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Greater Sage-Grouse (Centrocercus urophasianus) Habitat Selection in Northwestern Wyoming and Stable Isotope Analysis of Fecal Material

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ABSTRACT

Dramatic range-wide declines in Greater Sage-Grouse populations have prompted efforts to determine habitat characteristics that are selected by sage-grouse for foraging, nesting and brood-rearing areas in an effort to conserve this species. Managers at Heart Mountain and Y U Bench in northwestern Wyoming expressed the need to quantify various habitat characteristics and to determine key use areas at both study sites. Data were collected on a variety of habitat variables in spots selected by grouse for foraging, nesting, and brood-rearing activities. These variables were compared to the same variables measured at random points at both study sites. Significant differences existed between foraging/nesting habitat plots selected by sage-grouse and random habitat plots at both sites. Areas used most by sage-grouse for lekking, nesting, and brood-rearing were identified at both study locations. Data analyses indicated sage-grouse at Heart Mountain were choosing foraging and nesting areas dominated by junegrass while grouse at YU Bench were choosing foraging sites dominated by junegrass and nesting sites dominated by needle and thread grass.

Stable carbon and nitrogen isotope ratios were used to determine diet compositions of adults and chicks using avian fecal matter instead of tissue. Sage-grouse produce two different kinds of fecal material: intestinal droppings and cecal tars. Both types of fecal matter as well as various insect and plant species were collected at both field sites. Isotope analyses combined with mixing model analyses indicated that adult grouse at both sites were relying more on C_3 grasses than either forbs or sagebrush in the summer months compared to what has been previously reported. Mixing model results confirmed that insects were the main food item for chicks at these two locations but these results also indicated that chicks are consuming more C_3, C_4 and CAM plants than has been previously reported.

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DEDICATION

I would like to dedicate this dissertation to my best friend, Travis. He was my constant companion during my years in graduate school. He will be forever missed.

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CHAPTER 1. INTRODUCTION

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Dramatic range-wide declines in Greater Sage-Grouse populations have prompted efforts to conserve this unique avian species of the western United States and Canada. Sites owned by the Bureau of Land Management and The Nature Conservancy in northwestern Wyoming currently support Greater Sage-Grouse populations. In an effort to slow the downward spiral of this bird, certain sage-grouse conservation goals must be met. Managers at these locations wanted to begin their conservation efforts by accomplishing the following conservation objectives: (1) determine key areas of both large study sites that were being utilized by sage-grouse for lekking, nesting, and brood-rearing activities, (2) quantify the habitat characteristics that were being selected by sage-grouse for foraging, nesting and brood-rearing activities, and (3) use noninvasive stable isotope analyses combined with mixing models to investigate the primary food items being eaten by sage-grouse at both sites. I participated with the Bureau of Land Management and The Nature Conservancy in their conservation efforts by adopting these conservation objectives as my own dissertation research project. The chapters that follow this introduction give the reader background information about the Greater Sage-Grouse as well as a complete description of the key use areas that were determined, the quantification of the habitat characteristics selected by sage-grouse at both sites, background information about stable isotopes in general, and information about how stable isotopes were used in this particular study to determine the food items most important to sage-grouse at these sites.

CHAPTER 2. LITERATURE REVIEW

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INTRODUCTION

Meriwether Lewis provided the first written account of the Greater Sage-Grouse (*Centrocercus urophasianus*) in June of 1805 (Bent 1932). Lewis and Clark first encountered this species of grouse at the confluence of the Marias and Missouri Rivers in western Montana during their expedition (Bent 1932). Historically, sage-grouse inhabited sagebrush habitats in Alberta, Saskatchewan, British Columbia, Nevada, Colorado, Utah, Oregon, Washington, California, Montana, Wyoming, Idaho, North Dakota, South Dakota, Nebraska, Arizona, and New Mexico (Aldrich and Duvall 1955, Aldrich 1963, Schroeder 2004). Suitable habitat for Greater Sage-Grouse has decreased from an estimated 1,200,483 km^2 during presettlement days to only 668,412 km^2, which is almost a 56% reduction in available habitat (Schroeder 2004). Much of what remains of this biome has been altered in some way since presettlement times (West 1996). The present-day range of Greater Sage-Grouse includes southwestern Saskatchewan, southeastern Alberta, northeastern and eastern California, southeastern Oregon, central Washington, southern Idaho, eastern and southwestern Montana, most of Wyoming, northern Nevada, northwestern Colorado, northwestern and southwestern South Dakota, and southwestern portions of North Dakota (Connelly and Braun 1997, Schroeder et al. 2004). Greater Sage-Grouse have been extirpated from New Mexico, Arizona, Nebraska, and British Columbia (Schroeder et al. 2004). In 2000, the American Ornithologists' Union split the sage-grouse into two separate species, the Greater Sage-Grouse (*Centrocercus urophasianus*) and the Gunnison Sage-Grouse (*Centrocercus minimus*), based on new evidence of genetic differences as well as differences in courtship displays, plumage characteristics, and morphometrics (Young et al. 2000). Currently, Gunnison Sage-Grouse are found only in the Gunnison Basin of southwestern Colorado and adjacent San Juan County, Utah (Young et al. 2000).

Sage-grouse populations have undergone some level of decline range wide. Connelly and Braun (1997) estimated that sage-grouse populations have dropped by 47% in the last 50 years. Mining, agriculture, livestock overgrazing, recreation, urban development, oil and natural gas drilling, introduction of invasive weeds such as cheat grass, and wind energy development have all contributed to the decline of this obligate sagebrush species (Connelly et al. 2000, Crawford et al. 2004). Furthermore, the rapidly declining populations of this bird that remain now face another threat—West Nile Virus. It alone was responsible for a 25% decrease in some sage-grouse populations in Wyoming and Montana, USA, and Alberta, Canada in 2003 (Naugle et al. 2005).

Over the years, many petitions have been filed to list this species as threatened or endangered pursuant to the Endangered Species Act of 1973 (State of Wyoming Executive Department 2011). The United States Fish and Wildlife Service (USFWS) determined that listing the Greater Sage-Grouse as a threatened or an endangered species is warranted over all of its range. However, the USFWS has also determined that listing this species as threatened or endangered is currently precluded by higher priority listing actions (State of Wyoming Executive Department 2011). Therefore, Greater Sage-Grouse are currently considered a candidate species. The final listing determination for Greater Sage-Grouse is expected to be made by the USFWS in 2015. Several state and federal agencies have dedicated many resources to conserve Greater Sage-Grouse populations in Wyoming. Wyoming has developed a strategy called the Core Population Area strategy to coordinate the numerous on-going efforts to conserve the Greater Sage-Grouse (State of Wyoming Executive Department 2011). This strategy has become the blueprint for conservation measures in other states that have sage-grouse populations. Wyoming's

conservation plan is geared towards conservation of sage-grouse to prevent it from ever becoming listed as threatened or endangered under the Endangered Species Act of 1973.

DESCRIPTION AND LIFE HISTORY INFORMATION

The Greater Sage-Grouse (*Centrocercus urophasianus*) is the largest species of grouse in North America (Schroeder et al. 1999). This ground-dwelling, chicken-like bird can reach heights of up to two feet (Schroeder et al. 1999) and can weigh two to seven pounds (Beck and Braun 1978, Schroeder et al. 1999). Both sexes have grayish brown, buffy, and black feathers on their backs and sides as well as a black abdomen. Unlike females, males possess a large white ruff on the breast, long filoplumes on the back of the neck, a black throat, larger yellow superciliary combs, two olive green cervical apteria on the breast, and have longer tails (Johnsgard 1983).

This polygamous species is best known for its spectacular courtship displays, which are performed by male birds at open displaying arenas called leks. Each breeding season males gather together at the lek to perform their characteristic breeding displays to attract females. During the display, each male struts about with tail fanned and breast expanded outward while emitting popping sounds from the two exposed, inflated cervical apteria located on his breast (Schroeder et al. 1999).

Greater Sage-Grouse typically inhabit open areas situated at elevations of 3,000 to 9,500 feet that are dominated by various species of sagebrush (Girard 1937, Hays et al. 1998). Greater Sage-Grouse are considered to be sagebrush obligates. This bird is the only animal capable of surviving on sagebrush alone. This species exhibits low reproductive rates (Connelly 2000).

This fact paired with their extreme dependence upon sagebrush makes them extremely vulnerable to any alterations to sagebrush-steppe habitats they inhabit (Connelly 2000). Greater Sage-Grouse are particularly dependent on larger species of sagebrush, such as big sagebrush (*Artemisia tridentata*), three-tip sagebrush (*Artemisia tripartita*), and silver sagebrush (*Artemisia cana*), for food and cover throughout the year (Girard 1937, Hays et al. 1998, Schroeder et al. 1999). Although sage-grouse are most closely associated with habitats possessing larger species of sagebrush, these birds also utilize other types of sagebrush such as low sagebrush (*Artemisia arbuscula* Nutt.**)** and black sagebrush (*Artemisia nova* Nels.) Other types of native habitats used by these grouse are upland meadows, riparian meadows, and sagebrush grasslands (Patterson 1952, Dalke et al. 1963, Wallestad 1971). Despite their preference for sagebrush habitats, Greater Sage-Grouse also use human-altered habitats located adjacent to areas of sagebrush such as burns, roads, airstrips, and cropland (Patterson 1952, Hays et al. 1998, Rowland 2004).

Unlike other bird species, sage-grouse do not possess a muscular gizzard. Therefore, they cannot eat and digest seeds but instead must consume soft food items such as leafy vegetation (Wallestad 1975). Adult sage-grouse consume sagebrush year-round (Patterson 1952, Schneegas 1967, Klebenow 1973, Wallestad 1975, Call and Maser 1985). Martin (1951) found that sagebrush made up 71% of the total year-round diet. In late autumn, winter, and early spring, it comprises the bulk of their diet, especially in the winter when it makes up 100% of their diet (Patterson 1952, Schneegas 1967, Klebenow 1973, Wallestad 1975, Call and Maser 1985). Sagebrush species consumed include various subspecies of big sagebrush, low, silver, black and fringed sagebrush (*Artemisia frigida*) (Girard 1937, Rasmussen and Griner 1938, Patterson 1952, Leach and Hensley 1954, Wallestad et al. 1975, Remington and Braun 1985). Subspecies of big

sagebrush consumed include basin big, Wyoming big, and mountain big sagebrush. The latter two subspecies have less terpenes and are more nutritious than basin big sagebrush (Autenrieth et al. 1982). Welch et al. (1991) found sage-grouse preferred mountain big sagebrush over Wyoming and basin big sagebrush. Welch et al. (1991) also stated that even though these birds exhibit food preferences, the birds were capable of shifting their diets to include less preferred food items when preferred species became limited or unavailable. In May, Greater Sage-Grouse shift from a diet of exclusively sagebrush to one of primarily forbs and sagebrush (Rasmussen and Griner 1938, Leach and Hensley 1954, Patterson 1952, Wallestad et al. 1975). Forbs consumed include common dandelion (*Tarazacum officinale*), prickly lettuce (*Lactuca serriola*), snowberry (*Symhoricarpos rotundifolius*), cottonthorn (*Tetradymia spinosa*), rabbitbrush (*Chrysothamnus viscidiflorus*), Poaceae (grasses), sego lily (*Calochortus nuttallii*), legumes (Fabaceae), yarrow (*Achillea* spp.) and wild lettuce (*Lactuca* spp.) (Girard 1937, Leach and Hensley 1954, Martin 1970, Autenrieth et al. 1982, Schroeder et al. 1999). Barnett and Crawford (1994) found that consumption of various forbs, which are higher in protein, calcium, and phosphorus than sagebrush, improved the reproductive success of pre-laying hens. From May throughout the summer months, adults also consume small amounts of various insects, such as ants, beetles, grasshoppers, and the larvae of moths and butterflies (Moos 1941, Knowlton and Thornley 1942, Leach and Hensley 1954, Wallestad et al. 1975). Martin (1970) stated that insects comprised 2% of the adult Greater Sage-Grouse diet in spring and fall and 9% in summer.

