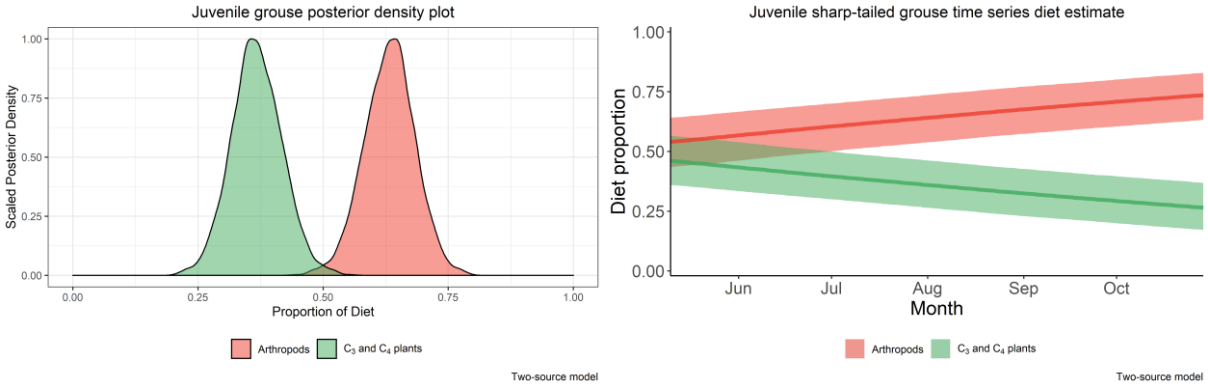
Adult male sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Arthropods	0.72	0.13	0.36 - 0.90
C_3 and C_4 plants	0.28	0.13	0.10 - 0.64

Adult male sharp-tailed grouse time series proportions

	Source	Median	95% CI
May	Arthropods	0.44	0.10 - 0.71
	C_3 and C_4 plants	0.56	0.29 - 0.90
August	Arthropods	0.71	0.35 - 0.90
	C_3 and C_4 plants	0.29	0.10 - 0.65
October	Arthropods	0.89	0.66 - 0.98
	C_3 and C_4 plants	0.11	0.02 - 0.34

Juvenile



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

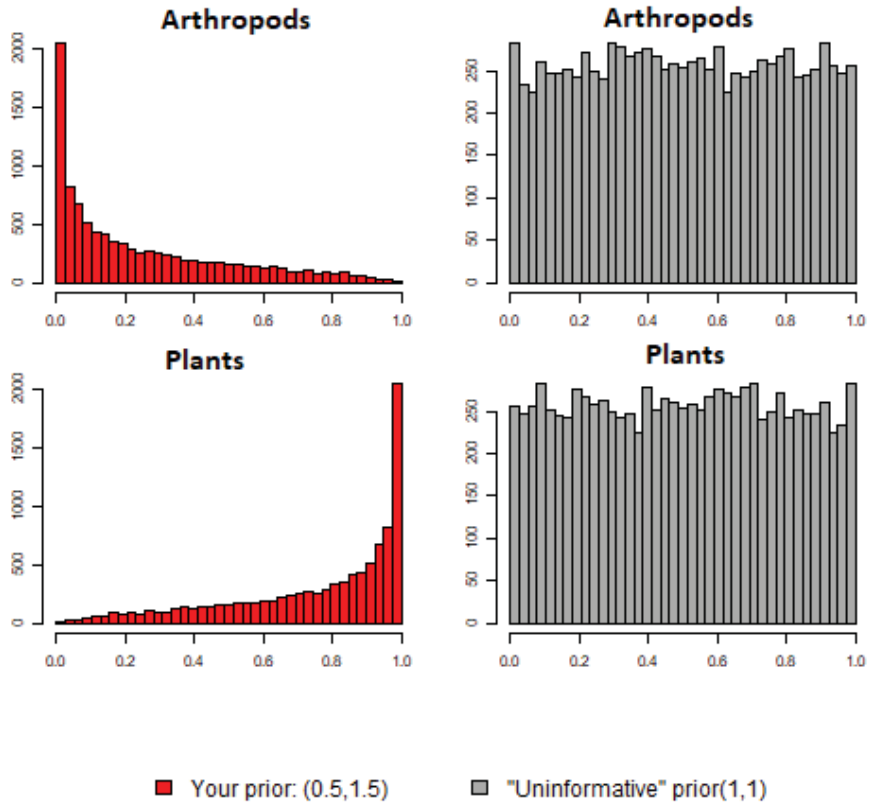
Juvenile sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Arthropods	0.63	0.05	0.53 - 0.73
C_3 and C_4 plants	0.37	0.05	0.27 - 0.47

Juvenile sharp-tailed grouse time series diet proportions

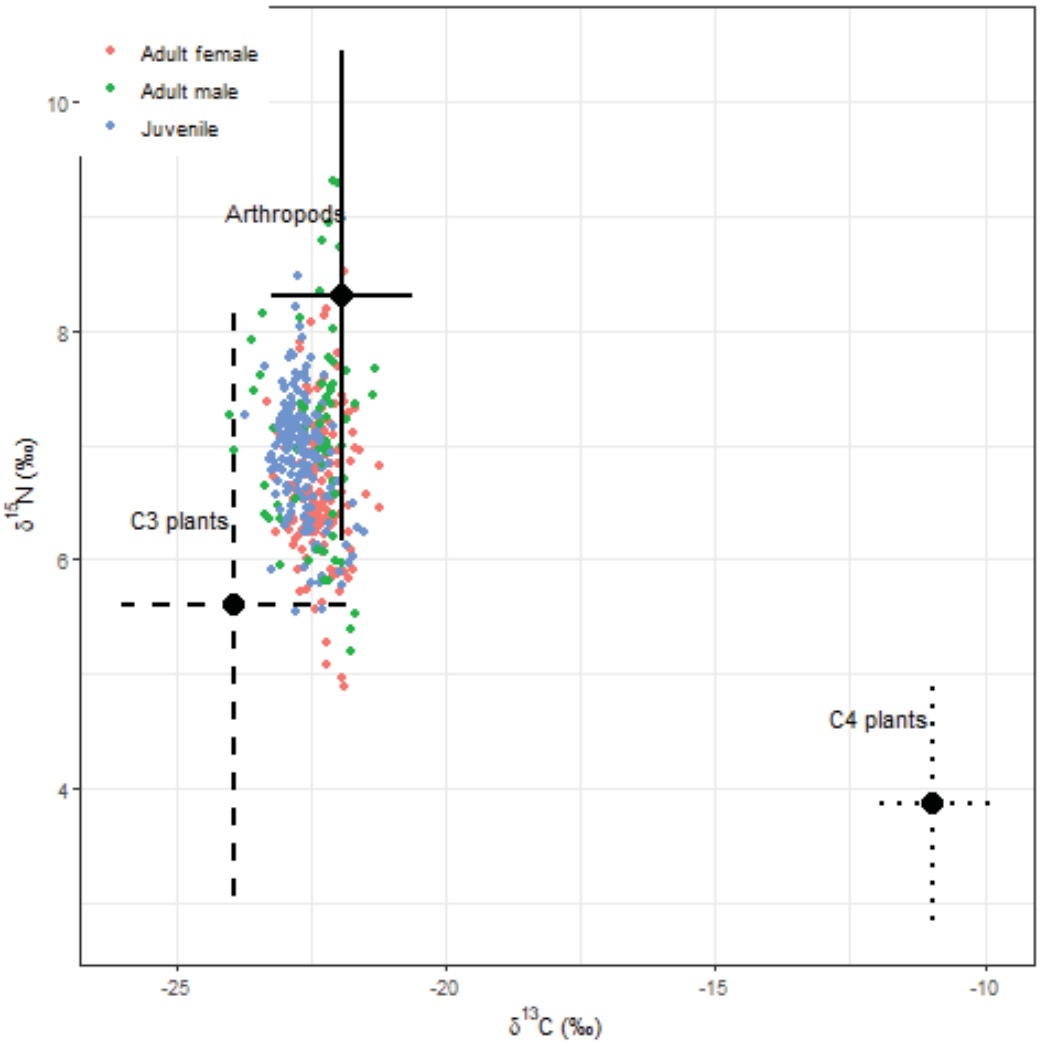
	Source	Median	95% CI
May	Arthropods	0.54	0.43 - 0.64
	C_3 and C_4 plants	0.46	0.36 - 0.57
August	Arthropods	0.64	0.54 - 0.74
	C_3 and C_4 plants	0.36	0.26 - 0.46
October	Arthropods	0.74	0.63 - 0.83
	C_3 and C_4 plants	0.26	0.17 - 0.37

Informative prior



APPENDIX 11.2: THREE-SOURCE MODEL INCLUDING C_4 PLANTS

Mixing space

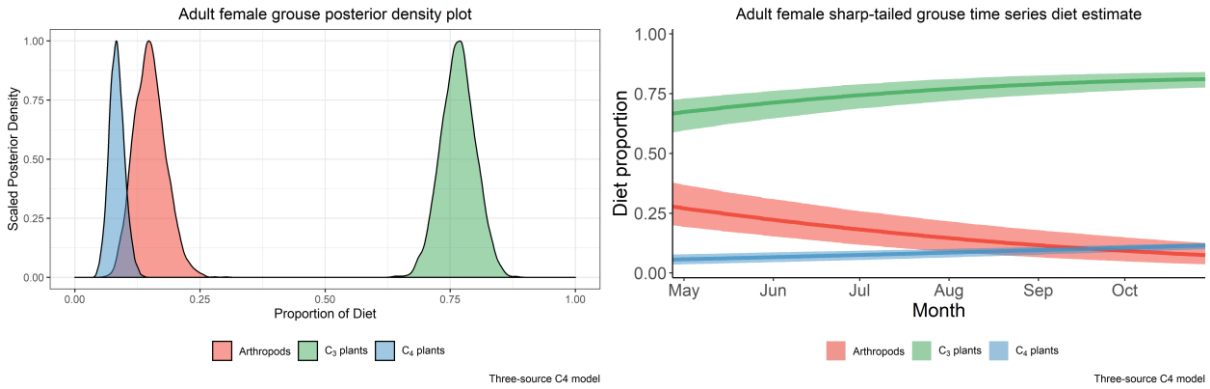


Sources corrected for trophic discrimination using TDF from Caut et al. (2009)

Model input summary statistics

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
Arthropods	4.464	2.131	-24.090	1.252	0.111	0.517	136
C3 plants	1.770	2.540	-26.070	2.060	0.030	0.470	103
C4 plants	0.030	1.000	-13.110	1.000	0.020	0.460	10

Adult female



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

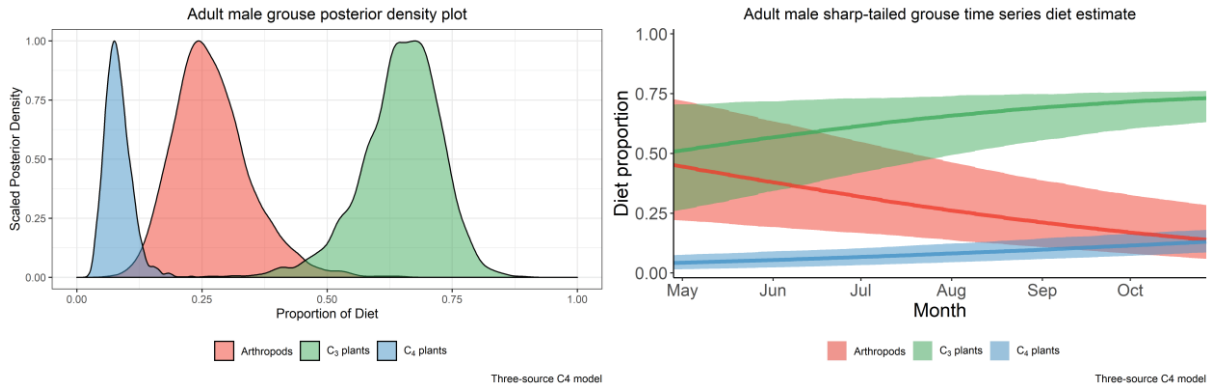
Adult female sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Arthropods	0.15	0.03	0.09 - 0.22
C_3 Plants	0.77	0.03	0.70 - 0.83
C_4 Plants	0.08	0.02	0.06 - 0.12

Adult female sharp-tailed grouse time series proportions

	Source	Median	95% CI
May	Arthropods	0.28	0.20 - 0.38
	C_3 Plants	0.67	0.59 - 0.72
	C_4 Plants	0.06	0.03 - 0.08
August	Arthropods	0.15	0.09 - 0.22
	C_3 Plants	0.77	0.72 - 0.81
	C_4 Plants	0.08	0.06 - 0.10
October	Arthropods	0.07	0.04 - 0.13
	C_3 Plants	0.81	0.78 - 0.84
	C_4 Plants	0.12	0.10 - 0.12

Adult male



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

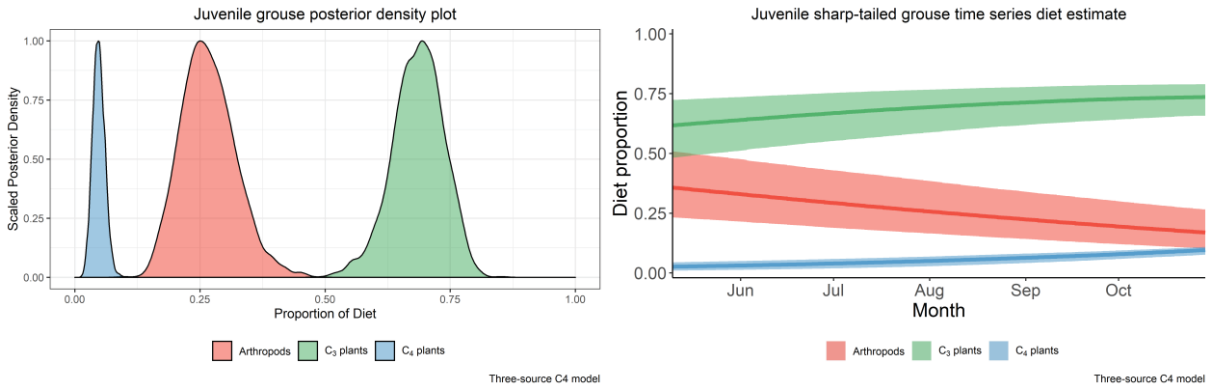
Adult male sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Arthropods	0.26	0.08	0.14 - 0.45
C_3 Plants	0.65	0.08	0.46 - 0.78
C_4 Plants	0.08	0.03	0.04 - 0.14

Adult male sharp-tailed grouse time series proportions

	Source	Median	95% CI
May	Arthropods	0.45	0.22 - 0.73
	C_3 Plants	0.51	0.26 - 0.70
	C_4 Plants	0.04	0.01 - 0.07
August	Arthropods	0.27	0.14 - 0.47
	C_3 Plants	0.65	0.48 - 0.74
	C_4 Plants	0.08	0.04 - 0.12
October	Arthropods	0.14	0.06 - 0.28
	C_3 Plants	0.73	0.63 - 0.76
	C_4 Plants	0.13	0.09 - 0.18