The diet of young grouse varies markedly from that of the adults. Insects are the main component of the chick diet, especially during the first three weeks of life, particularly ants from family Formicidae and beetles from family Scarabaeidae (Patterson 1952, Klebenow and Gray

1968, Peterson 1970). As chicks age, forbs replace insects as the most predominant food item in the diet of juveniles (Klebenow and Gray 1968, Peterson 1970, Wallestad et al. 1975, Johnson and Boyce 1990, Drut et al. 1994a, and Drut et al. 1994b). Rueblood (1954) found that forbs composed 54% to 60% of the summer diet of juvenile sage-grouse, while the diet of adult birds was 39% to 47% forbs. Klebenow and Gray (1968) found that Harkness gilia (*Leptosiphon harknessii*), loco (*Arabis convallarius*), common dandelion (*Taraxacum officinale*), goatsbeard (*Aruncus dioicus*), and sego lily (*Calochortus nuttallii)* were the top 5 forbs consumed by juvenile sage-grouse. In central Montana, Peterson (1970) found fringed sagebrush to be the food item most important for juvenile birds making the dietary transition from their late summer, forb-dominated diet to the sagebrush-dominated diet of the adult bird in winter. Once autumn arrives, the diet of both adults and juveniles becomes much less diverse and is comprised entirely of sagebrush leaves (Patterson 1952, Dalke et al. 1963, Klebenow and Gray 1968). Greater Sage-Grouse forage on the ground in open areas near cover, primarily during the morning and midafternoon to evening hours, nipping leaves and flowers off of living forbs and shrubs or pursuing insects across the ground (Girard 1937, Schroeder et al. 1999).

Sage-grouse have longer ceca than most other bird species and their digestive systems are designed to handle foods that are hard to digest such as sagebrush (Leopold 1953). They produce two distinct types of fecal droppings throughout the year: intestinal and cecal. Intestinal droppings are cylindrical, 2-3 centimeters long, and are various shades of light green (Schroeder et al. 1999). Terpenes in sagebrush are segregated from digestible substances, stored in the cecum, and excreted separately as cecal cast or tar. Cecal droppings are large, dark, blackish-green, liquid-like feces and are commonly found in the winter and early spring when the diet still consists of 100% sagebrush (Schroeder et al. 1999).

HABITAT REQUIREMENTS

Winter habitat

Characteristics of habitats used by sage-grouse vary throughout the year. During winter, Greater Sage-Grouse depend exclusively on sagebrush for food and shelter. Therefore, they tend to utilize dense sagebrush habitats at lower elevations, which will have less snow depth and taller sagebrush ensuring that they will have exposed sagebrush upon which to forage (Rasmussen and Griner 1938, Patterson 1952, Remington and Braun 1985, Schroeder et al. 1999, Connelly et al. 2000, Wyoming Game and Fish 2003, Crawford et al. 2004). Sage-grouse have demonstrated a preference for stands of medium to tall (25 to 80cm) sagebrush with 15 to 20% canopy coverage (Connelly et al. 2000). Winter is a less stressful time for sage-grouse because they only have one food source that is needed and they are able to find plenty of it relatively easy and may actually gain weight during the winter (Beck and Braun 1978). Sage-grouse have been reported to not be impacted by severe weather conditions unless snow completely covers the sagebrush (Hupp and Braun 1989).

Lekking habitat

In early spring, males gather together at a lek to perform their characteristic breeding displays to attract females (Patterson 1952). Lek sites are situated on sparsely vegetated sites that provide maximum visibility of displaying males (Patterson 1952). These sites are typically surrounded by areas of denser sagebrush vegetation that can provide food, nesting habitat and protection from predators, such as broad ridge tops and grassy openings (Patterson 1952, Braun et al. 1977, Wakkinen et al. 1992). Lek sites may be located in natural openings within sagebrush habitats or in openings produced by human disturbance such as burned areas, stock pond edges, dry lake

beds, airstrips, gravel pits, sheep bed grounds, roads, abandoned well locations, reservoirs, and cultivated fields (Patterson 1952, Dalke et al. 1963, Connelly et al. 1981, Gates 1985, Hays et al. 1998, Wyoming Game and Fish 2003). Leks tend to be located near habitat that is suitable nesting habitat (Patterson 1952, Connelly et al. 2011).

Nesting Habitat

Sage-grouse hens move to nesting areas within a few days of mating (Patterson 1952). Unlike lek areas that contain very little sagebrush, nesting areas are typically located near the lek area and typically contain a high percentage of sagebrush (Patterson 1952, Gill 1965, Wallestad 1975, Wakkinen et al. 1992). Successful nesting habitat has horizontal and vertical vegetation structural diversity composed of medium-height sagebrush and understories of native grasses and forbs to serve as herbaceous forage sources for pre-laying and nesting hens, to provide adequate concealment of nest and hen, and to provide a food source of insects (Sveum et al. 1998, Connelly et al. 2000). The majority of sage-grouse nests are built under sagebrush bushes of various species (Patterson 1952, Gill 1965). However, sometimes nests are built under other non-sagebrush shrub species that share the same habitat with sagebrush species. Some examples of other shrubs that have been documented as having been used for nest plants are four-wing saltbush (*Atriplex canesens*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus spp.),* eastern redcedar (*Juniperus virginiana*) and wheat stubble (*Triticum* spp.) (Patterson 1952, Herman-Brunson et al. 2009). Several studies have documented specific nesting habitat qualities selected by nesting sage-grouse. These studies revealed that sage-grouse hens tend to select areas with larger sagebrush bushes that have larger canopies and are taller compared to random habitat sites (Klebenow 1969, Wallestad and Pyrah 1974, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995). In southeastern Wyoming, Rothenmaier (1979)

found that sagebrush bushes used for nest sites were 30.6 cm high on average and that females selected nest plots with a mean sagebrush cover of 21.6 %. In western Wyoming, more than 80% of nests were found under bushes that were between 25 and 51 cm in height with an average nest bush height of 35.6cm (Patterson 1952). Numerous studies found that nests were usually found in areas that had taller live grass, more grass cover, and less bare ground than random habitat sites (Klebenow 1969, Wakkinen 1990). Gregg et al. (1994) stated that nest predation decreased as grass cover increased. Delong et al. (1995) suggested that thick herbaceous cover and adequate sagebrush cover were the two most important factors determining how protected nests were from predators and therefore how successful those nests were.

Brood-rearing habitat

After hatching, chicks are reared by hens in the vicinity of the nest site for 2-3 weeks (Berry and Eng 1985). In the first 3 weeks of life, the young follow the hen from the nesting site to nearby early brood-rearing habitats that are more open and forb- and insect-rich, but that have higher herbaceous cover than nest sites (Holloran 1999). Insects are crucial during the first week after hatching, and forbs provide calcium, phosphorus, and protein the chicks need as well much needed escape cover (Wallestad 1975, Barnett and Crawford 1994, Drut et al. 1994a, Drut et al. 1994b, Connelly 2000, Crawford et al. 2004). As food plants mature and become desiccated, hens tend to move their chicks to summer brood-rearing areas that are further away from nesting areas in search of more succulent forbs (Klebenow and Gray 1968). Late brood-rearing areas used during the summer occur in a variety of habitats —higher elevation summering grounds, riparian areas, wet meadows, and irrigated agricultural lands such as alfalfa fields (Patterson 1952, Connelly et al. 2011).

Autumn Habitat

As autumn approaches, Greater Sage-Grouse hens tend to continue utilizing irrigated agricultural lands, riparian areas along rivers, mixed sagebrush-grassland habitats in moist upland meadows and mid-slope draws where fall green-up of some cool-season grasses and forbs species occurs (Wyoming Game and Fish 2003). As these foods sources become desiccated or are killed by frost, these grouse begin to use their lower-elevation sagebrush wintering areas once again (Patterson 1952, Savage 1969, Wyoming Game and Fish 2003).

Sage Grouse Movements

Greater Sage-Grouse populations are nonmigratory or migratory, depending on the spatial arrangement of the different habitats they require year-round as well as vegetation cover, plant moisture conditions, elevation, topography, and severity of winter weather (Braun et al. 1977, Fischer et al. 1996 and 1997, Wyoming Game and Fish 2003). Migratory populations of these grouse typically migrate more than ten miles (Hays et al. 1998). Four seasonal movements or migrations per year have been observed in many migratory populations of this species: movements to breeding/nesting areas, movements to brood-raising areas, autumn movements, and movements to wintering grounds (Patterson 1952, Dalke et al. 1960, Gill and Glover 1965, Berry and Eng 1985). However, these movement patterns vary considerably between various populations (Connelly et al. 1988). Migrations of 50-100 miles from wintering grounds to lek sites have been reported (Hays et al. 1998).

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CHAPTER 3. VEGETATION CHARACTERISTICS OF HABITATS SELECTED BY GREATER SAGE-GROUSE (*Centrocercus urophasianus*) IN NORTHWESTERN WYOMING

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ABSTRACT

Dramatic range-wide declines in Greater Sage-Grouse populations have prompted efforts to determine habitat characteristics that are selected by sage-grouse for foraging, nesting and brood-rearing areas in an effort to conserve this species. Managers at Heart Mountain and Y U Bench in northwestern Wyoming expressed the need to quantify various habitat characteristics and to determine key use areas at both study sites. Data were collected on a variety of habitat variables in spots selected by grouse for foraging, nesting, and brood-rearing activities. These variables were compared to the same variables measured at random points at both study sites. Significant differences existed between foraging/nesting habitat plots selected by sage-grouse and random habitat plots at both sites. Areas used most by sage-grouse for lekking, nesting, and brood-rearing were identified at both study locations. Data analyses indicated sage-grouse at Heart Mountain were choosing foraging and nesting areas dominated by junegrass while grouse at YU Bench were choosing foraging sites dominated by junegrass and nesting sites dominated by needle and thread grass.

INTRODUCTION

Greater Sage-Grouse populations have declined drastically across their entire historic range due to habitat loss, habitat degradation, habitat fragmentation and various diseases and predation. Sagebrush ecosystems are important to not only sage-grouse but also to other species such as pronghorn antelope (*Antilocapra americana*), Brewer's sparrows (*Spizella brewerii*), sage

thrashers (*Oreoscoptes montanus*) and many others. Concerns over the decline of this unique bird have prompted people to take interest in conserving and managing the sagebrush ecosystems that are so important to the survival of sage-grouse and other sagebrush-dependent species such as those listed above.

HABITAT MANAGEMENT

Habitat manipulations have been used as a way of conserving and improving habitat for sage-grouse. The purpose of these treatments is to reduce sagebrush canopy cover and increase the density of grass and forb species. If those two things can be achieved from manipulation practices, better habitat for much needed insects, forbs and grasses can improve sage-grouse brood-rearing habitat. These manipulations fall into one of three categories: mechanical, chemical and biological treatments. None of these habitat manipulations include complete and total removal of all sagebrush but instead the goal of these treatments is the partial removal of sagebrush in hopes of regenerating its own regrowth and generating an increased growth response from any understory plants that are great for nest cover and attracting insects for young birds (Pyke 2011). Sagebrush is reduced by any of these three types of treatments but it is never completely eliminated from the habitat being treated.

Mechanical treatments

Mechanical treatments are designed to remove all or only a portion of the above ground portions of sagebrush shrubs or to completely remove and uproot them. These techniques include mowing sagebrush, chaining and removing sagebrush, disking, blading, railing, roller harrowing, and many more (Stoddart et al. 1975). Connelly et al. (2000a) reported that

mechanical treatments seemed to enhance sage-grouse brood-rearing habitat if sagebrush was treated in strips 4-8 meters wide. Dahlgren et al. (2006) found that in degraded sagebrush brood-rearing habitat, Dixie-harrow or Lawson-aerator treatments can successfully increase sage-grouse use of those habitats. Davies et al. (2012) found that mowing sagebrush reduced sagebrush cover enough to allow the growth of herbaceous vegetation. However, it has been suggested that impacts of these treatments may have a negative impact on sage-grouse (Klebenow 1970, Peterson 1970, Pyrah 1972). Swenson et al. (1987) found that sage-grouse populations declined in areas that had received mechanical treatments. Hess and Beck (2012) stated that having better livestock grazing practices and not treating areas of sagebrush were better management techniques than mowing sagebrush.

Chemical treatments

Chemical treatment of sagebrush is accomplished by aerially spraying sagebrush with various herbicides such as tebuthiron (Stoddart et al. 1975). In the past herbicides were used to kill off competing sagebrush bushes therefore increasing forage plants for livestock (Braun 1987). Herbicides are usually applied over larger areas than mechanical treatments and are extremely effective at reducing sagebrush canopy. Low amounts of herbicide applications are recommended because they are effective enough to decrease the density and canopy of sagebrush enough to increase grass and forb growth without overkilling sagebrush or killing existing grasses and forbs (Dahlgren et al. 2006). Some studies have shown that chemical treatments can be beneficial to sage-grouse especially by improving brood-rearing habitats (Autenrieth 1981, Olsen and Whitson 2002). However, some studies have shown how sage-grouse populations can be negatively affected by chemical treatments (Klebenow 1970, Peterson 1970, Pyrah 1972).

Biological treatments

Biological treatments include rotations of cattle grazing seasons or adjustments in the number of animals grazing and prescribed burns (Stoddart et al. 1975). Connelly et al. (2000a, 2000b) and Crawford et al. (2004) reported that if applied correctly, fire can be an important management tool for sagebrush habitats. Wright (1985) stated that fire is effective at lowering sagebrush density and canopy resulting in increases in forb and grass density. Several studies have demonstrated the benefits provided by prescribed burns to sagebrush habitats (Gates 1983, Pyle and Crawford 1996). Several studies have shown that fire can improve sagebrush habitats and increase use of them by sage-grouse (Klebenow 1970, Gates 1983, and Sime 1991). However, not all studies show positive impacts on sagebrush habitats and the sage-grouse populations inhabiting those habitats. Hulet (1983) and Hess and Beck (2012) found that fire had led to lek abandonment by sage-grouse. Connelly (2000a) stated that there was much lower male attendance at leks after burning had occurred. Fischer et al. (1996) found that fire reduced insect numbers postburn and he determined that fire does not enhance sage-grouse brood-rearing habitats. Knick et al. (2005) looked at 13 studies concerned with the effects of fire on sage-grouse. Five out of 13 of those studies examined the effects of fire on mountain big sagebrush habitats and only two of the five studies had positive outcomes while the other three were inconclusive. Two of the 13 studies reviewed by Knick et. al (2005) looked at fire's effects in a varied sagebrush landscape and both indicated negative impacts to sage-grouse and their habitat. Six of the 13 studies Knick reviewed looked at fire in sagebrush habitats dominated by Wyoming big sagebrush. Three of those studies showed sage-grouse were negatively impacted while the remaining three studies were found to be inconclusive. Hess and Beck (2012) stated that having

better livestock grazing practices and not treating areas of sagebrush were better management techniques than burning sagebrush.

VEGETATION CHARACTERISTICS OF HABITATS SELECTED BY SAGE-GROUSE

In addition to performing treatments to improve habitat quality for sage-grouse, it is important that habitat managers understand the areas that are most used by sage-grouse at their sites and what factors are determining whether or not sage-grouse utilize certain areas of certain habitats.

Several studies have looked at habitat characteristics selected by sage-grouse. Patterson (1952) found 90% of nests were built under sagebrush species. Braun (2001) stated that all subspecies of big sagebrush (*Artemisia tridentata tridentata, A. t. vaseyana, A. t. wyomingensis*) seem to be preferred more than other types wherever they are found. He also mentioned that sage-grouse will use other species of sagebrush such as low (*A. arbuscula*), silver (*A. cana*), threetip (*A. tripartita*), and black sagebrush (*A. nova*). Wallestad (1971) found that big sagebrush bushes 15-46 centimeters in height were the chosen plants utilized by sage grouse broods. Gregg et al. (1993) found that broodless hens selected nesting sites with more forb cover than hens with broods and all hens selected either big sagebrush species or low sagebrush under which to build their nests. Gregg (1991) found that at one site the birds chose nest sites in mountain big sagebrush (*A. t. vaseyana*) more than Wyoming big sagebrush (*A. t. wyomingensis*) but that at another site that trend was reversed. Gregg (1991) also noted that some hens chose to build their nests under rabbitbrush (*Chrysothamnus viscidiflorus*) and bitterbrush (*Purshia tridentata*) instead of using sagebrush bushes for nesting sites. Klebenow (1969) found no nests in areas that had more than 35% sagebrush coverage and birds at his study sites preferred threetip sagebrush more than big sagebrush subspecies. He also found that they did not use areas with dense sagebrush with little to no understory plants. Rasmussen and Griner (1938) found that

sage-grouse used silver sagebrush for nesting sites in Utah. Drut (1994) found that early in brooding season sage-grouse tended to use low sagebrush and then later switch to using big sagebrush subspecies. He also found that areas used by broods had greater forb frequency than random sites. Sveum et al. (1998) found that most nesting sites were located in big sagebrush bushes in areas with greater shrub cover, shrub height and litter than random locations surrounding the selected nesting sites. In southeastern Oregon, successful nests had greater cover of tall grass (>18 cm) and medium-height shrubs (40-80 cm) compared to failed nests (Gregg et al. 1994). On the same study area in Oregon, Delong et. al (1995) found that those with greater than 10% grass cover and medium-height sagebrush bushes were predated less than those with less than 10% grass cover. Holloran (2005) found that middle range sage densities were preferred by sage-grouse for nest sites more than too low or very dense stands. Several studies have reported percent grass cover at nest sites (Gray 1967, Klebenow 1969, Hulet 1986, Wakkinen 1990). However, out of those four studies, Klebenow (1969) is the only researcher that found greater grass cover at nest sites compared to random habitat sites.

Naugle et al. (2006) found that sage-grouse selected flatter, less rugged terrain away from any coniferous zones in winter. Klott (1993) found that sagebrush height, canopy width and grass height in used nesting sites were taller than random sites and that a mixture of big, low and mountain sagebrush were used for nesting sites. No other plants were used for nesting sites in his study. He also found that sage-grouse built nests away from livestock activities when grazing took place on tracts of land that also had sage-grouse present. According to Braun (2001), sage-grouse place nests under living sagebrush bushes with taller heights (30-80 cm) that possess canopy covers ranging from 15 to 25%. Areas used during early brooding are located within 300m to 1 km of nest sites and are dominated by forbs and grasses with about 15% or more

cover and grasses greater than 18 cm in height (Braun 2001). In Montana, successful nests had greater shrub cover surrounding the nest site and were associated with cover types that had a higher density of shrub cover than unsuccessful nests (Wallestad and Pyrah 1974). Other authors noted percent grass cover (Klebenow 1969) and grass height (Wakkinen 1990) were related to nest-site selection.

Davis (2003) found nests in several different cover types: Wyoming big sagebrush, mountain big sagebrush, low sagebrush, and mountain shrub. The majority of those nests were located under big sagebrush species (65%) (Davis 2003). Non-sagebrush plants used for nesting sites included bitterbrush, gray horsebrush (*Tetradymia canescens*), curlleaf mountain mahogany (*Cercocarpus ledfolius*), basin wildrye (*Elymus cinereus*) and western juniper (*Juniperous occidentalis*). Davis (2003) also stated that nest sites at his study areas had less forb cover and less tall grass coverage compared to random sites. Vegetative characteristics at successful nest sites were similar to unsuccessful nest sites but all nest sites greater amounts of medium height shrub cover (40-80 cm) than at random sites (Davis 2003).

STUDY SITES

The two study sites used in this study were Heart Mountain and Y U Bench near Cody, Wyoming. Heart Mountain has not received management manipulations. Y U Bench has had mechanical treatments in the form of sagebrush mowing and chaining. It is known that Greater Sage-Grouse utilize these two sites. However, at the time of this study, it was not currently known what areas of each site were being used by sage-grouse at various stages of the breeding season, especially for nesting and brood-rearing areas. The microhabitats sage-grouse were using had not been quantified at these two locations. My study addressed these two issues by

determining the locations which were most used by sage-grouse as well as collecting data on several habitat variables at the locations at which sage-grouse were found at both study sites. The information gathered in this study will help identify key use areas as well as habitat preferences at both study sites, thus enabling those involved in the management of these sites to identify priority areas for conservation and habitat management activities.

One objective of this study was to determine the areas of each large study site that sage-grouse were utilizing most for what type of activity. A second objective of this study was to quantify various habitat variables of each site and to determine habitat characteristics preferred by sage-grouse at these two locations.

METHODS

Study areas

Both of my study sites, Heart Mountain Ranch and Y U Bench, are located in the Bighorn Basin in Park County, Wyoming. The Bighorn Basin is a 161-kilometer wide plateau and intermontane basin located in north-central Wyoming. It is surrounded by the following mountain ranges: Absarokas to the west, Pryors to the north, Big Horns to the east, and the Owl Creek and Bridger ranges to the south (Figure 1). Since the Bighorn Basin is surrounded by mountains, a rain shadow covers it making it one of the most arid areas in Wyoming. It only receives 15-25 centimeters of precipitation per year. Most of this precipitation falls as snow instead of rain. The Bighorn Basin is characterized by multi-colored badlands and by gravelly arid soils that tend to have sandy subsoils (Dunnewald et al. 1927). Sagebrush, which tends to grow well in locations that have an arid, cold climate as well as this soil type, is the dominant vegetation cover in the Bighorn Basin. Just as the soil type and climatic conditions of the

Bighorn Basin determine the distribution of sagebrush, the distribution of a sagebrush-obligate species such as sage-grouse is determined by the distribution of sagebrush.