Juvenile



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

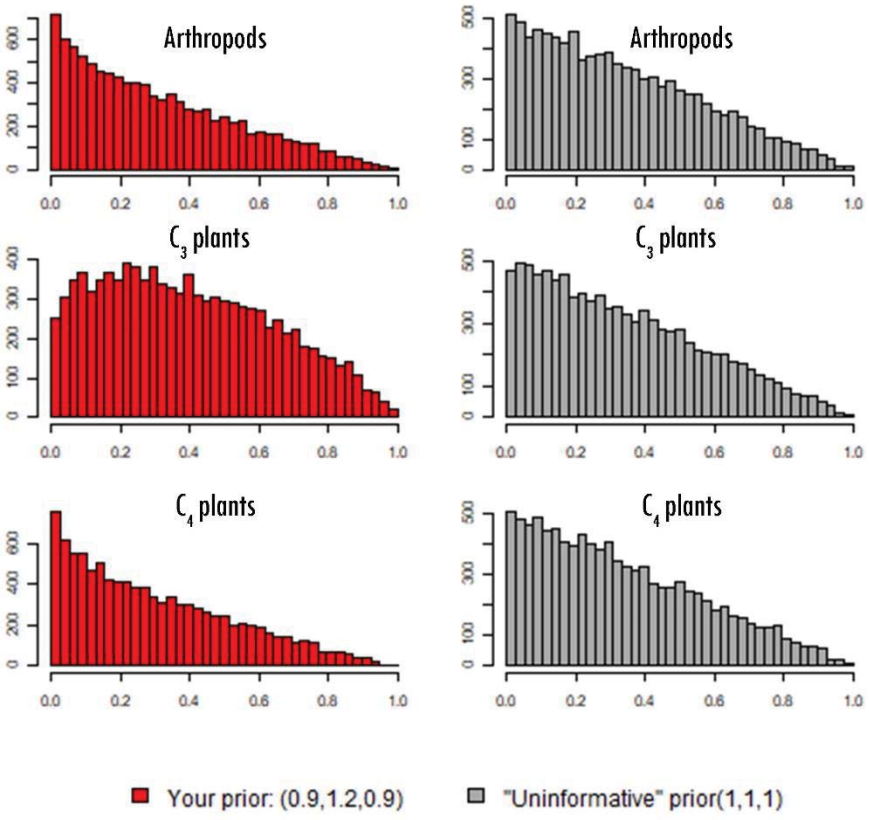
Juvenile sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Arthropods	0.26	0.05	0.17 - 0.39
C_3 Plants	0.69	0.05	0.58 - 0.78
C_4 Plants	0.05	0.01	0.02 - 0.07

Juvenile sharp-tailed grouse time series diet proportions

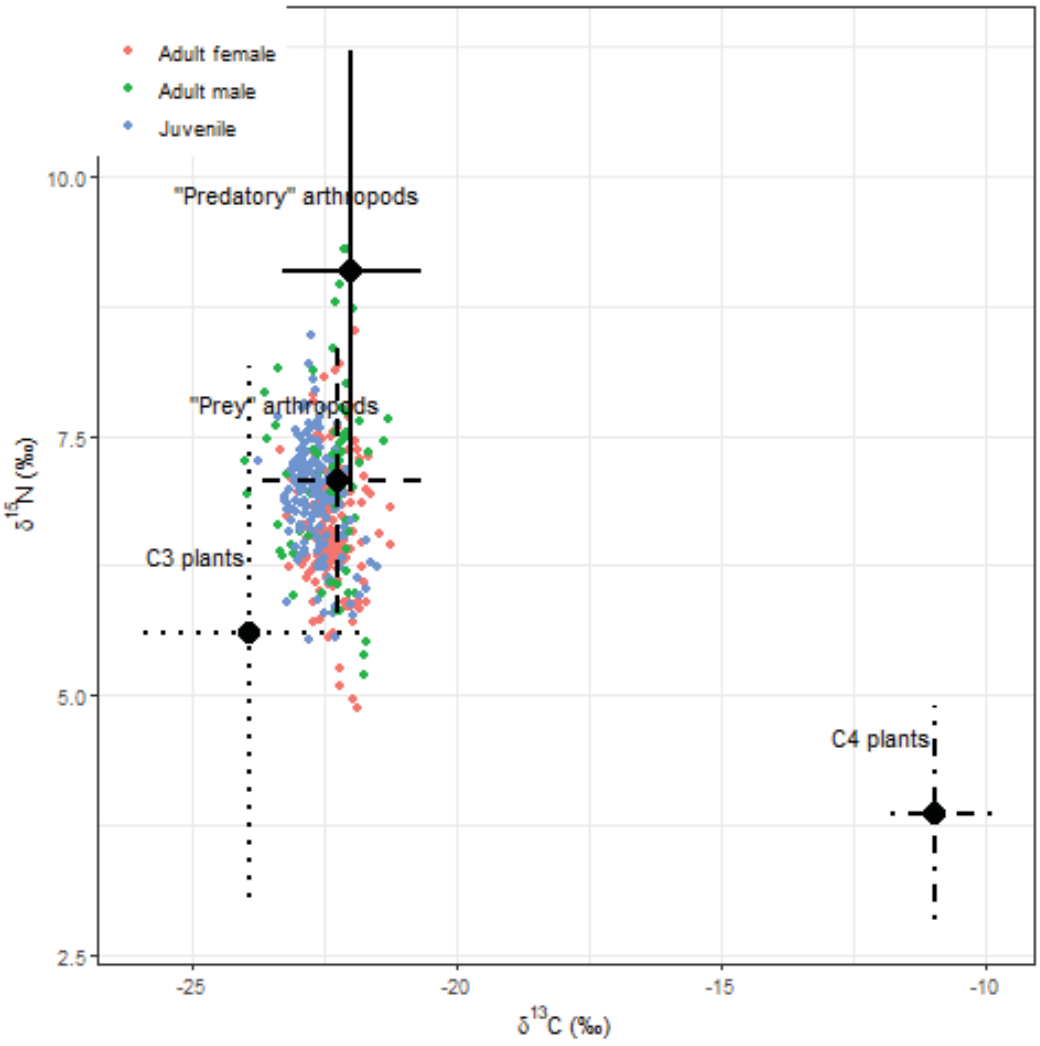
	Source	Median	95% CI
May	Arthropods	0.36	0.23 - 0.51
	C_3 Plants	0.62	0.48 - 0.72
	C_4 Plants	0.03	0.01 - 0.04
August	Arthropods	0.25	0.16 - 0.38
	C_3 Plants	0.70	0.59 - 0.77
	C_4 Plants	0.05	0.03 - 0.07
October	Arthropods	0.17	0.10 - 0.27
	C_3 Plants	0.74	0.66 - 0.79
	C_4 Plants	0.10	0.08 - 0.11

Informative prior



APPENDIX 11.3: FOUR-SOURCE TROPHIC MODEL INCLUDING C_4 PLANTS

Mixing space

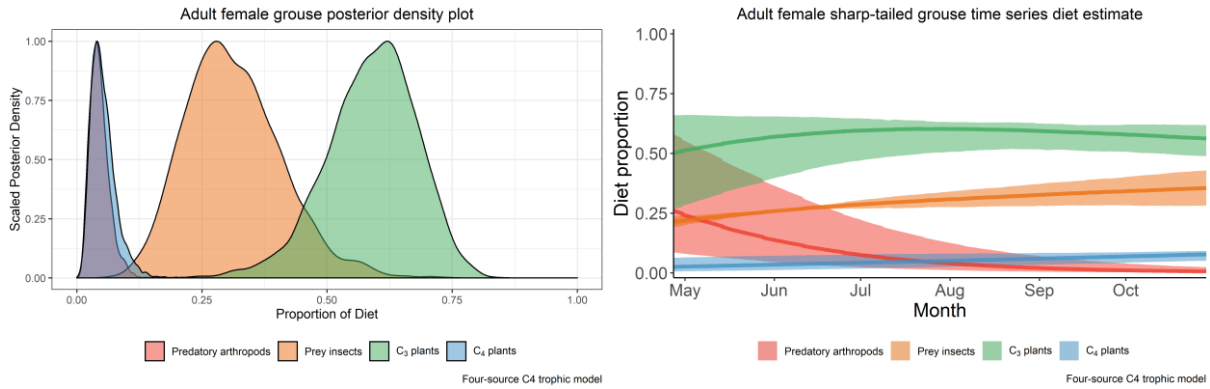


Sources corrected for trophic discrimination using TDF from Caut et al. (2009)

Model input summary statistica

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
"Predatory" arthropods	5.248	2.104	-24.138	1.266	0.107	0.520	96
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
C_3 plants	1.767	2.543	-26.066	2.058	0.027	0.466	103
C_4 plants	0.034	1.000	-13.105	1.000	0.016	0.459	10

Adult female



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

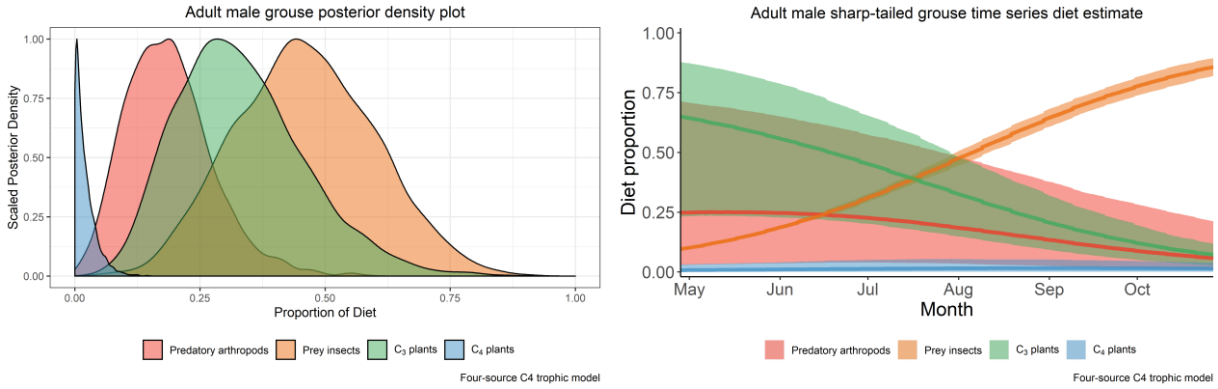
Adult female sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Predatory arthropods	0.04	0.02	0.02 - 0.09
Prey arthropods	0.30	0.10	0.15 - 0.53
C_3 Plants	0.60	0.09	0.39 - 0.74
C_4 Plants	0.05	0.02	0.02 - 0.11

Adult female sharp-tailed grouse time series proportions

	Source	Median	95% CI
May	Predatory arthropods	0.26	0.09 - 0.58
	Prey arthropods	0.21	0.15 - 0.19
	C_3 Plants	0.50	0.27 - 0.66
	C_4 Plants	0.03	0.01 - 0.06
August	Predatory arthropods	0.04	0.00 - 0.14
	Prey arthropods	0.31	0.28 - 0.34
	C_3 Plants	0.60	0.50 - 0.63
	C_4 Plants	0.05	0.02 - 0.08
October	Predatory arthropods	0.01	0.00 - 0.02
	Prey arthropods	0.36	0.29 - 0.44
	C_3 Plants	0.56	0.49 - 0.62
	C_4 Plants	0.08	0.05 - 0.09

Adult male



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

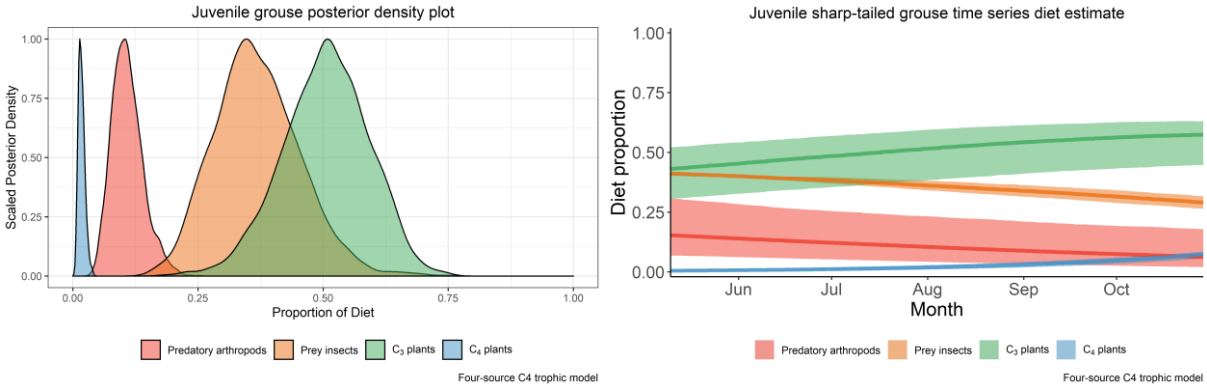
Adult male sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Predatory arthropods	0.18	0.09	0.05 - 0.39
Prey arthropods	0.46	0.14	0.21 - 0.74
C_3 Plants	0.32	0.13	0.13 - 0.62
C_4 Plants	0.01	0.02	0.00 - 0.07

Adult male sharp-tailed grouse time series proportions

	Source	Median	95% CI
May	Predatory arthropods	0.25	0.03 - 0.71
	Prey arthropods	0.10	0.06 - 0.06
	C_3 Plants	0.65	0.23 - 0.88
	C_4 Plants	0.01	0.00 - 0.03
August	Predatory arthropods	0.19	0.04 - 0.49
	Prey arthropods	0.45	0.35 - 0.40
	C_3 Plants	0.34	0.16 - 0.51
	C_4 Plants	0.01	0.00 - 0.05
October	Predatory arthropods	0.06	0.01 - 0.21
	Prey arthropods	0.86	0.76 - 0.83
	C_3 Plants	0.07	0.03 - 0.12
	C_4 Plants	0.01	0 .00 - 0.04

Juvenile



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

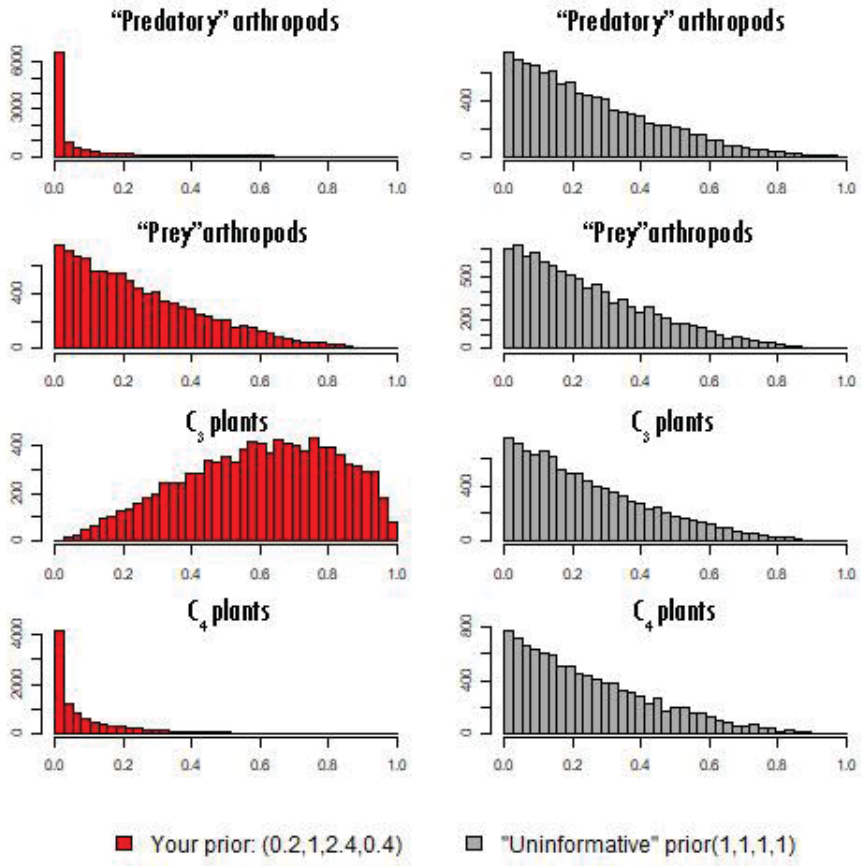
Juvenile sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Predatory arthropods	0.11	0.03	0.06 - 0.18
Prey arthropods	0.36	0.09	0.22 - 0.55
C_3 Plants	0.51	0.09	0.33 - 0.66
C_4 Plants	0.02	0.01	0.01 - 0.03

Juvenile sharp-tailed grouse time series diet proportions

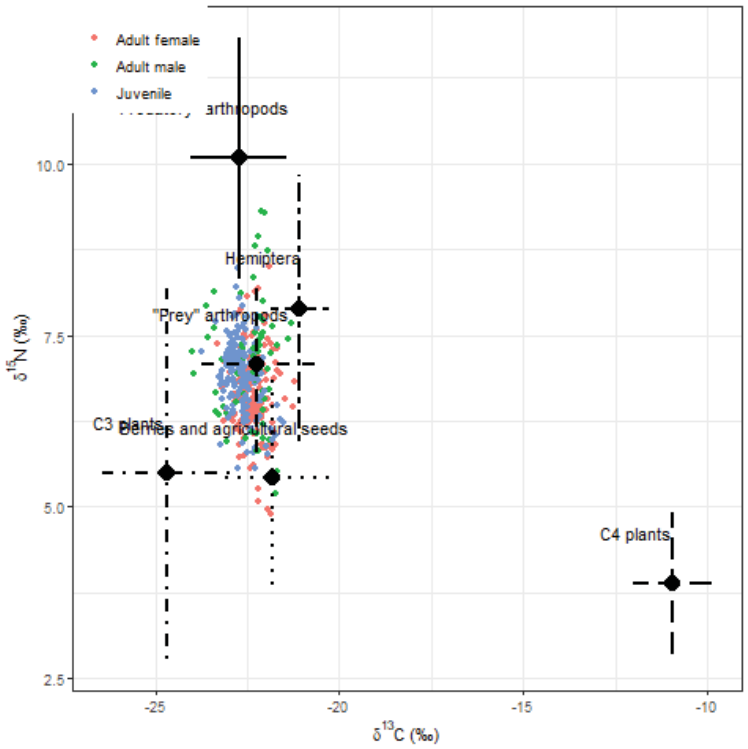
	Source	Median	95% CI
May	Predatory arthropods	0.15	0.07 - 0.31
	Prey arthropods	0.41	0.39 - 0.40
	C_3 Plants	0.43	0.31 - 0.52
	C_4 Plants	0.00	0.00 - 0.01
August	Predatory arthropods	0.10	0.04 - 0.23
	Prey arthropods	0.36	0.33 - 0.37
	C_3 Plants	0.52	0.39 - 0.60
	C_4 Plants	0.02	0.01 - 0.03
October	Predatory arthropods	0.06	0.02 - 0.18
	Prey arthropods	0.29	0.26 - 0.32
	C_3 Plants	0.57	0.45 - 0.63
	C_4 Plants	0.07	0.06 - 0.09

Informative Prior



APPENDIX 11.4: SIX-SOURCE MODEL (DID NOT CONVERGE)

Mixing space

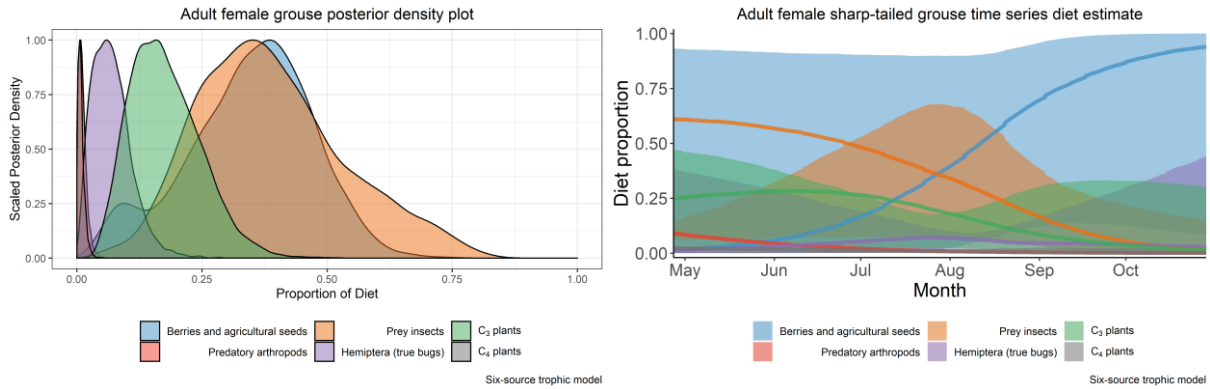


Sources corrected for trophic discrimination using TDF from Caut et al. (2009)

Model input summary statistics

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
Berries and agricultural seeds	1.582	1.544	-23.987	1.498	0.022	0.481	21
"Predatory" arthropods	6.241	1.739	-24.883	1.259	0.109	0.516	65
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
Hemiptera	4.050	1.924	-23.241	0.706	0.104	0.525	30
C3 plants	1.641	2.695	-26.858	1.706	0.029	0.466	71
C4 plants	0.034	1.000	-13.105	1.000	0.016	0.459	10

Adult female



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

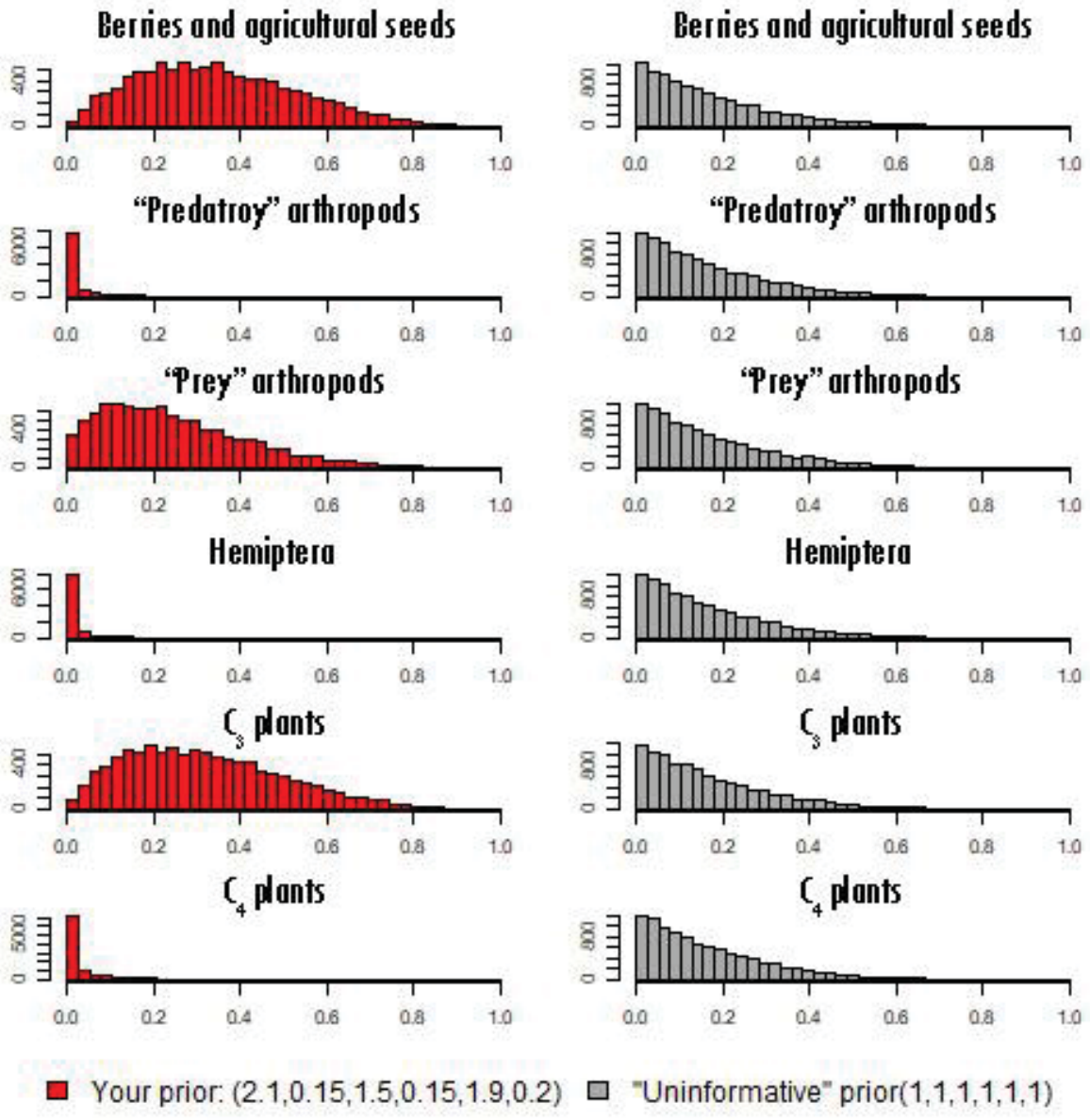
Adult female sharp-tailed grouse overall average diet proportions

	Median	SD	95% CI
Berries and agricultural seeds	0.36	0.12	0.08 - 0.56
Predatory arthropods	0.01	0.01	0.00 - 0.03
Prey arthropods	0.37	0.15	0.15 - 0.71
Hemiptera	0.07	0.04	0.01 - 0.16
C_3 Plants	0.17	0.07	0.07 - 0.33
C_4 Plants	0.01	0.01	0.00 - 0.02

Adult female sharp-tailed grouse time series proportions

	Source	Median	95% CI
May	Berries and agricultural seeds	0.02	0.00 - 0.93
	Predatory arthropods	0.09	0.00 - 0.00
	Prey arthropods	0.61	0.06 - 0.14
	Hemiptera	0.01	0.00 - 0.38
	C_3 Plants	0.25	0.01 - 0.47
	C_4 Plants	0.02	0.00 - 0.01
August	Berries and agricultural seeds	0.36	0.02 - 0.90
	Predatory arthropods	0.01	0.00 - 0.00
	Prey arthropods	0.36	0.07 - 0.68
	Hemiptera	0.07	0.01 - 0.11
	C_3 Plants	0.19	0.02 - 0.18
	C_4 Plants	0.01	0.00 - 0.02
October	Berries and agricultural seeds	0.94	0.08 - 1.00
	Predatory arthropods	0.00	0.00 - 0.01
	Prey arthropods	0.02	0.00 - 0.15
	Hemiptera	0.03	0.00 - 0.45
	C_3 Plants	0.01	0.00 - 0.30
	C_4 Plants	0.00	0.00 - 0.02

Informative priors



APPENDIX 12: FEATHER ISOTOPE VALUES

n = 375

*Feather condition: **BQ** = feather in blood quill, i.e. still growing. **BS** = visible bar streaking present

AHY = After-hatching-year, i.e. adult

HY = Hatching-year, i.e. juvenile

Bird ID	Sex	Age	Primary	Julian date	Feather condition*	Location	Year	%N	%C	d15N	d13C
4	♀	AHY	2	141		WR	2017	15.95	50.03	6.44	-23.08
4	♀	AHY	3	162		WR	2017	15.87	49.32	6.24	-23.15
4	♀	AHY	4	182		WR	2017	15.65	49.17	6.72	-23.20
4	♀	AHY	5	203		WR	2017	15.63	49.39	7.10	-23.11
4	♀	AHY	6	223		WR	2017	15.63	49.57	7.06	-23.05
4	♀	AHY	7	244		WR	2017	15.73	49.32	6.35	-22.60
4	♀	AHY	8	264		WR	2017	15.56	49.45	6.57	-22.31
4	♀	AHY	9	285	BQ	WR	2017	15.42	49.03	6.12	-22.26
7	♀	AHY	1	121	BS	WR	2017	15.36	46.54	6.37	-22.88
7	♀	AHY	2	141	BS	WR	2017	15.63	47.95	6.29	-22.93
7	♀	AHY	3	162	BS	WR	2017	15.42	47.25	6.35	-22.84
7	♀	AHY	4	182		WR	2017	15.52	47.63	6.52	-22.82
7	♀	AHY	5	203		WR	2017	15.33	47.78	6.26	-22.90
7	♀	AHY	6	223		WR	2017	15.35	48.18	6.33	-22.83
7	♀	AHY	7	244		WR	2017	15.27	47.98	6.09	-22.65
7	♀	AHY	8	264	BQ	WR	2017	15.62	46.81	5.72	-21.95
7	♀	AHY	9	285	BQ	WR	2017	15.39	48.51	6.38	-22.17
7	♀	AHY	10	304	BQ	WR	2017	15.40	47.74	5.85	-22.09
37	♀	AHY	1	121		WR	2017	15.42	47.72	7.53	-22.34
37	♀	AHY	2	141		WR	2017	15.59	48.21	7.20	-22.34
37	♀	AHY	3	162		WR	2017	15.49	47.79	7.05	-22.38
37	♀	AHY	4	182		WR	2017	15.42	48.18	6.62	-22.52
37	♀	AHY	5	203		WR	2017	15.47	48.92	6.58	-22.76
37	♀	AHY	6	223		WR	2017	15.45	48.46	6.74	-22.57
37	♀	AHY	7	244		WR	2017	15.47	48.60	6.59	-22.35
37	♀	AHY	8	264		WR	2017	15.49	48.65	6.73	-22.15
37	♀	AHY	9	285		WR	2017	15.39	48.30	5.61	-22.31
37	♀	AHY	10	304	BQ	WR	2017	15.69	48.84	5.09	-22.22
46	♀	AHY	1	121	BS	WR	2017	15.43	47.69	6.97	-22.97
46	♀	AHY	2	141		WR	2017	15.61	47.93	6.86	-22.89
46	♀	AHY	3	162		WR	2017	15.54	47.73	6.61	-22.91