Heart Mountain Ranch is owned by the Nature Conversancy and is located 18 kilometers north of Cody, Wyoming (44.6667° N, 109.1181° W) (Figure 2). Even though the entire ranch encompasses 6,070 hectares, my study area was concentrated on the eastern side of the mountain at an elevation of about 1,524 meters while the mountain's summit is at 2,476 meters. Heart Mountain is an untreated site. Y U Bench is owned by the Bureau of Land Management and is located about 48 kilometers east of Cody, Wyoming (44-23'10" N, 108-40'14" W) at an elevation of 1,637 meters (Figure 3). Y U Bench is a treated site. It has been treated mechanically by mowing the tops of sagebrush bushes to increase nutritious regrowth of leaves for sage-grouse. Some sagebrush has also been removed by chaining in hopes of increasing the growth of grasses and forbs. Both chaining and mowing were done in undulating strips several meters wide.

Habitat measurements

During the spring and summer seasons of 2005 and 2006, observers on foot attempted to locate Greater Sage-Grouse at both study sites. For every bird seen, the date, time, name of study site, the number, age, and sex of the bird or birds seen was recorded. In addition to this information, the GPS location of any bird or birds seen was recorded. In the approximate location at which birds were seen, a circular plot with a diameter of 6 meters was marked with survey flags using the approximate location from which the bird was seen as the center of the circular plot (James 1992). One flag marked the center of the plot and four other flags were used to mark the perimeter of the plot in which birds were observed foraging. Hereafter, I will refer to these plots as foraging plots. Within each circular various measurements and

observations were recorded and those included the following: tallest plant species, dominant grass species, dominant dicotyledonous plant species, number of sagebrush shrubs, number of sizeable rocks (rocks 8 centimeters or more in diameter were considered sizeable), average sagebrush canopy width, average height of sagebrush, live and dead sagebrush density,

average grass/forb height, and percent ground cover by the following: bare ground, small rocks/gravel (any stone under 8 cm in diameter), grasses/forbs, and sagebrush. Percent cover was determined by using the point intercept method (Mitchell and Hughes 1995, Herrick et al. 2005). After the 6 meter plot was measured and delineated with survey flags, a 150 cm long pin that was 2mm in diameter with a distal point that was sharpened down to less than 1 mm in diameter was dropped perpendicular to an outstretched 91 meter reel tape measure so that the tip of the pin hit the tape on the reel measure. This was done across the entire diameter of the plot circle in a 0 to 180 degree position and a 90 to 270 degree position within the 6 meter plot. Vegetation cover type was recorded every 8 centimeters within the 6 meter plots. The cover type present at the tip of the pin on each reading was recorded. Percentages were calculated for the four cover types: bare ground, gravel/rocks, grass/forb, and sagebrush. For comparing foraging sites to overall habitat characteristics, a random sample of the surrounding habitat was obtained for each foraging site sample. Direction each random site was from the center of the foraging plot was determined by a random number generator on a smartphone which had been set to pick random numbers from 1 to 360. The number given was then set on a compass and that was the direction of travel taken from the center of the foraging plot to the center of the random habitat plot. The distance from the center of the foraging plot to the center of the new random habitat plot was determined again by the random number generator which was set to generate numbers from 25 to 100 and whatever number was picked became the distance in meters traveled from the

foraging plot's center to the random habitat plot's center. These random habitat plots were also 6 meters in diameter and marked by survey flags in the same manner as described for the foraging plots. The same types of data were collected at the random habitat plots using the same equipment and protocols as those used for the foraging plots. In addition to these data, other data were collected from both sites such as number of hens with broods and number of chicks per brood when encountered.

Nest searches were also performed. Great care was taken to prevent disturbing active nests. Therefore, all nest searches took place late in the field season to maximize the likelihood that nesting activities were over for the season. No nests were found with hens still incubating eggs and all nests found either already had eggs that were hatched or had eggs that had been eaten by nest predators such as Common Ravens (*Corvus corax*). When nests were found, the plant under which they were located became the center of a nest plot that was treated the same way as the foraging plots in terms of methods and types of data collected. The only additional data recorded for the nest plots were the height and canopy width in centimeters of the actual nest plant. Random habitat plots were made for every nest site discovered using the same methods and protocols that were used for the random habitat plots that corresponded to the foraging plots.

Data Analysis

Descriptive statistics, plus the following statistical tests: chi square analysis, principle components analysis, multivariate analysis of variance (MANOVA) and Duncan Multiple Range tests were used to identify those vegetation factors important for sage-grouse as well as differences in habitat variables between study sites. JMP and SAS statistical software packages were used to analyze the data collected in this study (SAS 2000, JMP 2005). PCA was used to

determine basic patterns in the data (Williams 1983) and it is commonly employed without transforming the variables to improve normality (Bonaccorso and Guillermo 2002). The patterns shown by PCA were analyzed further using MANOVA and following the lead of Anderson and Shugart (1974) the variables were retained untransformed.

RESULTS

Key use areas by Greater Sage-Grouse at my study sites

Areas most used by sage-grouse at Heart Mountain (east side) (Figure 4) and Y U Bench (Figure 5) for various activities are delineated in various colors. Yellow areas on both maps are lek locations for the two study sites, areas where birds were seen in foraging plots repeatedly are outlined in red, and areas in which nests were found are outlined in white. At the Heart Mountain (east side) site, most birds were found fairly far back from an area where the entrance road crosses a canal. They usually were found on either side of the entrance road into the site especially on the north side of the road which is the same side of the entrance road the lek was located on. There are two small plateaus or mesas north of the road that were separated by fairly deep draws. Several birds but no nests were found in these draws. Most birds seen in the draws were hens with broods. All nests found at Heart Mountain were found on the north side of the entrance road. The lek at Y U Bench was located on the opposite side of the road from the area at which most of my encounters with birds occurred. At Y U Bench, birds were encountered from the roadside all the way to the back edge where the bench dropped off unlike the situation at Heart Mountain where birds were never seen close to the main highway leading up to the entrance gate and road. Nests located at Y U Bench were all located on the southeastern edge of the bench right before it drops off to the Greybull River area below.

Foraging Plots and Random Habitat Plots

Comparing Heart Mountain foraging plots to random habitat plots indicated that the mean values of all these variables in foraging plots were higher than those of the random habitat plots except for number of sizeable rocks, percent cover by rocks, and percent cover by bare ground. Foraging plots at Heart Mountain on average had fewer large rocks, less rocky ground cover, and less bare ground cover than the available habitat around them (Table 1). At Heart Mountain means for all habitat variables were significantly higher in the foraging plots compared to the means of those same variables in the random habitat plots (MANOVA, $p<0.0001$) with the exception of the following variables: total number of sizeable rocks, percent cover by bare ground, and percent rocky ground cover. The means of these three variables were significantly lower in the foraging plots compared to the random habitat plots (MANOVA, $p<0.0001$). Categorical variables measured for both plot types at Heart Mountain included tallest plant, most dominant dicotyledonous plant, and most dominant grass species in each plot. Sagebrush was the tallest plant in 67% of the foraging plots. In 26% of the foraging plots, junegrass was the tallest plant while needle and thread grass was the tallest plant in only 7% of the foraging plots. Junegrass was the most dominant grass species in 82% of the foraging plots and needle and thread grass was the most prevalent grass species in only 18% of the foraging plots at Heart Mountain. Sagebrush was the most dominant dicotyledonous plant in 100% of the foraging plots. Sagebrush was the tallest plant in 67% of the random habitat plots. In 27% of the random habitat plots, junegrass was the tallest plant while needle and thread grass was the tallest plant in only 6% of the random habitat plots. Junegrass was the most dominant grass species in 81% of the random habitat plots and needle and thread grass was the most prevalent grass species in only 19% of the random habitat plots. Squirreltail was the least prevalent grass species being found in only 6% of the random habitat plots but never being seen in foraging plots at Heart Mountain.

Sagebrush was the most dominant dicotyledonous plant in 100% of the random habitat plots. At Heart Mountain, areas dominanted by junegrass were chosen by sage-gouse as foraging areas significantly more than areas dominated by other grass types ($X^2=40.96$, $df=1$, $p<0.0001$).

At Y U Bench, the mean values of all variables in foraging plots were higher than those of random habitat plots except for number of sizeable rocks, percent cover by bare ground, and percent cover by rocks (Table 1). Foraging plots at Y U Bench had fewer large rocks, less rocky ground cover, and less bare ground than the available habitat around them (Table 1). At Y U Bench, the means for all measured habitat variables were significantly higher in the foraging plots compared to the means of those same variables in the random habitat plots (MANOVA, $p<0.0001$) with the exception of the following variables: total number of sizeable rocks, percent cover by bare ground, and percent rocky/gravel ground cover. These three variables were significantly lower in the foraging plots compared to the random habitat plots (MANOVA, $p<0.0001$). Categorical variables measured for both plot types at Y U Bench included tallest plant, most dominant dicotyledonous plant, and most dominant grass species in each plot. Sagebrush was the tallest plant in 47% of the foraging plots. In 41% of the foraging plots, junegrass was the tallest plant while needle and thread grass was the tallest plant in only 9% of the foraging plots. Squirreltail grass was the tallest plant in 3% of the foraging plots. Junegrass was the most dominant grass species in 79% of the foraging plots, needle and thread grass was the most prevalent grass species in 16% of the foraging plots, and 5% of the foraging plots contained squirreltail grass as the dominant grass species. Sagebrush was the most dominant dicotyledonous plant in 100% of the foraging plots. Sagebrush was the tallest plant in 54% of the random habitat plots. In 37% of the random habitat plots, junegrass was the tallest plant

while needle and thread grass was the tallest plant in only 9% of the random habitat plots. Junegrass was the most dominant grass species in 63% of the random habitat plots and needle and thread grass was the most prevalent grass species in only 31% of the random habitat plots. Squirreltail was the least prevalent grass species being found in only 6% of the random habitat plots. Sagebrush was the most dominant dicotyledonous plant in 100% of the random habitat plots. At Y U Bench, areas dominated by junegrass were chosen as foraging areas significantly more than areas dominated by any other grass type ($X^2=95.67$, $df=2$, $p<0.0001$).

All habitat variables differed significantly between both study sites (MANOVA, $p<0.0001$). Duncan Multiple Range tests also indicated that all nine variables differed significantly between sites.