46		AHY	4	182		WR	2017	15.60	47.78	6.64	-22.85
46		AHY	5	203		WR	2017	15.50	48.67	6.27	-22.95
46		AHY	6	223		WR	2017	15.50	48.66	6.17	-22.77
46		AHY	7	244		WR	2017	15.54	48.80	5.56	-22.42
46		AHY	8	264		WR	2017	15.49	48.54	5.27	-22.21
46		AHY	9	285	BQ	WR	2017	15.46	47.94	4.97	-21.94
46		AHY	10	304	BQ	WR	2017	14.94	45.05	4.89	-21.87
67		AHY	1	121		WR	2017	15.53	47.22	7.37	-21.86
67		AHY	2	141	BS	WR	2017	15.60	48.06	6.85	-22.00
67		AHY	3	162	BS	WR	2017	15.58	48.16	6.43	-22.19
67		AHY	4	182		WR	2017	15.50	48.02	6.32	-22.45
67		AHY	5	203		WR	2017	15.30	48.30	6.61	-22.60
67		AHY	7	244		WR	2017	15.36	48.56	6.81	-22.30
67		AHY	8	264		WR	2017	15.38	48.44	6.37	-22.14
67		AHY	9	285	BQ	WR	2017	15.46	48.64	6.23	-21.79
67		AHY	10	304	BQ	WR	2017	15.45	48.29	5.83	-21.81
165		AHY	1	121		TR	2018	14.20	44.14	8.18	-22.21
165		AHY	2	141		TR	2018	15.39	47.73	8.12	-22.26
165		AHY	3	162	BS	TR	2018	14.75	46.18	7.58	-22.24
165		AHY	4	182	BS	TR	2018	14.57	45.32	7.16	-22.46
165		AHY	5	203	BS	TR	2018	14.75	47.02	6.80	-22.39
165		AHY	6	223		TR	2018	15.01	48.00	6.33	-22.59
165		AHY	7	244		TR	2018	14.15	46.00	6.32	-22.30
165		AHY	8	264		TR	2018	13.88	45.42	5.91	-21.71
165		AHY	9	285	BQ	TR	2018	14.43	46.13	6.09	-21.76
165		AHY	10	304	BQ	TR	2018	14.20	45.76	6.47	-21.80
167		AHY	1	121		WR	2018	15.66	48.82	7.37	-23.31
167		AHY	3	162	BS	WR	2018	16.00	49.76	6.58	-22.57
167		AHY	4	182	BS	WR	2018	15.73	49.08	6.29	-22.41
167		AHY	5	203		WR	2018	15.69	49.01	6.13	-22.47
167		AHY	6	223		WR	2018	15.72	49.08	5.74	-22.58
167		AHY	7	244	BS	WR	2018	15.88	49.46	5.72	-22.70
167		AHY	8	264	BQ	WR	2018	15.84	49.47	5.91	-22.72
167		AHY	9	285	BQ	WR	2018	15.47	48.31	6.00	-22.58
167		AHY	10	304	BQ	WR	2018	15.76	49.03	6.51	-22.46
168		AHY	1	121	BS	WR	2018	15.61	48.37	6.60	-22.53
168		AHY	2	141	BS	WR	2018	15.65	48.58	6.63	-22.52
168		AHY	3	162	BS	WR	2018	15.72	48.55	6.73	-22.46
168		AHY	4	182	BS	WR	2018	15.16	47.27	6.78	-22.43
168		AHY	5	203	BS	WR	2018	9.67	30.34	6.68	-22.31
168		AHY	6	223		WR	2018	15.78	49.41	6.50	-22.30

168		AHY	7	244	BS	WR	2018	15.68	49.16	6.32	-22.09
168		AHY	8	264	BS	WR	2018	15.65	49.19	6.30	-22.11
168		AHY	9	285	BQ	WR	2018	15.51	48.57	6.22	-22.26
168		AHY	10	304	BQ	WR	2018	14.93	45.15	6.38	-22.06
171		AHY	1	121		WR	2018	14.97	46.58	7.52	-22.60
171		AHY	2	141		WR	2018	15.02	46.78	7.47	-22.54
171		AHY	3	162		WR	2018	15.02	47.27	7.32	-22.29
171		AHY	4	182		WR	2018	14.86	46.58	7.09	-22.34
171		AHY	5	203		WR	2018	14.25	46.31	6.45	-22.42
171		AHY	6	223		WR	2018	14.24	46.21	6.23	-22.50
173		AHY	1	121		WR	2018	15.81	49.56	6.36	-22.29
173		AHY	2	141		WR	2018	15.61	48.65	6.06	-22.31
173		AHY	3	162		WR	2018	15.67	49.31	6.24	-22.40
173		AHY	4	182		WR	2018	15.65	49.23	6.38	-22.41
173		AHY	5	203		WR	2018	15.63	49.47	6.41	-22.37
173		AHY	6	223		WR	2018	15.59	49.13	6.41	-22.53
173		AHY	7	244		WR	2018	15.50	49.09	6.57	-22.54
173		AHY	8	264		WR	2018	15.52	49.03	6.52	-22.64
173		AHY	9	285	BQ	WR	2018	15.59	49.38	6.44	-22.55
173		AHY	10	304	BQ	WR	2018	15.73	49.54	6.29	-22.35
174		AHY	1	121		WR	2018	15.68	49.01	6.91	-22.22
174		AHY	2	141		WR	2018	15.82	49.28	6.21	-22.68
174		AHY	3	162	BS	WR	2018	15.72	49.20	6.13	-22.80
174		AHY	4	182	BS	WR	2018	15.62	48.88	6.25	-22.66
174		AHY	5	203		WR	2018	15.54	49.09	6.08	-22.42
174		AHY	6	223		WR	2018	15.45	48.82	6.47	-22.27
174		AHY	7	244		WR	2018	15.52	48.60	6.15	-22.45
174		AHY	8	264		WR	2018	15.78	49.03	5.90	-22.11
174		AHY	9	285		WR	2018	15.61	49.05	5.89	-22.05
174		AHY	10	304		WR	2018	15.64	48.64	5.87	-22.00
178		AHY	1	121	BS	TR	2018	15.51	47.34	8.51	-21.90
178		AHY	2	141		TR	2018	15.43	47.08	7.80	-21.99
178		AHY	3	162		TR	2018	15.44	47.51	7.36	-22.03
178		AHY	4	182		TR	2018	15.57	48.24	7.09	-22.07
178		AHY	5	203		TR	2018	15.43	48.35	6.98	-22.27
178		AHY	6	223		TR	2018	15.59	48.73	7.01	-22.34
178		AHY	7	244		TR	2018	15.45	48.31	6.94	-21.60
178		AHY	8	264		TR	2018	15.43	48.30	6.82	-21.23
178		AHY	9	285	BQ	TR	2018	15.61	48.78	6.96	-22.01
178		AHY	10	304	BQ	TR	2018	15.40	47.88	7.11	-22.24
181		AHY	1	121	BS	TR	2018	15.40	46.37	8.06	-22.51

181		AHY	2	141	BS	TR	2018	15.51	47.80	7.30	-22.67
181		AHY	3	162		TR	2018	15.53	48.47	6.84	-22.61
181		AHY	4	182		TR	2018	15.60	48.06	6.95	-22.43
181		AHY	5	203		TR	2018	15.76	49.23	6.94	-22.50
181		AHY	6	223		TR	2018	15.83	49.26	6.83	-22.72
181		AHY	7	244		TR	2018	15.63	48.64	6.93	-22.51
181		AHY	8	264	BQ	TR	2018	15.84	49.32	6.79	-22.32
181		AHY	10	304	BQ	TR	2018	15.61	49.02	6.84	-22.69
183		AHY	1	121		TR	2018	15.53	47.97	7.68	-22.01
183		AHY	2	141		TR	2018	15.44	47.75	7.44	-21.92
183		AHY	3	162		TR	2018	15.28	47.11	7.28	-21.81
183		AHY	4	182		TR	2018	16.00	49.54	7.31	-21.68
183		AHY	5	203		TR	2018	15.39	48.04	7.11	-21.73
183		AHY	6	223		TR	2018	15.45	48.09	6.86	-21.77
183		AHY	7	244		TR	2018	15.63	48.43	6.58	-21.93
183		AHY	8	264		TR	2018	15.76	48.94	6.50	-22.12
183		AHY	9	285	BQ	TR	2018	15.69	48.81	7.20	-22.19
183		AHY	10	304	BQ	TR	2018	15.74	48.90	7.49	-22.36
187		AHY	1	121		TR	2018	15.38	48.27	7.89	-22.68
187		AHY	2	141		TR	2018	15.07	47.38	7.84	-22.69
187		AHY	3	162		TR	2018	14.66	46.23	7.01	-22.47
187		AHY	4	182		TR	2018	15.56	48.85	7.13	-22.23
187		AHY	5	203		TR	2018	14.29	45.93	6.83	-22.14
187		AHY	6	223		TR	2018	14.92	47.53	6.98	-21.69
187		AHY	7	244		TR	2018	14.15	45.56	6.46	-21.24
187		AHY	8	264	BQ	TR	2018	14.11	45.21	6.56	-21.47
187		AHY	9	285	BQ	TR	2018	14.83	46.61	6.40	-21.98
187		AHY	10	304	BQ	TR	2018	14.87	47.17	5.90	-21.88
53		HY	1	152	BS	WR	2017	15.53	48.50	7.11	-22.62
53		HY	2	174	BS	WR	2017	15.57	48.53	7.03	-22.57
53		HY	3	196	BS	WR	2017	15.68	48.94	7.00	-22.70
53		HY	4	218	BS	WR	2017	15.56	48.56	6.93	-22.59
53		HY	5	239	BS	WR	2017	15.37	48.28	6.55	-22.44
53		HY	6	261		WR	2017	15.54	48.96	6.09	-22.40
53		HY	8	304		WR	2017	15.57	48.94	5.89	-21.97
53		HY	9	132		WR	2017	15.51	49.02	6.67	-22.73
53		HY	10	132		WR	2017	15.29	48.17	6.74	-22.63
56		HY	1	152		WR	2017	15.55	48.16	7.16	-22.34
56		HY	2	174		WR	2017	15.53	48.61	7.24	-22.34
56		HY	3	196	BS	WR	2017	15.53	48.22	7.36	-22.29
56		HY	4	218	BS	WR	2017	15.48	48.42	7.36	-22.30

56		HY	5	239		WR	2017	15.53	48.70	7.07	-22.34
56		HY	6	261		WR	2017	15.37	48.27	6.80	-22.28
56		HY	7	283		WR	2017	15.53	48.66	6.54	-22.13
56		HY	8	304		WR	2017	15.41	48.41	6.49	-21.70
56		HY	9	132		WR	2017	15.39	48.37	6.87	-22.42
56		HY	10	132		WR	2017	15.33	48.29	6.93	-22.42
60		HY	1	152	BS	WR	2017	15.81	48.82	8.47	-22.74
60		HY	2	174		WR	2017	15.64	48.67	8.20	-22.80
60		HY	3	196		WR	2017	15.48	48.33	7.76	-22.90
60		HY	4	218		WR	2017	15.57	48.48	7.80	-22.85
60		HY	5	239		WR	2017	15.46	48.61	7.79	-22.81
60		HY	6	261		WR	2017	15.47	48.55	7.47	-22.75
60		HY	7	283		WR	2017	15.47	48.78	6.54	-22.64
60		HY	8	304		WR	2017	15.47	48.86	6.11	-22.39
60		HY	9	132		WR	2017	15.29	48.43	7.55	-23.04
60		HY	10	132		WR	2017	15.21	48.25	7.51	-22.98
64		HY	1	152		WR	2017	15.44	47.32	6.24	-22.22
64		HY	2	174		WR	2017	15.69	48.98	7.25	-23.01
64		HY	3	196		WR	2017	15.61	48.78	7.32	-22.87
64		HY	4	218		WR	2017	15.53	48.66	7.42	-22.88
64		HY	5	239		WR	2017	15.50	48.85	7.23	-22.86
64		HY	6	261		WR	2017	15.61	49.05	6.74	-22.85
64		HY	7	283		WR	2017	15.54	48.79	6.23	-22.60
64		HY	8	304		WR	2017	15.62	48.92	5.79	-22.32
64		HY	9	132		WR	2017	15.36	48.52	7.23	-23.06
64		HY	10	132		WR	2017	15.45	48.62	7.09	-23.04
99		HY	1	152		WR	2017	15.59	48.65	6.87	-22.87
99		HY	2	174		WR	2017	15.59	48.94	6.85	-22.96
99		HY	3	196		WR	2017	15.53	48.77	7.02	-22.99
99		HY	4	218		WR	2017	15.63	48.95	6.81	-22.83
99		HY	5	239		WR	2017	15.57	49.17	6.38	-22.63
99		HY	6	261		WR	2017	15.63	49.21	6.13	-22.42
99		HY	7	283		WR	2017	15.64	49.22	6.32	-22.16
99		HY	8	304	BQ	WR	2017	15.61	49.21	6.03	-21.72
99		HY	9	132		WR	2017	15.27	48.88	6.79	-23.06
99		HY	10	132		WR	2017	15.57	49.19	6.64	-22.94
169		HY	1	152	BS	WR	2018	15.50	48.61	7.77	-22.50
169		HY	2	174	BS	WR	2018	15.64	49.10	7.68	-22.56
169		HY	3	196	BS	WR	2018	15.57	48.97	7.57	-22.56
169		HY	4	218		WR	2018	15.56	48.94	7.44	-22.61
169		HY	5	239		WR	2018	15.53	47.57	6.93	-22.46