Nest Plots and Random Habitat Plots

At Heart Mountain, the averages of the same variables measured for the foraging versus random habitat plot comparisons were higher than those of the surrounding habitat except for number of sizeable rocks, percent cover by bare ground, and percent cover by rocks (Table 2). Surrounding habitat plots had more rock coverage, more sizeable rocks as well as more bare ground than the plots containing the nests. All categories of numerical variables measured were significantly different between plot types (MANOVA, $p<0.0001$). In addition to these variables, actual nest plant heights and canopy widths were recorded and on average nest plant height and canopy width were 80 cm and 163 cm, respectively. Comparisons were also made between plot types between some categorical variables that were collected from each site. All of the nest plots were located on flat terrain as opposed to sloped terrain. In all the nest plots the dominant dicotyledonous plant was Wyoming big sagebrush and the dominant grass was

junegrass in 53% of the plots, needle and thread grass in 35% of the plots, and squirreltail grass in only 12% of the plots. In 41% of the samples Wyoming big sagebrush was the tallest plant in nest plots, 29% of the nest plots had junegrass as the tallest plant, 18% of the nest plots had needle and thread grass as the tallest plant and squirreltail was the tallest plant in only 12% of the nest plots. Results for random habitat plots were exactly the same in terms of the terrain and the dominant dicot. However, junegrass was always the most dominant grass and Wyoming big sagebrush was always the tallest plant in the random habitat plots. At Heart Mountain, areas dominated by junegrass were chosen as nesting areas significantly more than areas dominated by any other grass species ($X^2=25.343$, $df=2$, $p<0.0001$).

At Y U Bench, the averages of the same variables measured for the foraging versus random habitat plot comparisons were higher than those of the surrounding habitat except for number of sizeable rocks, percent cover by bare ground, and percent cover by rocks (Table 2). Surrounding habitat plots on average had more rock coverage (gravel), more sizeable rocks as well as more bare ground than the plots containing the nests. All categories of variables measured were significantly different between plot types (MANOVA, $p<0.0001$). In addition to these variables, average nest plant heights and canopy widths were calculated and were 84.4 cm and 130.4 cm, respectively. Comparisons of categorical variables that were collected from each site were also made between plot types at Y U Bench. All of the nest plots were located on flat terrain as opposed to sloped terrain. In all of the nest plots the dominant dicot was Wyoming big sagebrush and the dominant grass was needle and thread grass in 56% of the plots, junegrass in 38% of the plots, and squirreltail grass in only 6% of the plots. In 38% of the plots Wyoming big sagebrush was the tallest plant, 23% of plots contained junegrass as the tallest plant, 23% of the plots had needle and thread grass as the tallest plant, and squirreltail was the tallest plant in

only 16% of the plots. Results for random habitat plots were exactly the same in terms of the terrain and the dominant dicot. However, junegrass was the most dominant grass in 46% of the plots while needle and thread grass was the most dominant grass in 54% of the plots. No random habitat plots had squirreltail grass as the dominant grass species. At Y U Bench, there was a significant difference between grass types being chosen in nesting plots ($X^2 = 38.48$, $df=2$, $p<0.0001$) with areas dominated by needle and thread grass being chosen significantly more than other grass species for nesting sites. The overwhelming majority of random habitat plots had Wyoming big sagebrush as the tallest plant (86%) while the remaining 14% was split evenly among junegrass and needle and thread grass.

Nest Plots and Foraging Plots

Comparisons were also made between nest plots and foraging plots. At Heart Mountain, average grass height and average sagebrush canopy width, were significantly higher in nesting plots compared to foraging plots (MANOVA, $p<0$ .001). No significant differences were found between any of the other numerical habitat variables at Heart Mountain. At Y U Bench, the only numerical habitat variable that was significantly different between nesting and foraging plots was average sagebrush height. Average sagebrush heights in nesting plots were significantly lower than those of the foraging plots at Y U Bench (MANOVA, $p<0.001$).

Principal Components Analysis (PCA)

For the Heart Mountain foraging and random habitat plot data, the first 3 PCs accounted for 66% of the variance among the data (Table 3). Percent cover of sage, total sagebrush bushes, sagebrush canopy width, sagebrush height, percent rock cover, and percent cover of bare ground explained the most variation in habitat characteristics between foraging and random habitat

plots for PC1 (Figure 6). The percent cover of grass and the total sizeable rocks in an area explained most of the variation between foraging and random habitat plots in PC2 (Figure 6). Lastly, percent cover of bare ground and grass explained most of the variation between plot types at Heart Mountain for PC3 (Figure 6).

For the Heart Mountain nest and random habitat plot data, the first 3 PCs accounted for 89% of variance among the data (Table 3). Average grass/forb height, average sagebrush height, average sagebrush canopy width, percent bare ground and number of sizeable rocks explained the most variation in habitat characteristics between nest plots and random habitat plots for PC1 (Figure 7). The percent sagebrush and grass cover in plots explained most of the variation between nest plots and random habitat plots in PC2 (Figure 7). Lastly, total sagebrush bushes and percent cover by bare ground and explained the most variation for PC3 (Figure 7).

For the Y U Bench foraging and random habitat plot data, the first 3 PCs accounted for 72% of variance among the data (Table 3). Percent cover of sagebrush, average grass/forb height, average sagebrush canopy width, and percent cover of rock and bare ground explained the most variation in habitat characteristics between foraging and random habitat plots for PC1 (Figure 8). The total sizeable rocks and average sagebrush height explained most of the variation between foraging and random habitat plots in PC2 (Figure 8). Lastly, percent cover of grass, average canopy width, and total number of sagebrush bushes explained the most variation for PC3 (Figure 8).

For the Y U Bench nest and random habitat plot data, the first 3 PCs accounted for 80% of variance among the data (Table 3). Average sagebrush height, average grass/forb height, average sagebrush canopy width, total sizeable rocks, and percent cover of bare ground and

sagebrush explained the most variation in habitat characteristics between nest plots and random habitat plots for PC1 (Figure 9). The percent cover of rock, bare ground and grass explained most of the variation between nest plots and random habitat plots in PC2 (Figure 9). Lastly, percent cover of grass and sagebrush as well as the total number of sagebrush bushes explained the most variation for PC3 (Figure 9).

DISCUSSION

Results for foraging plots versus random habitat plots at both study sites indicated that sage-grouse were being found significantly more in areas that had fewer large rocks, less bare ground, and less gravel/rocky ground cover than the available habitat surrounding the locations in which they were actually being found. Chi-square analyses of categorical data collected at foraging and random habitat plots at both sites show there is a significant difference between the grass types that dominated the areas within which birds were being found. Sage-grouse at both sites were choosing to forage in locations that were dominated by sagebrush as well as junegrass. Sage-grouse were choosing areas with junegrass significantly more than areas predominated by other available grass species such as needle and thread grass and squirreltail grass. Almost all of the birds found at Heart Mountain were found on flat terrain in my study just as Naugle (2006) had found in his study.

Data analyses of nest site plots versus random habitat plots at both study sites showed that sage-grouse hens were choosing nesting sites on flat terrain only and only placing those nests under Wyoming big sagebrush bushes as opposed to using other less prevalent sagebrush species that were available. Unlike some researchers such as Gregg (1991) and Davis (2003), I did not find any nests under non-sagebrush type plants.

On average, sage-grouse hens were choosing nest bushes that were at least 81 centimeters tall with canopy widths of at least 163 centimeters wide. These numbers were greater than the much published range of 40-80cm for sagebrush height (Gregg et al. 1994, Braun 2001). MANOVA results for nesting plots versus random habitat plots at both study sites indicated that sage-grouse nests were being found in areas that had significantly fewer large rocks, less bare ground, and less gravel/rocky ground cover than the available habitat surrounding the locations in which they were found. Nests at both study sites were found in significantly taller and wider sagebrush with significantly more grass cover than random habitat sites just as Klott (1993) found in his study. None of the nests found in my study were seen under any other plant species other than sagebrush. Klott also (1993) never found nests under any other type of bush such as rabbitbrush. He only found them under sagebrush plants. Chi-square analysis results indicated that nests were primarily found in plots dominated by junegrass significantly more than areas dominanted by any other grass species present at Heart Mountain. However, in all corresponding random habitat plots, junegrass was the most dominant grass species 100% of the time. This means that even though junegrass was the most prevalent and available grass in the vicinities nest sites were chosen, some hens still chose sites dominated by other grasses such as needle and thread grass and squirreltail grass. Nests at Y U Bench were found in plots where needle and thread grass was the most dominant grass species significantly more than areas dominated by any other grass species such as junegrass or squirreltail grass.

Therefore, hens at Heart Mountain forage and nest more in junegrass while hens at Y U Bench seem to prefer to forage in areas with lots of junegrass but seem to prefer nesting in areas where needle and thread grass is the most dominant grass species.

According to analyses comparing nest plot characteristics to foraging plot characteristics, it appears that taller grass heights and wider sagebrush canopies are more important to Heart Mountain grouse for nesting rather than for foraging areas. These same analyses seem to indicate that grouse at Y U Bench tend to nest in areas where sagebrush bushes are shorter on average than sagebrush bushes in their chosen foraging areas.

Both the MANOVA and Duncan Multiple Range tests highlighted some of the contrasts between both study sites even though they are both semiarid sagebrush steppe habitats at fairly high elevations. Y U Bench had significantly more gravel cover but significantly less large stones compared to Heart Mountain. Y U Bench had fewer sagebrush bushes in the plots and the sagebrush tended to be shorter in height with wider canopies than sagebrush at Heart Mountain. Plots at Heart Mountain tended to have more sagebrush bushes in the plots sampled but the bushes tended to be taller with more narrow canopies than those of Y U Bench. Y U Bench had more grass and less spots of bare ground than plots at Heart Mountain as well. Grass was also taller at Y U Bench on average.

Duncan multiple range tests performed on data from both sites indicated the following: (1) sage-grouse were found in taller sagebrush on average than the surrounding habitat at both sites (2) sage-grouse were found in areas with more sagebrush bushes than the surrounding habitat at both sites (3) sage-grouse were found where the sagebrush bushes tended to have wider canopies than those bushes of the surrounding habitat at both sites (4) sage-grouse were found in areas with significantly fewer sizeable rocks than the surrounding habitat at both study sites (5) sage-grouse were found in areas with less bare ground significantly more often than they were found in areas with more bare ground at both sites and the percent cover by bare ground between both plot types at both sites was significantly different (6) sage-grouse were found in areas with

higher percent coverage by sagebrush bushes than the surrounding habitat at both sites (7) sage-grouse were found in areas of higher percent grass cover than the surrounding habitat at both sites (8) sage-grouse were found in areas with lower percent coverage of rock than the surrounding habitat at both sites and (9) sage-grouse were found in areas where the average grass/forb height was higher than the surrounding habitat plots at both sites.

The Greater Sage-Grouse is currently a species of management concern. According to my principal components analyses results, sage-grouse at both sites utilized areas of those sites that had more sagebrush, less rocks and bare ground, and taller and wider sagebrush bushes for day-to-day foraging activities. For nesting, plentiful sagebrush, wider sagebrush bushes, less bare ground and rocks were also important to sage-grouse hens seeking suitable places to build nests. However, one extra component was revealed by principal components analyses on nest site data from both study sites that was important to sage-grouse---the average grass/forb height in an area. Nests were found under sagebrush bushes with taller heights and wider canopies but nests were also found under those bushes that were surrounded by taller grasses/forbs. Moving forward with information obtained in this study, habitat managers at both sites can perhaps focus their management activities in the key use areas delineated on Figures 4 and 5 and possibly use any information from this study to improve or maintain the habitat that sage-grouse at both sites showed a preference to.