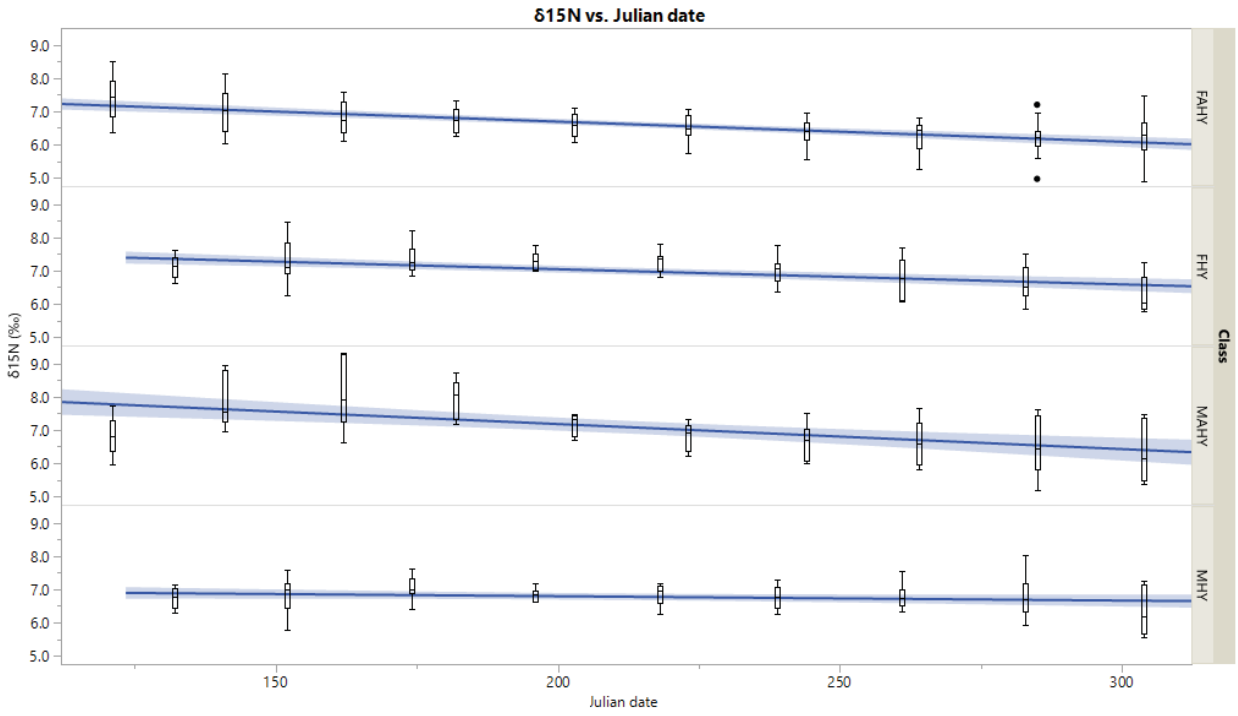
169		HY	6	261		WR	2018	15.56	49.07	6.10	-22.33
169		HY	7	283		WR	2018	15.56	49.04	5.85	-22.29
169		HY	8	304	BQ	WR	2018	15.77	49.48	5.78	-21.94
169		HY	9	132		WR	2018	15.58	49.13	7.63	-22.62
169		HY	10	132		WR	2018	15.58	49.39	7.38	-22.59
179		HY	1	152	BS	TR	2018	15.57	48.62	7.00	-22.65
179		HY	2	174	BS	TR	2018	15.59	49.01	7.11	-22.67
179		HY	3	196	BS	TR	2018	15.52	48.84	7.03	-22.61
179		HY	4	218	BS	TR	2018	16.49	51.60	7.06	-22.58
179		HY	5	239	BS	TR	2018	15.54	48.86	6.82	-22.55
179		HY	6	261		TR	2018	15.56	48.85	6.76	-22.60
179		HY	7	283		TR	2018	15.66	49.31	6.48	-22.88
179		HY	8	304	BQ	TR	2018	15.58	49.20	5.91	-23.22
179		HY	9	132		TR	2018	15.49	48.87	7.13	-22.71
179		HY	10	132		TR	2018	15.62	49.20	6.83	-22.66
180		HY	1	152		TR	2018	15.48	48.59	7.04	-23.05
180		HY	2	174		TR	2018	15.79	49.72	7.05	-23.03
180		HY	3	196		TR	2018	15.51	48.99	7.27	-23.01
180		HY	4	218		TR	2018	15.46	48.74	7.37	-22.97
180		HY	5	239		TR	2018	15.68	49.74	7.10	-22.94
180		HY	6	261		TR	2018	17.00	53.68	7.69	-23.35
180		HY	7	283	BQ	TR	2018	14.30	45.09	7.49	-22.96
180		HY	8	304	BQ	TR	2018	15.62	49.41	7.25	-23.73
180		HY	9	132		TR	2018	15.41	48.95	7.14	-23.10
180		HY	10	132		TR	2018	15.43	48.84	7.16	-23.06
186		HY	1	152		TR	2018	14.70	46.06	7.93	-22.64
186		HY	2	174	BS	TR	2018	15.68	49.22	7.62	-22.77
186		HY	4	218	BS	TR	2018	15.50	48.71	7.13	-22.87
186		HY	5	239	BS	TR	2018	15.52	48.65	7.22	-22.88
186		HY	6	261		TR	2018	15.62	49.09	7.22	-22.72
186		HY	7	283		TR	2018	15.66	49.32	7.27	-22.43
186		HY	8	304	BQ	TR	2018	15.48	48.72	7.17	-22.08
186		HY	9	132		TR	2018	15.43	48.71	7.56	-22.76
186		HY	10	132		TR	2018	15.77	49.70	7.28	-22.89
1		AHY	1	121		WR	2017	15.73	48.54	5.95	-23.06
1		AHY	2	141		WR	2017	15.44	47.77	6.95	-22.76
1		AHY	3	162		WR	2017	15.51	48.39	6.63	-22.59
45		AHY	5	203		WR	2017	15.50	48.90	6.68	-22.08
45		AHY	6	223		WR	2017	15.59	49.15	6.21	-22.07
45		AHY	7	244		WR	2017	15.42	48.64	5.99	-22.05
45		AHY	8	264		WR	2017	15.54	48.88	5.98	-21.90

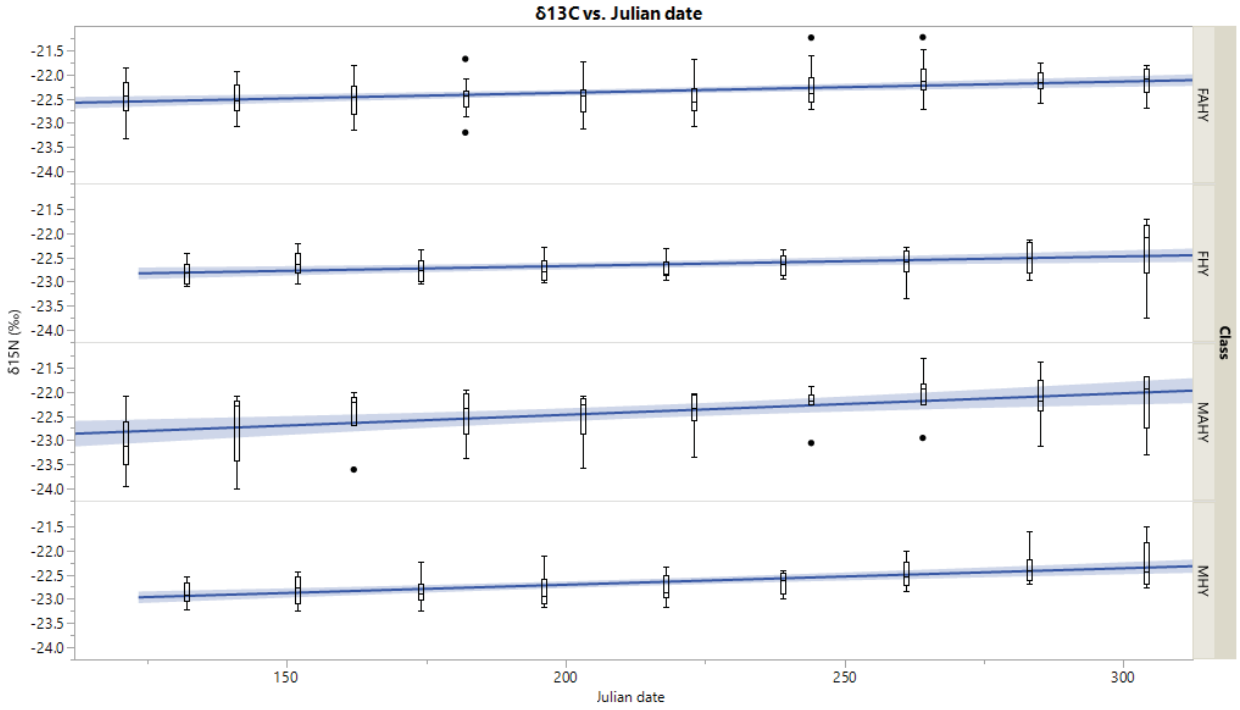
45	♂	AHY	9	285	BQ	WR	2017	15.77	49.01	5.20	-21.75
45	♂	AHY	10	304	BQ	WR	2017	15.58	48.97	5.38	-21.75
52	♂	AHY	1	121	BS	WR	2017	15.62	48.84	6.53	-22.78
52	♂	AHY	2	141	BS	WR	2017	15.57	49.00	7.53	-22.30
52	♂	AHY	3	162	BS	WR	2017	15.57	48.72	7.76	-22.16
52	♂	AHY	4	182	BS	WR	2017	15.60	49.01	8.00	-22.07
52	♂	AHY	5	203	BS	WR	2017	15.33	48.36	7.35	-22.14
52	♂	AHY	6	223		WR	2017	15.43	48.82	6.92	-22.20
52	♂	AHY	7	244		WR	2017	15.67	48.97	6.07	-22.26
52	♂	AHY	8	264		WR	2017	15.56	49.16	5.81	-22.26
52	♂	AHY	9	285		WR	2017	15.44	48.71	5.82	-22.19
52	♂	AHY	10	304		WR	2017	15.51	49.02	5.52	-21.69
102	♂	AHY	1	121		WR	2017	15.79	49.37	7.72	-22.08
102	♂	AHY	2	141		WR	2017	15.72	49.03	7.53	-22.08
102	♂	AHY	3	162		WR	2017	15.72	49.31	7.25	-22.20
102	♂	AHY	4	182		WR	2017	15.75	49.43	7.19	-22.34
102	♂	AHY	5	203		WR	2017	15.51	49.08	6.84	-22.30
102	♂	AHY	6	223		WR	2017	15.51	49.12	6.57	-22.04
102	♂	AHY	7	244		WR	2017	15.45	48.97	6.71	-21.89
102	♂	AHY	8	264		WR	2017	15.57	49.41	6.40	-22.07
102	♂	AHY	9	285	BQ	WR	2017	15.56	49.31	6.08	-22.38
102	♂	AHY	10	304	BQ	WR	2017	15.56	49.28	5.98	-22.54
170	♂	AHY	2	141		TR	2018	15.62	48.73	7.61	-23.42
170	♂	AHY	3	162		TR	2018	15.68	48.95	8.12	-22.69
170	♂	AHY	4	182		TR	2018	15.61	48.85	7.36	-22.68
170	♂	AHY	6	223		TR	2018	15.59	49.12	6.96	-22.35
170	♂	AHY	7	244	BS	TR	2018	15.47	48.57	6.98	-22.18
170	♂	AHY	8	264	BS	TR	2018	15.55	48.92	7.00	-21.93
170	♂	AHY	9	285	BS	TR	2018	15.64	49.16	6.96	-22.28
172	♂	AHY	1	121		TR	2018	15.62	45.51	6.65	-23.36
172	♂	AHY	2	141		TR	2018	15.77	47.85	8.79	-22.28
172	♂	AHY	3	162		TR	2018	16.15	47.97	9.29	-22.02
172	♂	AHY	4	182		TR	2018	15.43	47.82	8.34	-22.32
172	♂	AHY	5	203		TR	2018	15.61	48.99	7.31	-22.63
172	♂	AHY	6	223		TR	2018	15.62	48.99	7.16	-22.58
172	♂	AHY	7	244		TR	2018	15.63	49.00	7.03	-22.22
172	♂	AHY	8	264		TR	2018	15.68	49.13	7.23	-21.84
172	♂	AHY	9	285	BQ	TR	2018	15.59	48.82	7.64	-21.83
172	♂	AHY	10	304	BQ	TR	2018	15.60	48.79	7.46	-22.13
177	♂	AHY	1	121		TR	2018	15.13	45.75	6.95	-23.94
177	♂	AHY	2	141		TR	2018	15.84	48.15	7.26	-24.01

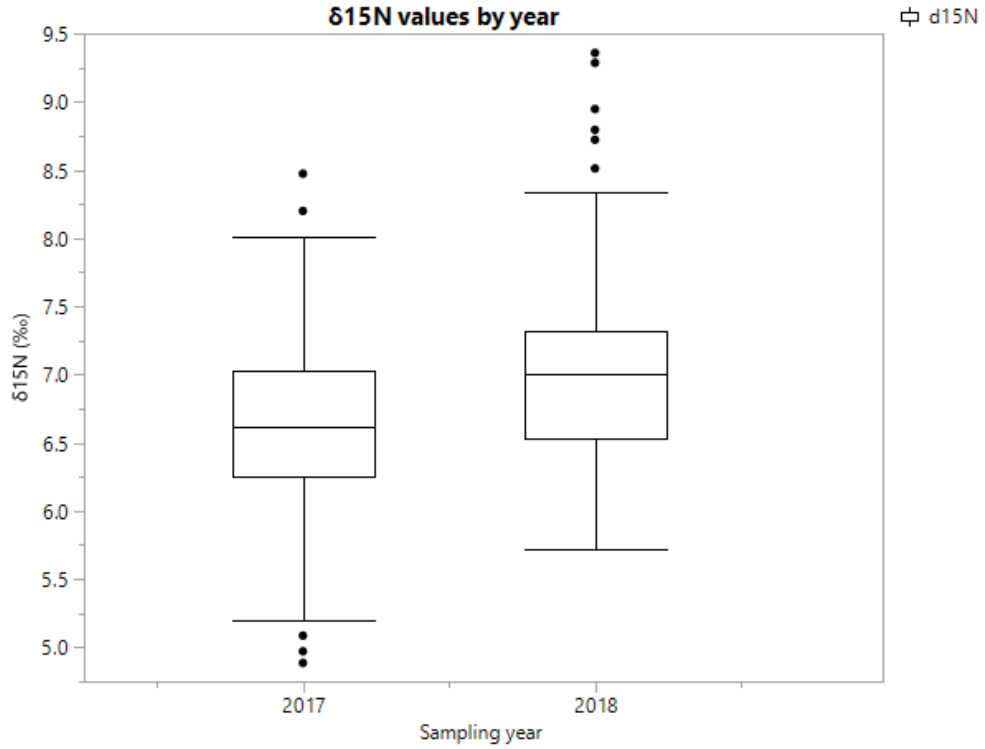
177		AHY	3	162		TR	2018	16.04	48.11	7.92	-23.60
177		AHY	4	182	BS	TR	2018	15.83	48.20	8.14	-23.38
177		AHY	5	203		TR	2018	15.60	47.77	7.47	-23.56
177		AHY	6	223		TR	2018	15.69	48.59	6.39	-23.33
177		AHY	7	244		TR	2018	15.51	48.14	6.36	-23.06
177		AHY	8	264		TR	2018	15.78	49.21	6.58	-22.95
177		AHY	9	285	BQ	TR	2018	15.71	48.89	6.46	-23.12
177		AHY	10	304	BQ	TR	2018	15.75	48.52	6.35	-23.28
182		AHY	1	121		TR	2018	15.81	48.53	7.14	-23.18
182		AHY	2	141		TR	2018	13.99	42.51	8.95	-22.18
182		AHY	3	162		TR	2018	10.80	35.32	9.30	-22.10
182		AHY	4	182		TR	2018	15.56	48.12	8.72	-21.96
182		AHY	5	203		TR	2018	15.58	48.85	7.42	-22.21
182		AHY	6	223		TR	2018	15.54	48.60	7.31	-22.32
182		AHY	7	244		TR	2018	15.58	48.74	7.51	-22.13
182		AHY	8	264		TR	2018	15.74	49.36	7.67	-21.30
182		AHY	9	285		TR	2018	15.65	48.93	7.44	-21.37
182		AHY	10	304	BQ	TR	2018	15.49	48.41	7.35	-21.68
15		HY	1	152	BS	WR	2017	15.47	48.17	6.29	-22.99
15		HY	2	174	BS	WR	2017	15.48	48.05	6.41	-22.86
15		HY	3	196	BS	WR	2017	15.57	48.53	6.62	-22.56
15		HY	4	218	BS	WR	2017	15.56	48.70	6.87	-22.34
15		HY	5	239	BS	WR	2017	15.75	49.01	6.76	-22.53
15		HY	6	261		WR	2017	15.51	48.62	6.76	-22.52
15		HY	7	283		WR	2017	15.71	48.89	6.84	-22.18
15		HY	8	304		WR	2017	15.73	48.82	5.97	-21.81
15		HY	9	132		WR	2017	15.50	48.92	6.61	-22.75
15		HY	10	132		WR	2017	15.64	48.75	6.52	-22.63
44		HY	1	152		WR	2017	15.72	48.71	5.79	-22.49
44		HY	2	174		WR	2017	15.69	48.58	7.35	-22.80
44		HY	3	196		WR	2017	15.73	49.10	7.18	-22.91
44		HY	4	218		WR	2017	15.70	48.90	7.07	-22.81
44		HY	5	239		WR	2017	15.70	48.91	6.82	-22.64
44		HY	6	261		WR	2017	15.93	49.47	6.45	-22.57
44		HY	7	283		WR	2017	15.88	49.32	5.92	-22.63
44		HY	8	304		WR	2017	15.81	48.97	5.55	-22.77
44		HY	9	132		WR	2017	15.79	49.30	7.14	-22.92
44		HY	10	132		WR	2017	15.69	48.88	7.07	-22.88
50		HY	1	152		WR	2017	15.65	48.70	7.07	-22.43
50		HY	2	174		WR	2017	15.55	48.01	7.61	-22.23
50		HY	3	196	BS	WR	2017	15.58	48.84	6.62	-22.11

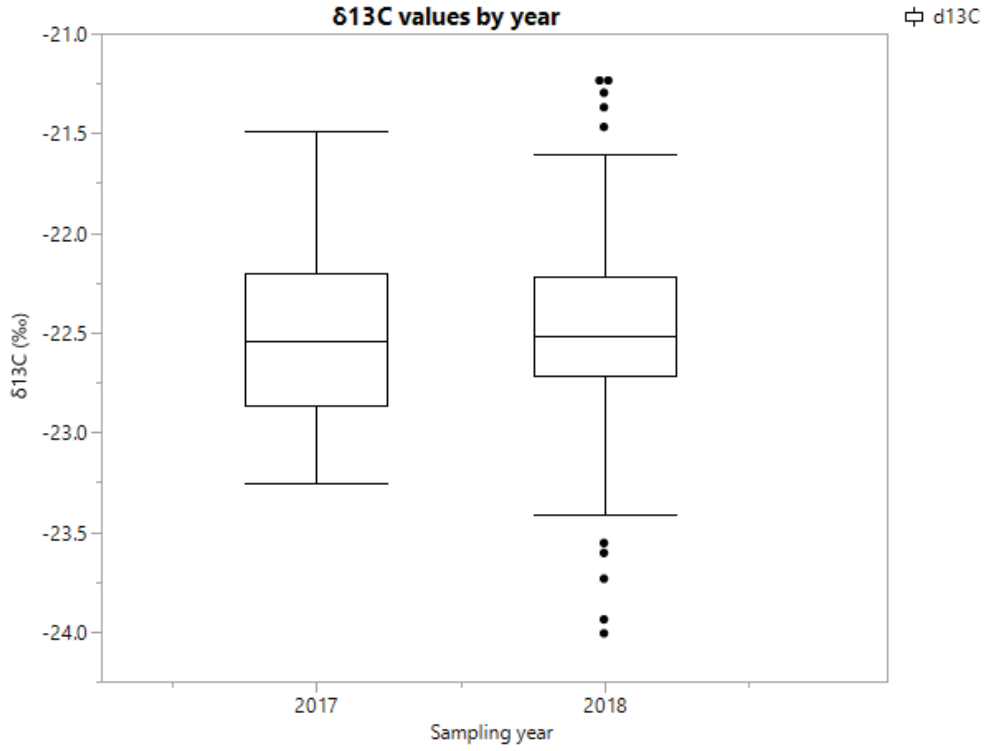
50		HY	4	218	BS	WR	2017	15.45	48.51	6.25	-22.51
50		HY	5	239	BS	WR	2017	15.53	48.89	6.24	-22.57
50		HY	6	261	BS	WR	2017	15.70	48.83	6.33	-22.50
50		HY	7	283	BS	WR	2017	15.52	48.69	6.54	-22.20
50		HY	8	304	BS	WR	2017	15.67	48.79	6.13	-21.85
50		HY	9	132		WR	2017	15.60	49.12	6.44	-22.59
50		HY	10	132		WR	2017	15.73	49.21	6.29	-22.58
51		HY	1	152		WR	2017	15.71	49.00	6.88	-23.25
51		HY	2	174		WR	2017	15.65	48.85	6.91	-23.23
51		HY	3	196		WR	2017	15.62	48.81	6.98	-23.17
51		HY	4	218		WR	2017	15.60	48.57	7.04	-22.94
51		HY	5	239		WR	2017	15.51	48.69	6.71	-22.45
51		HY	6	261		WR	2017	15.54	48.88	6.68	-22.01
51		HY	7	283		WR	2017	15.61	48.93	6.28	-21.62
51		HY	8	304	BQ	WR	2017	15.57	48.92	6.23	-21.49
51		HY	9	132		WR	2017	15.46	48.76	6.79	-23.12
51		HY	10	132		WR	2017	15.58	49.02	6.62	-22.90
101		HY	1	152		WR	2017	15.78	49.15	7.17	-23.11
101		HY	2	174		WR	2017	15.86	49.18	6.87	-23.03
101		HY	3	196		WR	2017	15.59	48.95	6.77	-23.03
101		HY	4	218		WR	2017	15.56	48.76	6.59	-22.96
101		HY	5	239		WR	2017	15.60	49.15	6.36	-22.88
101		HY	6	261		WR	2017	15.59	49.19	6.74	-22.68
101		HY	7	283		WR	2017	15.51	48.90	6.45	-22.49
101		HY	8	304		WR	2017	15.73	49.64	5.56	-22.28
101		HY	9	132		WR	2017	15.53	49.05	6.43	-23.05
101		HY	10	132		WR	2017	15.51	49.05	6.35	-22.94
166		HY	1	152		TR	2018	15.75	46.25	7.60	-22.70
166		HY	2	174		TR	2018	15.76	46.94	7.19	-22.95
166		HY	3	196		TR	2018	15.83	47.76	6.68	-23.12
166		HY	4	218		TR	2018	15.84	48.37	6.57	-23.17
166		HY	5	239		TR	2018	15.53	47.92	7.27	-23.00
166		HY	6	261		TR	2018	15.67	48.91	7.53	-22.83
166		HY	7	283		TR	2018	15.59	48.58	8.04	-22.69
166		HY	8	304		TR	2018	15.59	48.72	7.26	-22.72
166		HY	9	132		TR	2018	15.52	48.58	6.79	-23.22
166		HY	10	132		TR	2018	15.51	48.25	6.86	-23.21
176		HY	1	152		TR	2018	15.51	48.58	7.19	-22.84
176		HY	2	174		TR	2018	15.49	48.64	7.00	-22.92
176		HY	3	196		TR	2018	15.63	48.91	6.95	-22.95
176		HY	4	218		TR	2018	15.51	48.39	7.10	-22.94

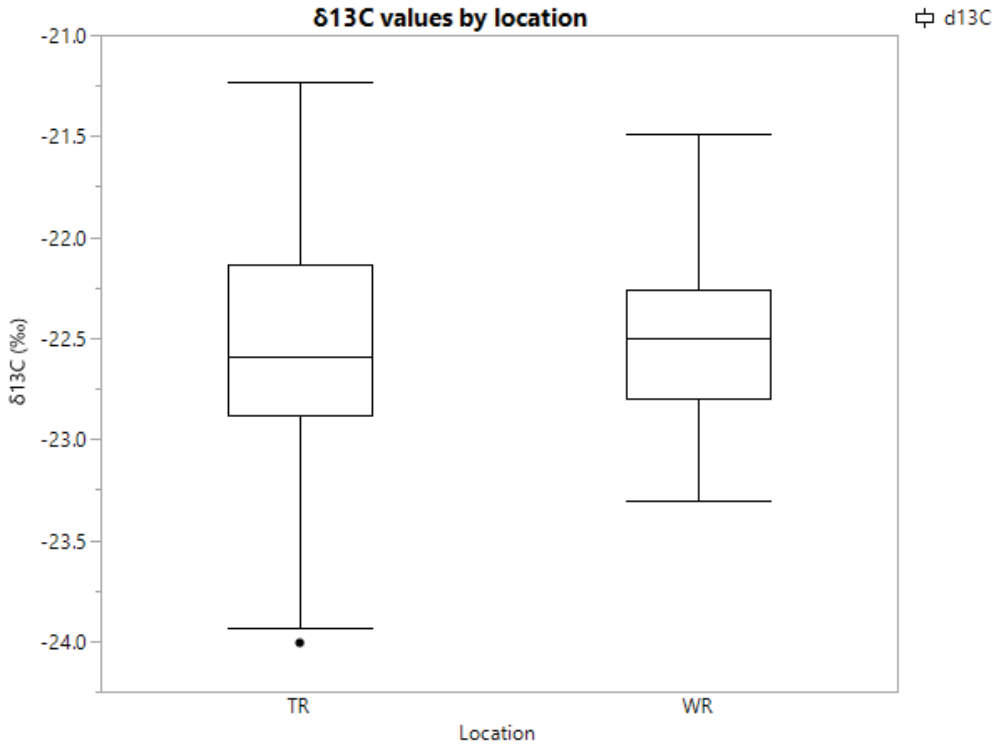
176	♂	HY	5	239		TR	2018	15.56	48.91	6.98	-22.88
176	♂	HY	6	261		TR	2018	15.56	48.85	7.04	-22.73
176	♂	HY	7	283		TR	2018	15.62	48.97	7.23	-22.60
176	♂	HY	8	304		TR	2018	15.65	49.28	7.18	-22.59
176	♂	HY	9	132		TR	2018	15.46	48.59	7.07	-22.97
176	♂	HY	10	132		TR	2018	15.53	48.90	6.85	-22.96
200	♂	HY	1	152		TR	2018	15.59	48.97	6.95	-22.69
200	♂	HY	2	174		TR	2018	15.56	48.84	6.97	-22.65
200	♂	HY	3	196		TR	2018	15.68	49.25	6.92	-22.64
200	♂	HY	4	218		TR	2018	15.82	49.46	7.20	-22.55
200	♂	HY	5	239		TR	2018	15.56	48.76	7.11	-22.41
200	♂	HY	6	261		TR	2018	15.50	48.90	6.94	-22.13
200	♂	HY	7	283		TR	2018	15.64	49.18	7.03	-22.33
200	♂	HY	8	304	BQ	TR	2018	15.75	49.41	7.09	-22.63
200	♂	HY	9	132		TR	2018	15.53	49.18	7.15	-22.74
200	♂	HY	10	132		TR	2018	15.43	48.72	6.92	-22.54

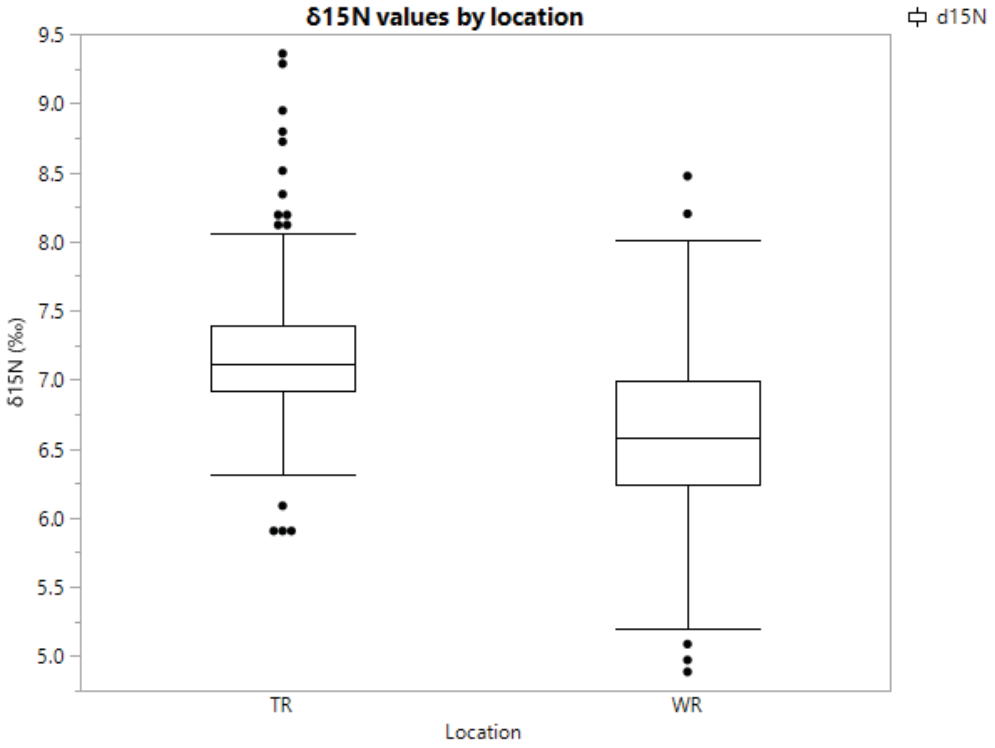


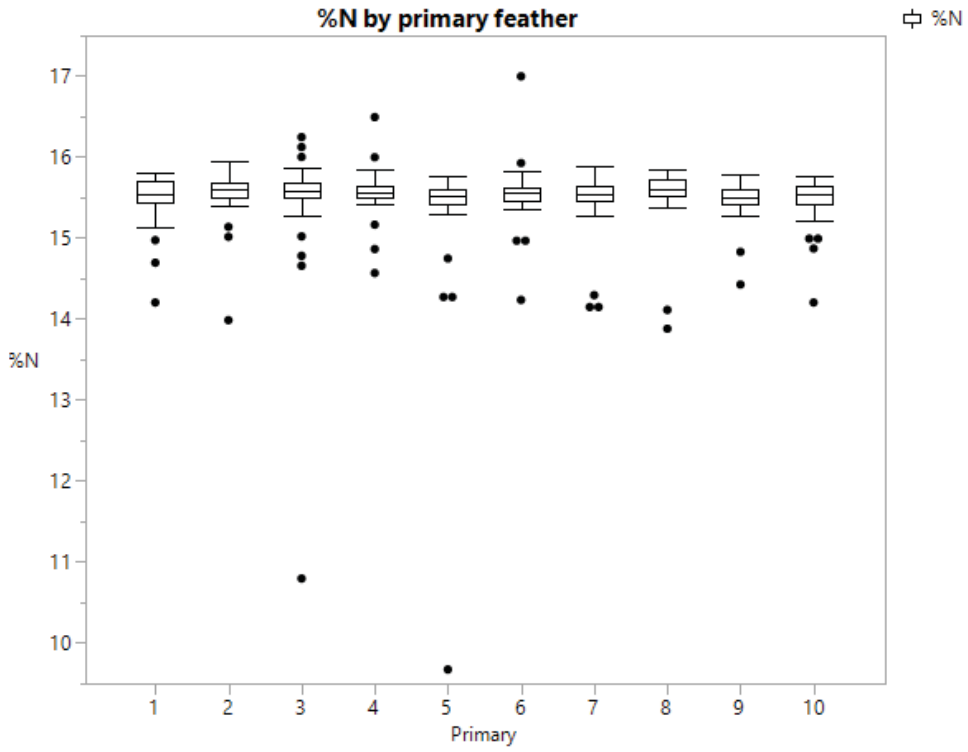

δ13C vs. Julian date
δ15N (‰)
-21.5
-22.0
-22.5
-23.0
-23.5
-24.0
FAHY
FHY
MAHY
MHY
Class
150
200
250
300
Julian date