Even though this study focused on the habitat characteristics selected by sage-grouse at these sites, there are other factors that may drive habitat selection by sage-grouse that were outside the scope of this study such as tall structures and predator abundance. Beck et al. (2006) demonstrated that sage-grouse exhibit avoidance behavior to tall structures such as transmission lines in Idaho. Transmission lines provide ideal perching places for aerial predators such as

hawks and eagles (Beck et al. 2006). Sage-grouse prefer nesting farther away from tall structures so this is one confounding factor that may drive nest-site selection. Ritchie et al. (1994) found that there was more nest predation at untreated sites rather than at treated sites. He attributed this to the fact that untreated sites probably attract more potential prey items that in turn attract more predators. Increased numbers of predators in an area inevitably leads to higher predation rates such as higher sage-grouse predation. He also stated that nest cover is really only valuable with aerial predators and that most of the predators detected in his study turned out to be mammalian predators such as badgers which hunt by olfaction. Other studies have demonstrated that common mammalian predators are foxes and coyotes. Therefore, sage-grouse may be selecting a given habitat for more reasons than just what vegetation characteristics are present.

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APPENDIX A: TABLES AND FIGURES

FIGURE 1. Topographic map of Bighorn Basin, Wyoming, USA. Map provided by Google Earth (2009).

FIGURE 2. Map of Heart Mountain Ranch study site in Park County, Wyoming, USA. Map provided by the Bureau of Land Management (2005).

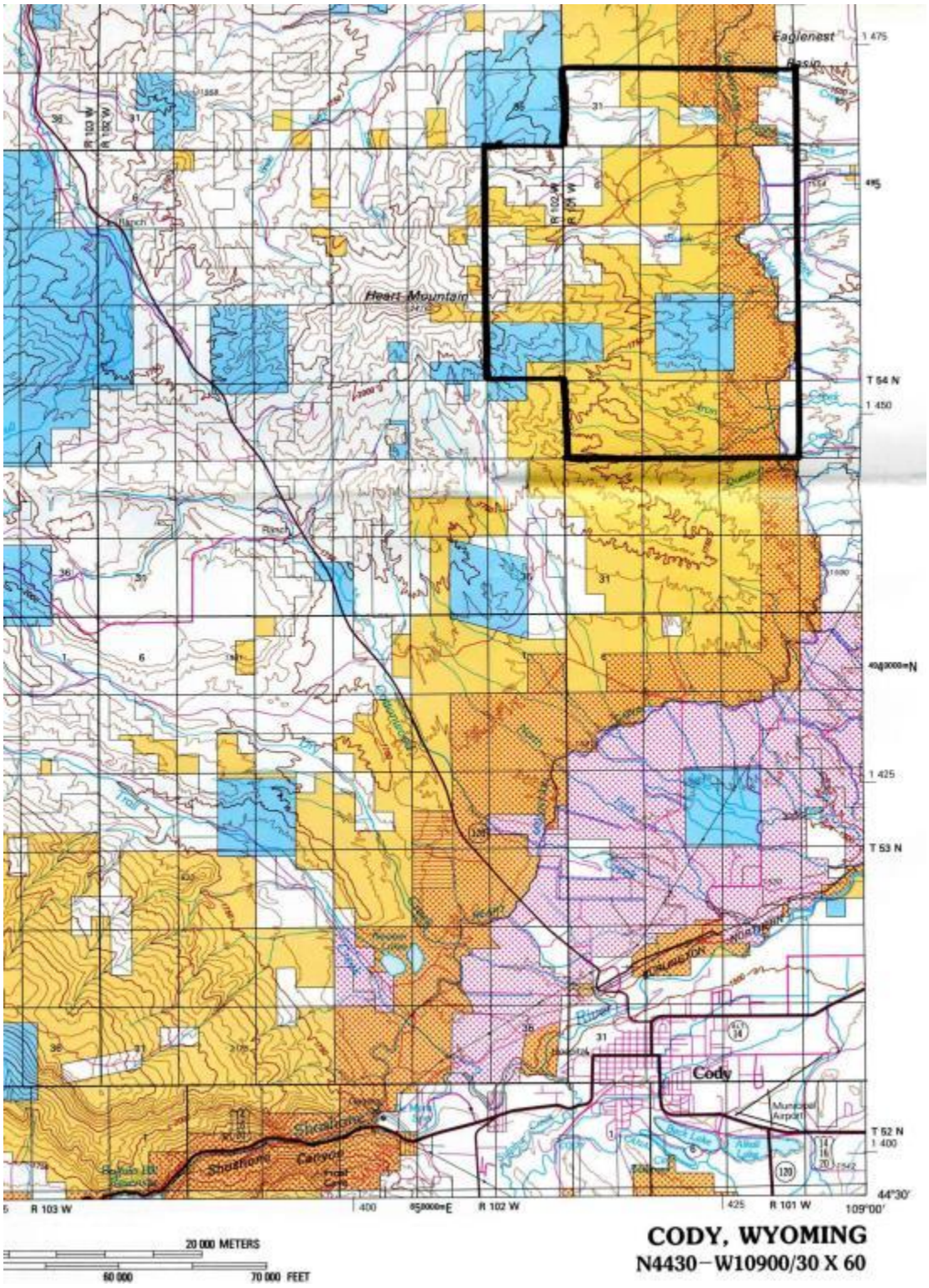


FIGURE 3. Map of Y U Bench study site in Park County, Wyoming, USA. Map provided by the Bureau of Land Management (2005).

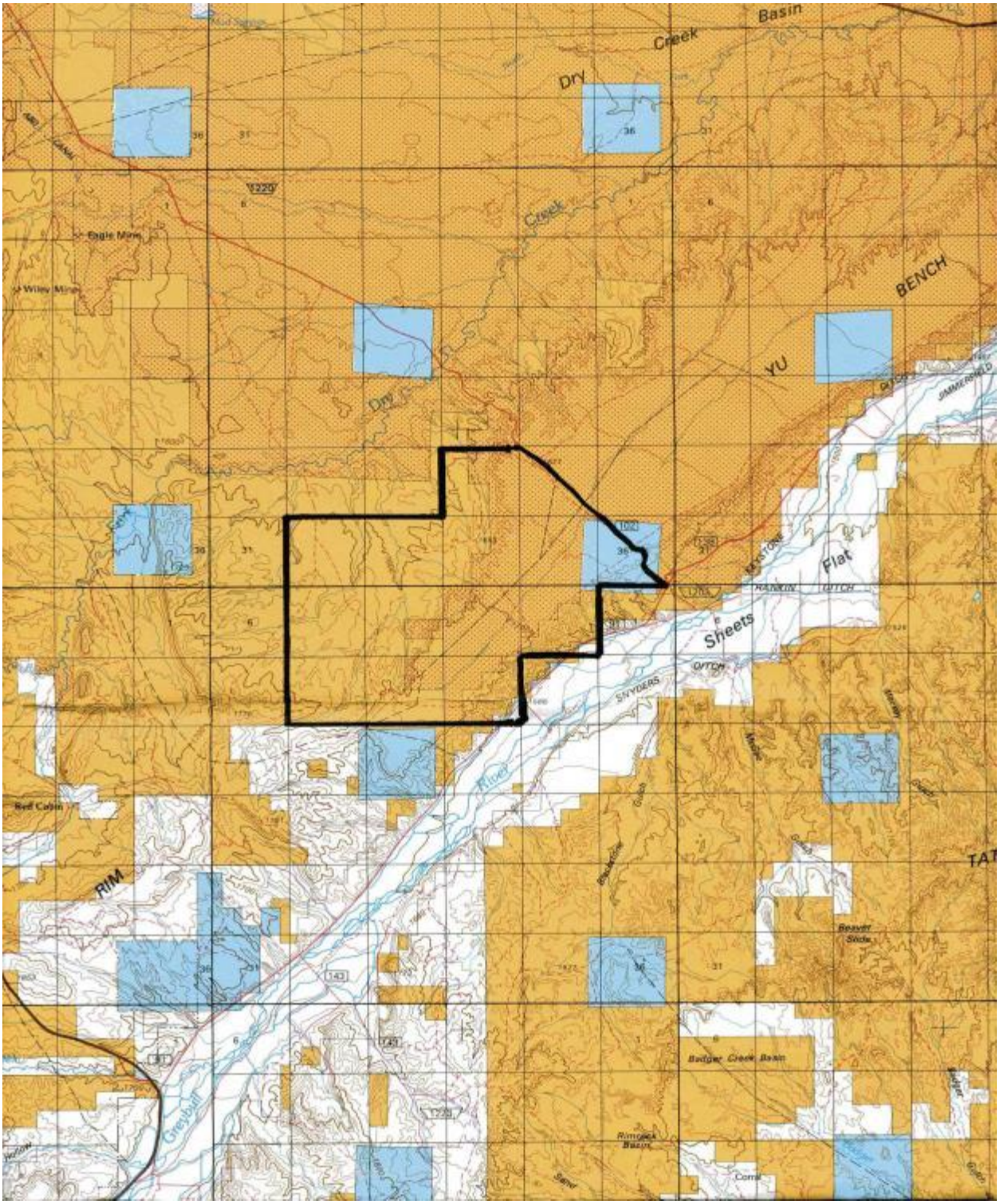


FIGURE 4. Topographic map of my Heart Mountain study site near Cody, Wyoming. Areas delineated by a yellow line are lek areas, areas delineated by red lines are areas where grouse where found foraging, and areas enclosed by white lines are areas of this study site in which nests were located. Map provided by Google Earth (2009).

FIGURE 5. Topographic map of my study site at Y U Bench near Cody, Wyoming. Areas delineated by a yellow line are lek areas, areas delineated by red lines are areas where grouse where found foraging, and areas enclosed by white lines are areas of this study site in which nests were located. Map provided by Google Earth (2009).