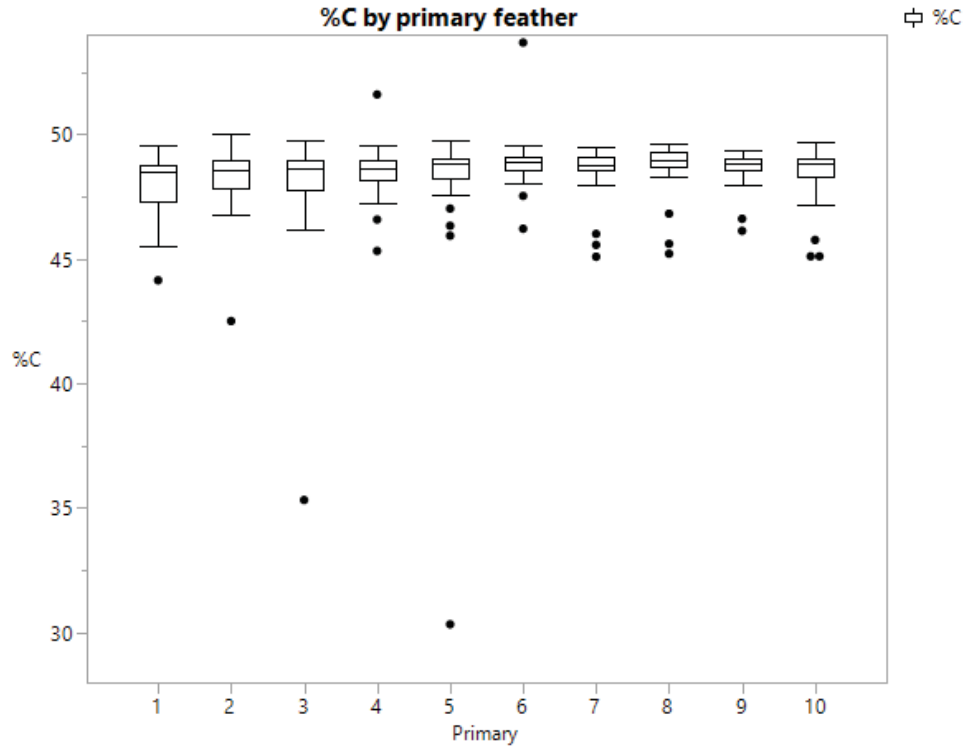

δ15N values by year
d15N
δ15N (‰)
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
2017
2018
Sampling year


δ13C values by year
d13C
-21.0
-21.5
-22.0
-22.5
-23.0
-23.5
-24.0
δ13C (‰)
2017
2018
Sampling year


δ13C values by location
d13C
-21.0
-21.5
-22.0
-22.5
-23.0
-23.5
-24.0
δ13C (‰)
TR
WR
Location


δ15N values by location
d15N
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
δ15N (‰)
TR
WR
Location


%N by primary feather
%N
17
16
15
14
13
12
11
10
%N
1
2
3
4
5
6
7
8
9
10
Primary


%C by primary feather
%C
50
45
40
35
30
%C
1
2
3
4
5
6
7
8
9
10
Primary

APPENDIX 13: GELMAN RUBIN AND GEWEKE DIAGNOSTICS RESULTS

Model	Class	Gelman-Rubin results			Geweke results				Meets '5% within +/-1.96' criteria		
		0 > 1.01	0 > 1.05	0 > 1.1	Chain 1	Chain 1	Chain 3	Variables	Chain 1	Chain 1	Chain 3
Three-source trophic	Adult female	0	0	0	32	16	149	650	5%	2%	23%
	Adult male	0	0	0	6	80	4	315	2%	25%	1%
	Juvenile	0	0	0	44	48	27	768	6%	6%	4%
Four-source trophic	Adult female	5	0	0	24	22	199	824	3%	3%	24%
	Adult male	148	41	16	41	8	161	400	10%	2%	40%
	Juvenile	10	0	0	249	71	232	973	26%	7%	24%
Two-source	Adult female	0	0	0	7	21	108	476	1%	4%	23%
	Adult male	6	2	0	7	10	3	230	3%	4%	1%
	Juvenile	0	0	0	59	16	9	563	10%	3%	2%
Three-source C4	Adult female	0	0	0	182	22	10	650	28%	3%	2%
	Adult male	0	0	0	21	7	10	315	7%	2%	3%
	Juvenile	6	0	0	299	14	36	768	39%	2%	5%
Four-source trohic C4	Adult female	55	0	0	21	26	37	824	3%	3%	4%
	Adult male	10	0	0	15	122	232	400	4%	31%	58%
	Juvenile	0	0	0	175	135	59	973	18%	14%	6%
Six-source	Adult female	1141	981	868	465	816	953	1172	40%	70%	81%
Three-source trophic no prior	Adult female	0	0	0	72	145	67	650	11%	22%	10%
Three-source trophic no lipid correction	Adult female	0	0	0	50	32	15	650	8%	5%	2%
Three-source trophic Torres-poche TDF	Adult female	0	0	0	26	46	67	650	4%	7%	10%
Three-source trophic SIDER TDF	Adult female	4	0	0	34	49	210	650	5%	8%	32%

APPENDIX 14.1: SENSITIVITY ANALYSIS

Model structure from the *three-source trophic* model was used to assess model sensitivity to changing various model parameters such as priors, trophic discrimination factor, and lipid correction.

Summary of effects

Three-source Trophic model 'unchanged' estimate

Source	Median	SD	95% CI
"Predatory" arthropods	0.08	0.03	0.03 - 0.16
"Prey" arthropods	0.68	0.07	0.53 - 0.82
C_3 Plants	0.23	0.07	0.11 - 0.37

Three-source Trophic with no lipid correction overall estimate

	Median	SD	95% CI
"Predatory" arthropods	0.06	0.03	0.02 - 0.14
"Prey" arthropods	0.78	0.07	0.63 - 0.90
C_3 Plants	0.15	0.06	0.06 - 0.29

Three-source Trophic with no prior overall estimate

	Median	SD	95% CI
"Predatory" arthropods	0.09	0.03	0.04 - 0.17
"Prey" arthropods	0.70	0.07	0.54 - 0.82
C_3 Plants	0.20	0.07	0.10 - 0.36

Three-source Trophic with Torres-poche TDF overall estimate

	Median	SD	95% CI
"Predatory" arthropods	0.08	0.04	0.03 - 0.18
"Prey" arthropods	0.78	0.06	0.63 - 0.88
C_3 Plants	0.13	0.05	0.06 - 0.25

Three-source Trophic with SIDER TDF overall estimate

	Median	SD	95% CI
"Predatory" arthropods	0.18	0.07	0.08 - 0.34
"Prey" arthropods	0.65	0.08	0.48 - 0.80
C_3 Plants	0.16	0.05	0.08 - 0.27

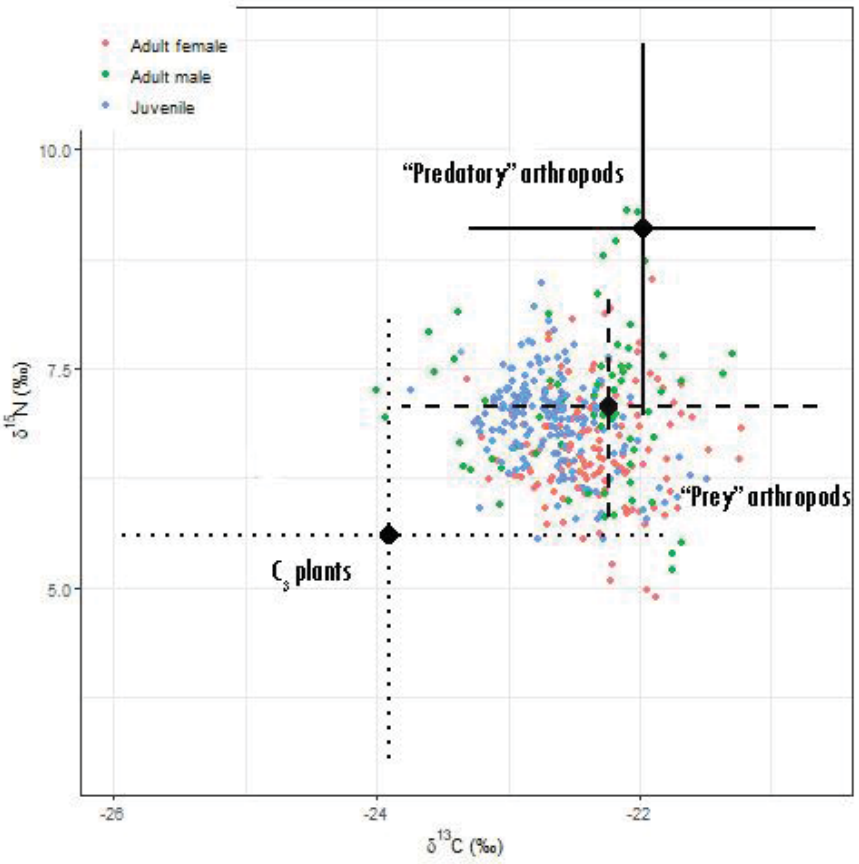
Lower value than unchanged model

Higher value than unchanged model

No significant differences (95% Cis overlap)

APPENDIX 14.2: THREE-SOURCE TROPHIC MODEL WITHOUT INFORMATIVE PRIOR

Mixing space

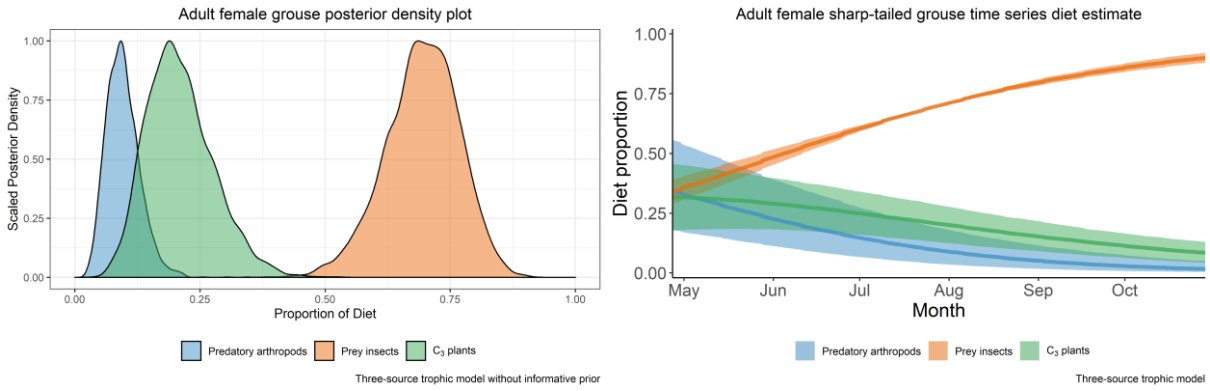


Corrected for trophic discrimination using TDF from Caut et al. (2009)

Model input summary statistics

Three-source trophic:

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
"Predatory" arthropods	5.248	2.104	-24.138	1.266	0.107	0.520	96
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
C_3 plants	1.767	2.543	-26.066	2.058	0.027	0.466	102



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

Three-source Trophic with no prior overall estimate

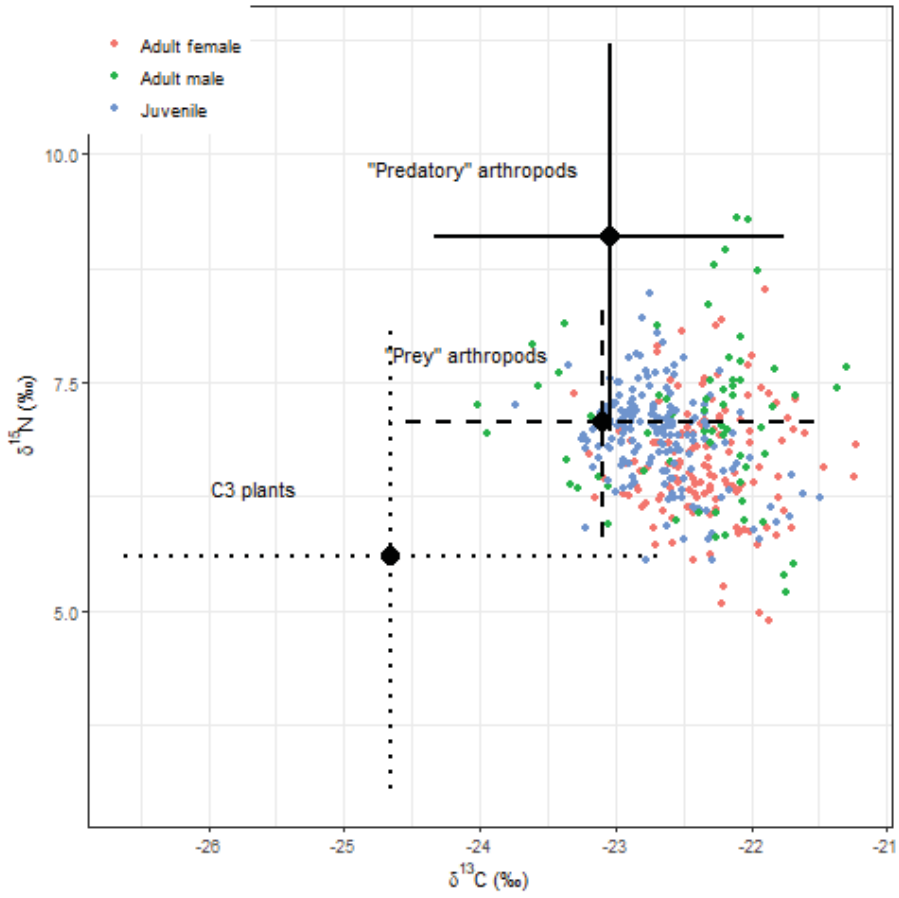
	Median	SD	95% CI
"Predatory" arthropods	0.09	0.03	0.04 - 0.17
"Prey" arthropods	0.70	0.07	0.54 - 0.82
C_3 Plants	0.20	0.07	0.10 - 0.36

Time series diet proportions for 'no prior' model

	Source	Median	95% CI
May	"Predatory" arthropods	0.34	0.18 - 0.56
	"Prey" arthropods	0.34	0.27 - 0.36
	C_3 Plants	0.32	0.18 - 0.46
August	"Predatory" arthropods	0.09	0.04 - 0.19
	"Prey" arthropods	0.70	0.68 - 0.68
	C_3 Plants	0.21	0.13 - 0.28
October	"Predatory" arthropods	0.02	0.00 - 0.05
	"Prey" arthropods	0.90	0.87 - 0.91
	C_3 Plants	0.08	0.04 - 0.13

APPENDIX 14.3: THREE-SOURCE TROPHIC MODEL WITH NO LIPID CORRECTION

Mixing space

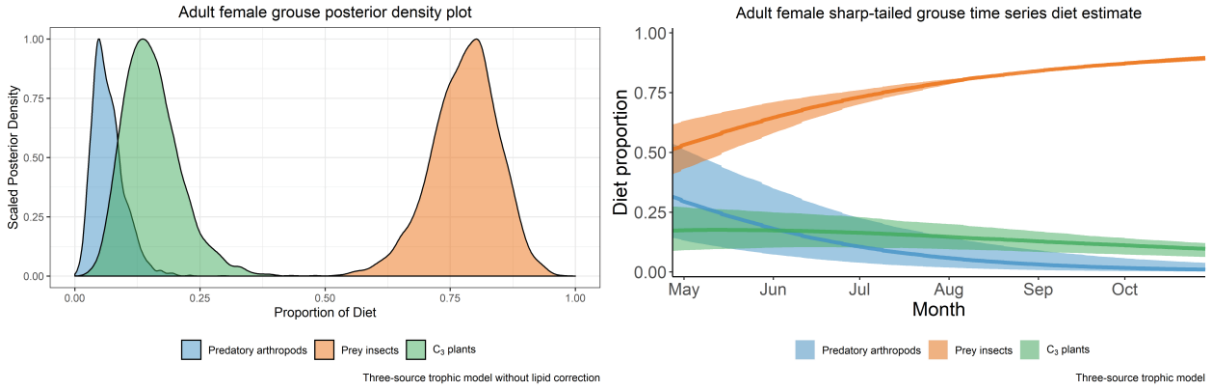


Corrected for trophic discrimination using TDF from Caut et al. (2009)

Model input summary statistics

Three-source trophic:

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
"Predatory" arthropods	5.248	2.104	-24.138	1.266	0.107	0.520	96
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
C_3 plants	1.767	2.543	-26.066	2.058	0.027	0.466	102



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

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Three-source Trophic with no lipid correction overall estimate

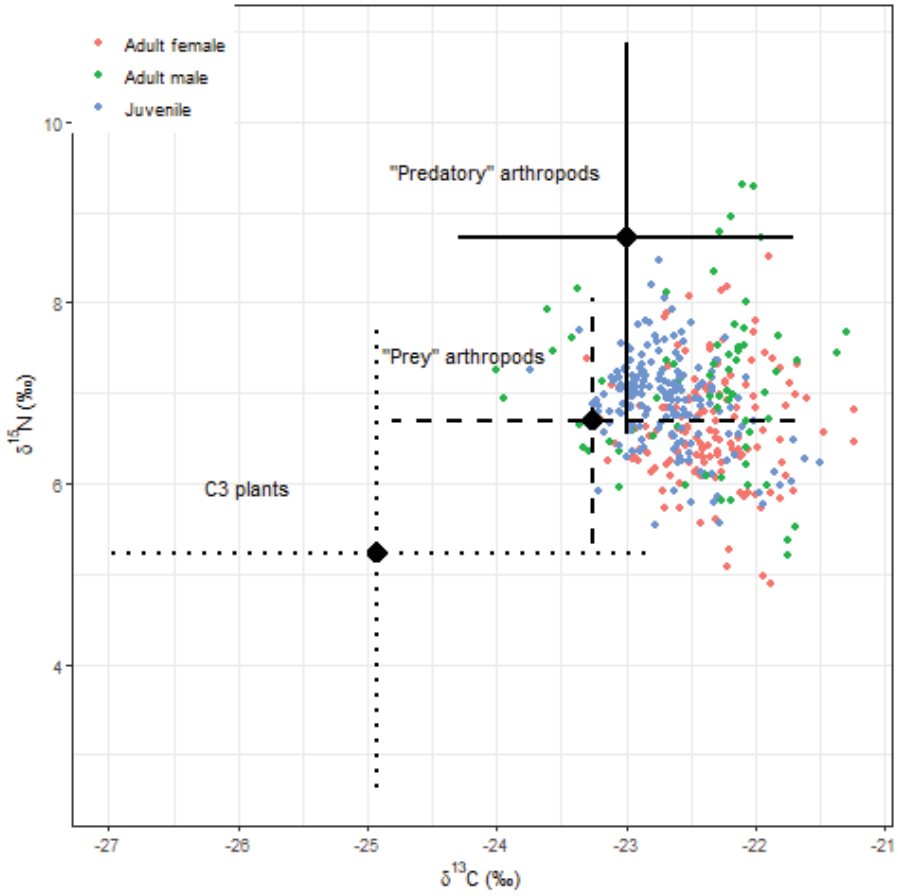
	Median	SD	95% CI
"Predatory" arthropods	0.06	0.03	0.02 - 0.14
"Prey" arthropods	0.78	0.07	0.63 - 0.90
C_3 Plants	0.15	0.06	0.06 - 0.29

Time series diet proportions for 'no lipid correction' model

	Source	Median	95% CI
May	"Predatory" arthropods	0.31	0.14 - 0.54
	"Prey" arthropods	0.51	0.38 - 0.58
	C_3 Plants	0.17	0.09 - 0.27
August	"Predatory" arthropods	0.06	0.02 - 0.15
	"Prey" arthropods	0.79	0.75 - 0.78
	C_3 Plants	0.15	0.10 - 0.20
October	"Predatory" arthropods	0.01	0.00 - 0.04
	"Prey" arthropods	0.89	0.88 - 0.90
	C_3 Plants	0.10	0.06 - 0.12

APPENDIX 14.4: THREE-SOURCE TROPHIC MODEL USING TDF FROM TORRES-POCHE (2017)

Mixing space

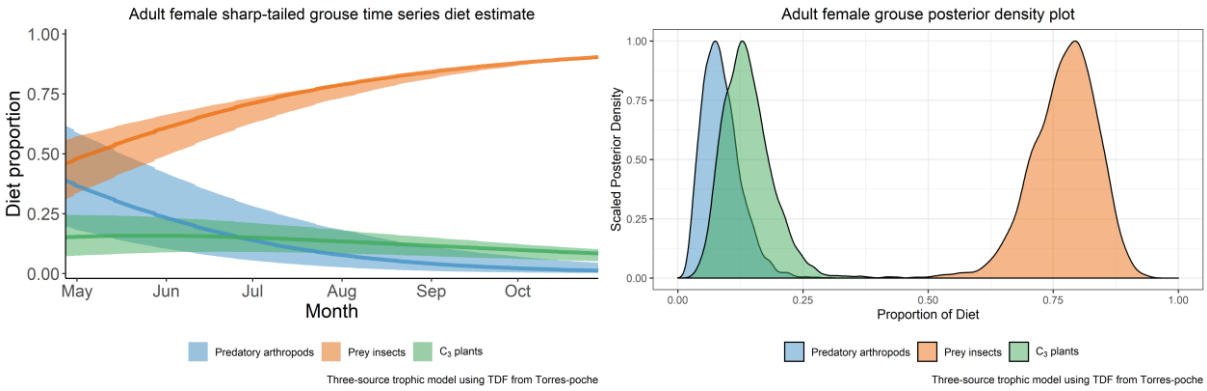


TDF experimentally derived for captive Attwater's prairie chickens (*Tympanuchus cupido attwateri*) by Torres-poche (2017): $\Delta\delta^{15}N$ = 3.46 ± 0.53‰ and $\Delta\delta^{13}C$ = 1.14 ± 0.28‰

Model input summary statistics

Three-source trophic:

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
"Predatory" arthropods	5.248	2.104	-24.138	1.266	0.107	0.520	96
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
C_3 plants	1.767	2.543	-26.066	2.058	0.027	0.466	102



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

Three-source Trophic with Torres-poche TDF overall estimate

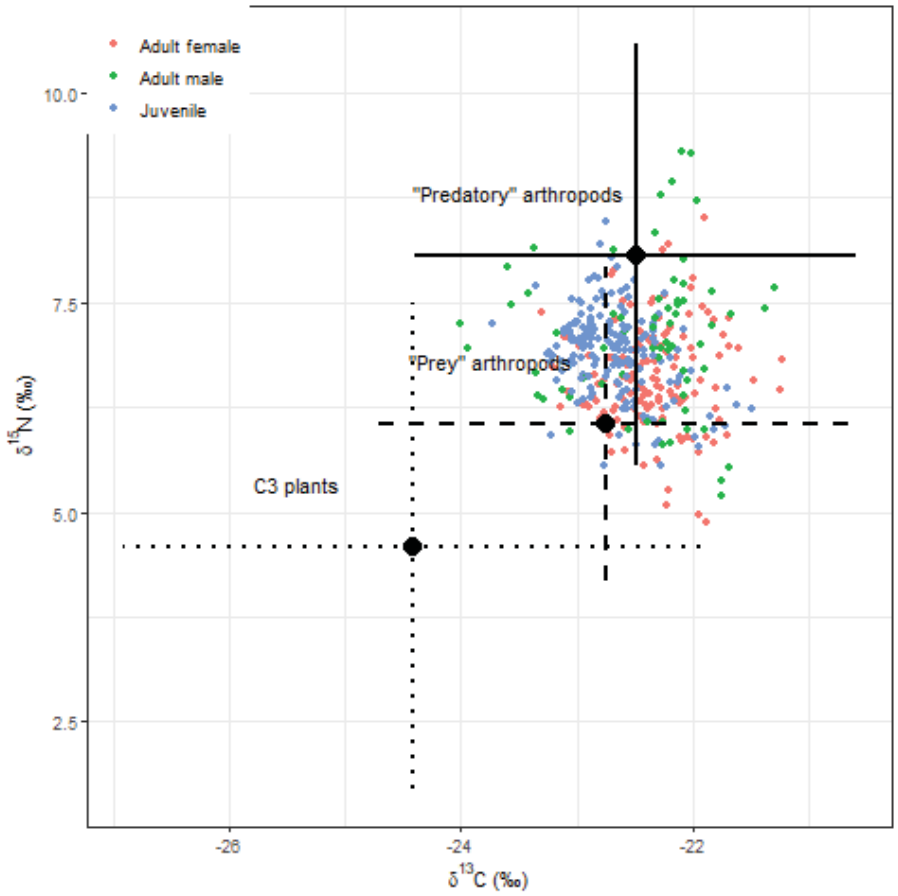
	Median	SD	95% CI
"Predatory" arthropods	0.08	0.04	0.03 - 0.18
"Prey" arthropods	0.78	0.06	0.63 - 0.88
C_3 Plants	0.13	0.05	0.06 - 0.25

Time series diet proportions using Torres-poche TDF

	Source	Median	95% CI
May	"Predatory" arthropods	0.39	0.20 - 0.62
	"Prey" arthropods	0.46	0.31 - 0.56
	C_3 Plants	0.15	0.07 - 0.25
August	"Predatory" arthropods	0.08	0.03 - 0.19
	"Prey" arthropods	0.78	0.72 - 0.79
	C_3 Plants	0.14	0.08 - 0.19
October	"Predatory" arthropods	0.01	0.00 - 0.04
	"Prey" arthropods	0.90	0.90 - 0.90
	C_3 Plants	0.08	0.05 - 0.10

APPENDIX 14.5: THREE-SOURCE TROPHIC MODEL WITH TDF DERIVED USING SIDER

Mixing space



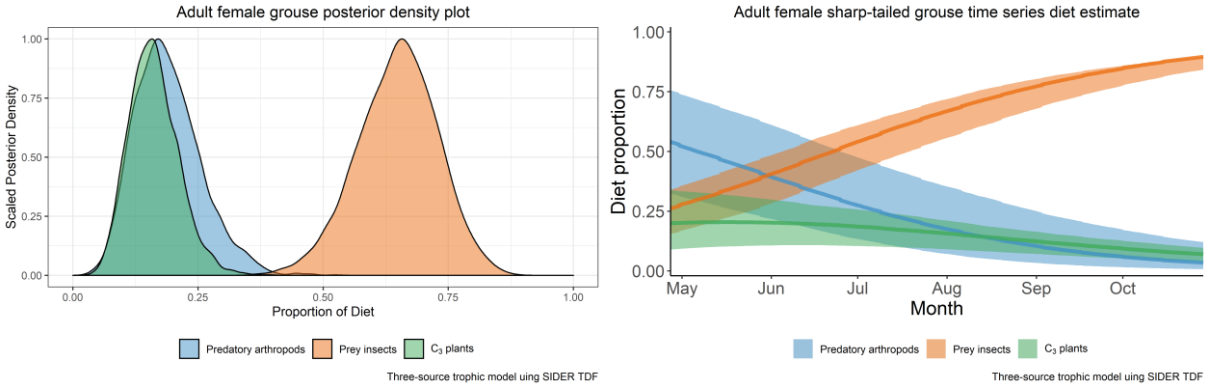
TDF derived using the SIDER (Stable Isotope Discrimination Estimation in R) (Healy et al. 2017) and the following SIDER recipe: species = "Tympanuchus_phasianellus", habitat = "terrestrial", taxonomic.class = "aves", tissue = "feather", diet.type = "omnivore", tree = combined_trees

$\Delta\delta^{15}N = 2.82 \pm 1.40‰$ and $\Delta\delta^{13}C = 1.64 \pm 1.42‰$

Model input summary statistics

Three-source trophic:

Source	Mean $\delta^{15}N$	SD $\delta^{15}N$	Mean $\delta^{13}C$	SD $\delta^{13}C$	N Conc	C Conc	n
"Predatory" arthropods	5.248	2.104	-24.138	1.266	0.107	0.520	96
"Prey" arthropods	3.231	1.249	-24.390	1.541	0.119	0.516	40
C_3 plants	1.767	2.543	-26.066	2.058	0.027	0.466	102



Left: Posterior density plot of diet proportions representing the probability distributions for each food source. Right: Time series estimates of food source proportions. The lines represent the median values and associated 95% credible intervals.

Three-source Trophic with SIDER TDF overall estimate

	Median	SD	95% CI
"Predatory" arthropods	0.18	0.07	0.08 - 0.34
"Prey" arthropods	0.65	0.08	0.48 - 0.80
C_3 Plants	0.16	0.05	0.08 - 0.27

Time series diet proportions using SIDER TDF

	Source	Median	95% CI
May	"Predatory" arthropods	0.54	0.32 - 0.76
	"Prey" arthropods	0.26	0.15 - 0.34
	C_3 Plants	0.20	0.09 - 0.34
August	"Predatory" arthropods	0.19	0.08 - 0.37
	"Prey" arthropods	0.65	0.54 - 0.71
	C_3 Plants	0.16	0.09 - 0.22
October	"Predatory" arthropods	0.03	0.01 - 0.12
	"Prey" arthropods	0.90	0.84 - 0.90
	C_3 Plants	0.07	0.04 - 0.10

APPENDIX 15: SHARP-TAILED GROUSE NECROPSY DATA

Bird ID	Collection site	Class	Weight (g)	Age	Sex	Bursa present?	Bursa depth (mm)	Ceacum length (cm)	Large intestine (cm)	Small intestine (cm)
165	TR	F-AHY	620	AHY	F	No		62.0	13.4	117.0
167	WR	F-AHY	670	AHY	F	No		48.8	14.8	117.0
168	WR	F-AHY	750	AHY	F	No		59.0	14.0	141.0
171	WR	F-AHY	750	AHY	F	No		51.4	13.0	124.4
173	WR	F-AHY	680	AHY	F	No		43.4	14.8	127.4
174	WR	F-AHY	800	AHY	F	No		57.0	7.0	118.2
178	TR	F-AHY	770	AHY	F	No		63.2	16.0	135.8
181	TR	F-AHY		AHY	F	No		62.4	13.6	135.4
183	TR	F-AHY		AHY	F	No		45.0	12.0	122.4
185	TR	F-AHY		AHY	F	No		66.0	13.0	130.6
187	TR	F-AHY		AHY	F	No		54.0	14.4	121.0
201	TR	F-AHY	770	AHY	F	No		64.4	12.4	144.8
169	WR	F-HY	690	HY	F	Yes	14	50.6		
179	TR	F-HY		HY	F	Yes	13	51.2	12.8	127.0
180	TR	F-HY		HY	F	Yes	14	57.4	14.0	129.8
186	TR	F-HY		HY	F	Yes	14	61.0	12.0	123.2
170	TR	M-AHY	860	AHY	M	No		58.6	15.0	136.0
172	TR	M-AHY	900	AHY	M	No		71.6	13.0	132.0
177	TR	M-AHY		AHY	M	No		57.4	13.6	130.6
182	TR	M-AHY	820	AHY	M	No		55.2	15.6	136.0
184	TR	M-AHY		AHY	M	No		55.4	14.4	135.0
166	TR	M-HY	730	HY	M	Yes	14	60.0	12.8	130.8
176	TR	M-HY		HY	M	Yes	13	55.0		
200	TR	M-HY		HY	M	Yes	12	48.8		

Intestinal morphology of a sharp-tailed grouse. From the right: crop (absent); proventriculus; gizzard; small intestine; large intestine and cloaca (top), and 2 long ceca (57 cm on average) splitting from the junction of the small and large intestine.