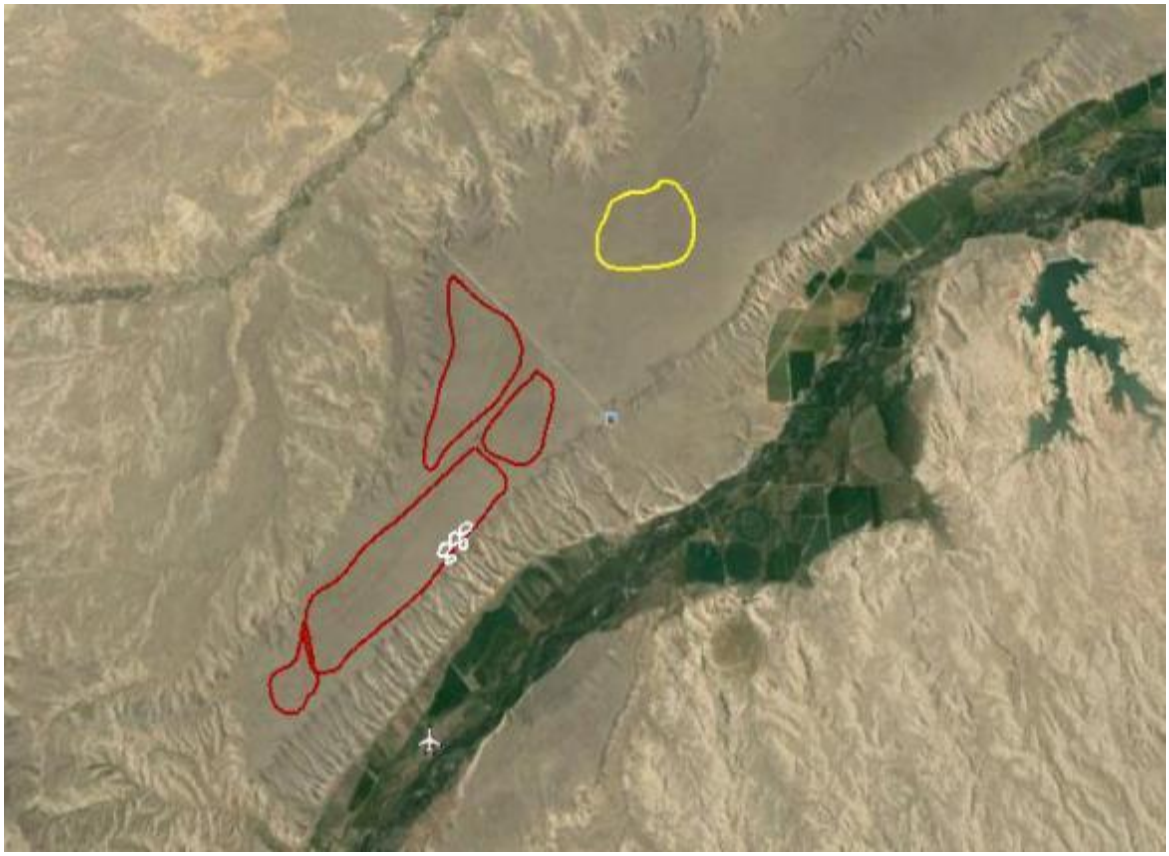


TABLE 1. Descriptive statistics for habitat characteristics of Heart Mountain and Y U Bench foraging plots and random habitat plots for the spring/summer seasons of 2005-2006. In the descriptive statistics columns, the heading for each descriptive statistic has (HM) for Heart Mountain or (YU) for Y U Bench.

Characteristics	Mean (HM)	Standard Error (HM)	Mean (YU)	Standard Error (YU)
Foraging plots				
Average grass/forb height (cm)	34.7	0.286	91.0	0.327
Average sage height (cm)	76.6	0.589	84.0	0.826
Total number of sage clumps	33.1	0.481	27.7	0.671
Average sage canopy width (cm)	97.1	0.637	102.3	0.764
Number of sizeable rocks	4.4	0.428	3.3	0.253
Percent cover bare ground (%)	12.1	0.485	8.2	0.436
Percent cover sagebrush (%)	44.1	0.612	42.9	0.656
Percent cover grass (%)	39.0	0.465	41.8	0.419
Percent cover rock (%)	4.8	.270	7.0	0.301
Random habitat plots				
Average grass/forb height (cm)	24.8	0.576	69.1	0.723
Average sage height (cm)	67.7	0.528	64.1	0.560
Total number of sage clumps	27.0	0.426	22.8	0.500
Average sage canopy width (cm)	75.8	0.431	77.3	0.481
Number of sizeable rocks	6.9	0.313	3.8	0.405
Percent cover bare ground (%)	18.2	0.425	17.4	0.399
Percent cover sagebrush (%)	36.4	0.407	34.0	0.320
Percent cover grass (%)	34.9	0.382	38.1	0.344
Percent cover rock (%)	8.1	0.307	12.8	0.331

TABLE 2. Descriptive statistics for nest site characteristics and random habitat plots which were measured at Heart Mountain and YU Bench during the spring/summer seasons of 2005-2006. In the descriptive statistics columns, the heading for each descriptive statistic has (HM) for Heart Mountain or (YU) for Y U Bench.

Characteristics	Mean (HM)	Standard Error (HM)	Mean (YU)	Standard Error (YU)
Actual nest sites				
Nest plant height (cm)	80.4	2.770	84.4	1.680
Nest plant canopy width (cm)	162.8	5.846	130.4	2.020
Average sage height (cm)	76.3	4.466	91.4	1.700
Average grass/forb height (cm)	81.1	0.892	59.3	1.090
Total number of sage clumps	36.8	2.630	32.4	2.330
Average sage canopy width (cm)	108.8	0.649	102.8	1.290
Number of sizeable rocks	3.3	1.110	4.7	1.930
Percent cover bare ground (%)	10.0	1.770	7.4	0.836
Percent cover sagebrush (%)	47.0	6.540	45.7	2.360
Percent cover grass (%)	40.8	6.630	39.7	1.550
Percent cover rock (%)	2.3	0.829	6.3	1.700
Random habitat plots				
Average sage height (cm)	42.2	1.410	54.2	1.240
Average grass/forb height (cm)	44.6	1.080	42.5	1.300
Total number of sage clumps	32.9	1.410	30.8	1.980
Average sage canopy width (cm)	74.2	1.040	79.1	1.330
Number of sizeable rocks	12.5	3.590	10.2	2.380
Percent cover bare ground (%)	16.0	2.640	16.0	1.110
Percent cover sagebrush (%)	41.3	3.316	37.9	1.440
Percent cover grass (%)	38.0	5.630	36.2	1.830
Percent cover rock (%)	5.4	2.911	9.9	2.140

TABLE 3. Eigenvalues and principal components analysis proportion of variance generated for sage-grouse foraging site, random habitat site, nest site, and random nest habitat site characteristics at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006. The proportion of variance among the data that each principal component accounted for in each column is within parentheses.

	Heart Mountain		**Y U Bench**	
	Foraging/Random Sites	Nest/Random Sites	Foraging/Random Sites	Nest/Random Sites
PC 1	3.40 (37.7%)	4.74 (52.6%)	4.04 (44.9%)	4.14 (46.0%)
PC 2	1.49 (16.5%)	1.89 (21.0%)	1.31 (14.6%)	1.61 (17.8%)
PC 3	1.06 (11.8%)	1.40 (15.5%)	1.12 (12.4%)	1.45 (16.2%)
Total %	66%	89%	72%	80%

FIGURE 6. Principal components analysis biplot for sage-grouse foraging site selection and habitat site characteristics at Heart Mountain study site during the spring/summer seasons of 2005-2006.

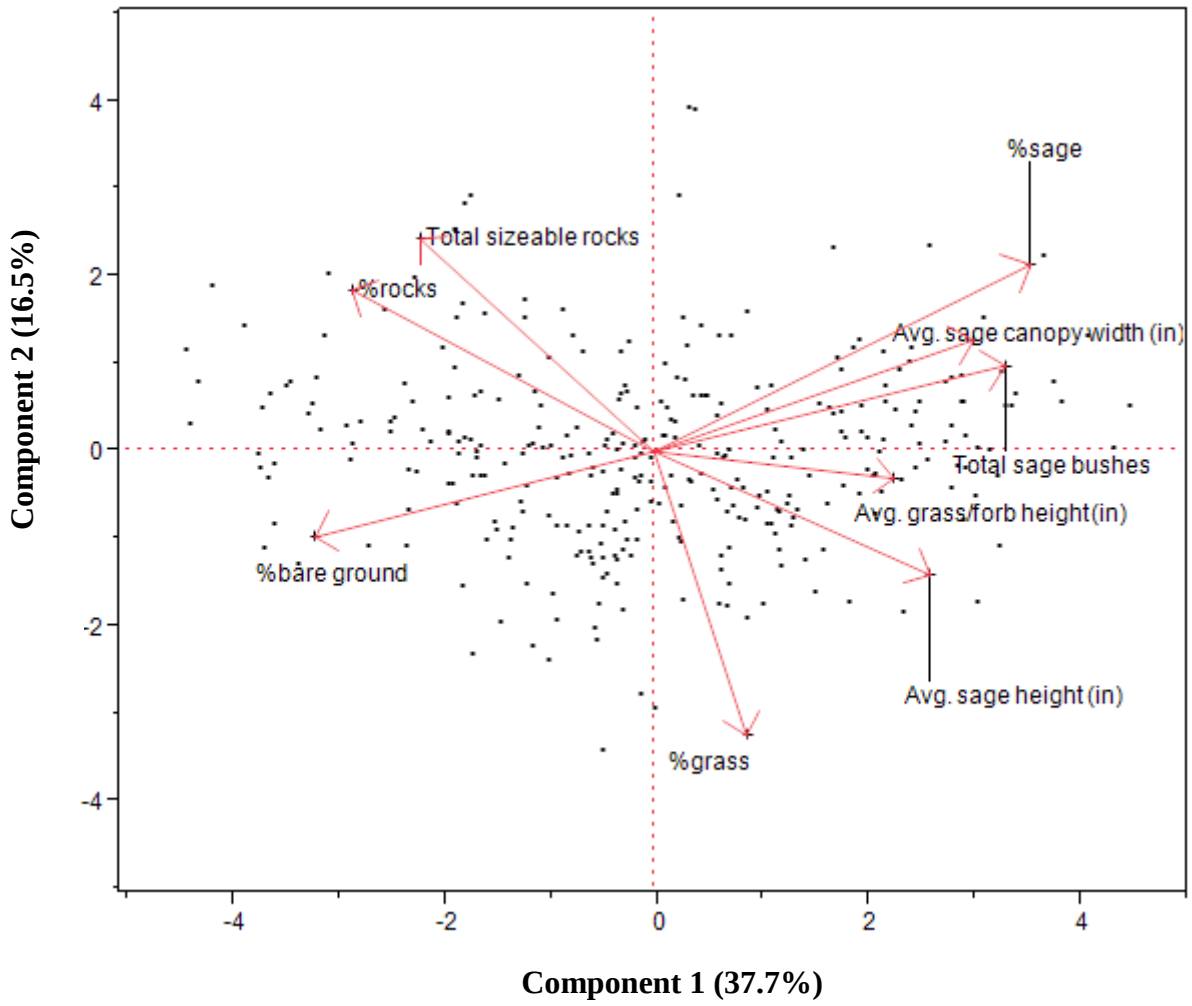


FIGURE 7. Principal components analysis biplots for nest site selection by hens at Heart Mountain study site during the spring/summer seasons of 2005-2006.

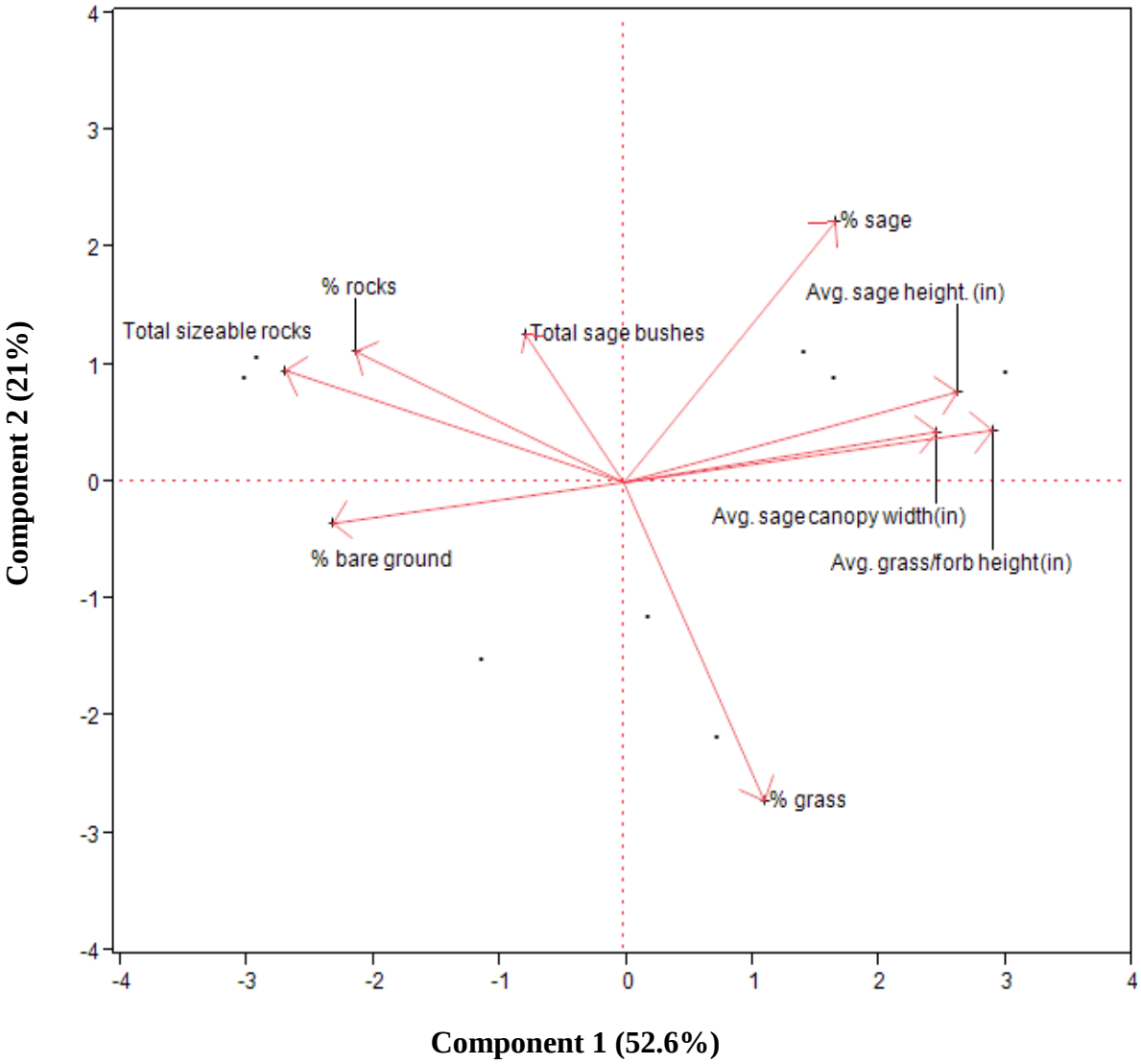


FIGURE 8. Principal components analysis biplot for sage-grouse foraging site selection and habitat site characteristics at Y U Bench study site during the spring/summer seasons of 2005-2006.

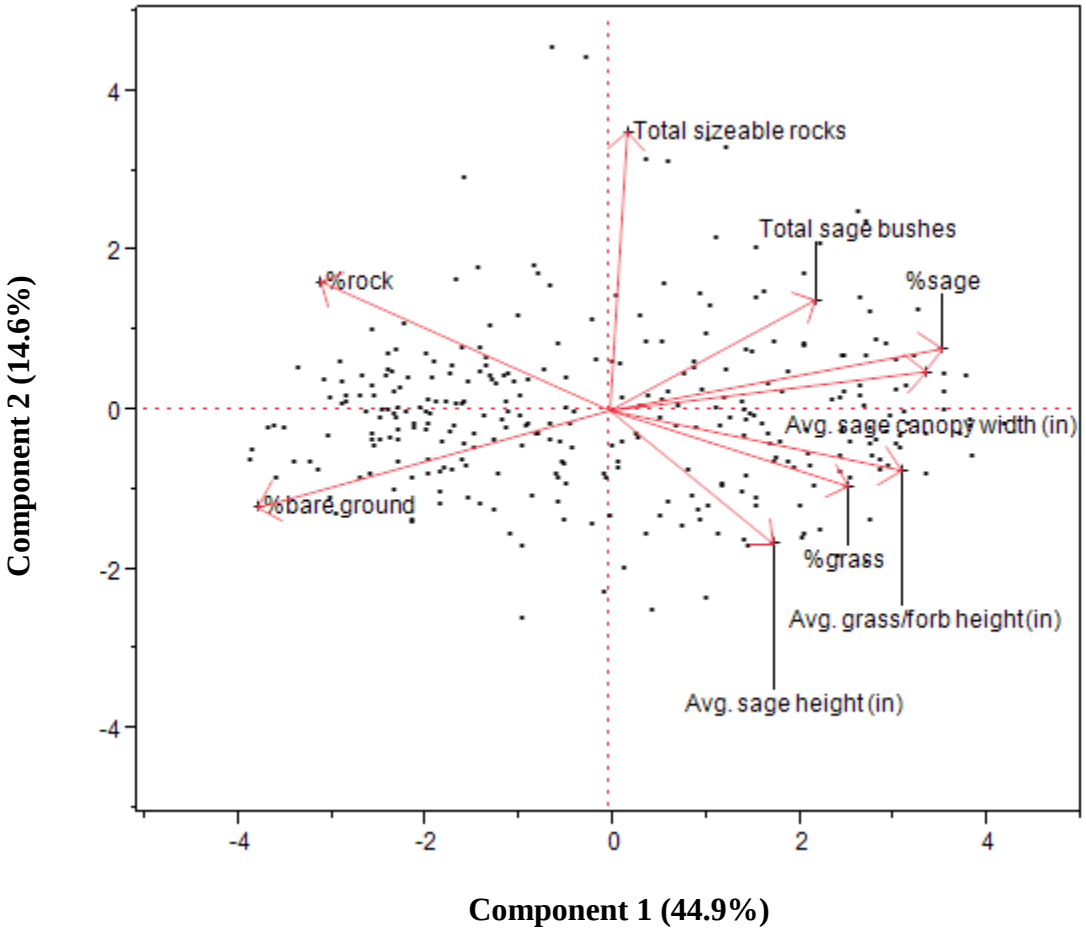
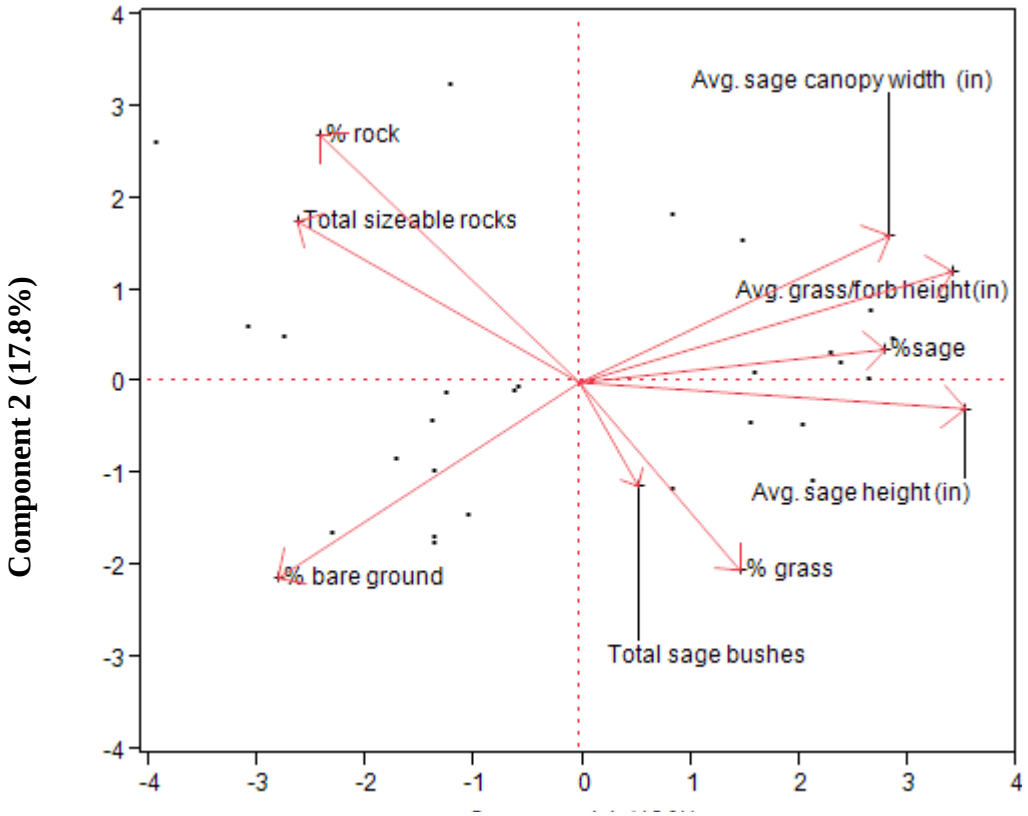


FIGURE 9. Principal components analysis biplot for sage-grouse hen nest site selection and random habitat characteristics at Y U Bench study site during the spring/summer seasons of 2005-2006.



CHAPTER 4. CARBON AND NITROGEN STABLE ISOTOPE ANALYSES OF GREATER SAGE-GROUSE INTESTINAL PELLETS AND CECAL TAR FROM NORTHWESTERN WYOMING

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ABSTRACT

Stable carbon and nitrogen isotope ratios were used to determine diet compositions using avian fecal matter instead of tissue. Sage-grouse produce two different kinds of fecal material: intestinal droppings and cecal tars. Both types of fecal matter were collected at both field sites during the summers of 2005 and 2006. Commonly encountered insects and plants from both study sites were also collected to provide a baseline for food item carbon and nitrogen stable isotopes ratios. Carbon isotope analyses of adult intestinal pellets indicate no significant difference in ratios from diet and nitrogen isotope analyses show that nitrogen is depleted compared to diet. However, cecal tar samples were significantly depleted in nitrogen even more than the nitrogen isotope ratios of intestinal pellets. Without showing the usually accepted 3-4‰ stepwise enrichment occurring at each trophic level, fecal nitrogen stable isotope ratios alone could not be reliable in determining diet composition and trophic level position. Chick intestinal pellet carbon stable isotope ratios varied but seemed to be most similar to the average carbon isotope ratio of scarab beetles found at both sites. Chick intestinal pellet nitrogen stable isotope ratios show depletion relative to scarab beetles and enrichment relative to ant and grasshopper nitrogen values. Mixing model analyses of carbon and nitrogen ratios of all three fecal types indicated that adult sage-grouse ingested more C_3 grasses and less forbs and sagebrush in the summer months than previously reported. Mixing models also indicated that although adults are eating mostly sagebrush in late spring, adults also appear to be eating more rabbitbrush and

greasewood than most previous studies have shown. Mixing models confirmed insects are the most important item in the diets of chicks. However, these same results also indicated chicks may be ingesting small amounts of food types that are atypical dietary components of young chicks such as both C_3 and C_4 grasses and CAM plants.

INTRODUCTION

Most chemical elements, such as hydrogen, carbon, and nitrogen, occur naturally in different forms called isotopes. Isotopes of various chemical elements possess the same number of protons but differ in the number of neutrons contained within their nucleus. Therefore, different isotopes of the same element vary in atomic mass. There are two types of isotopes: radioactive and stable. Unlike radioactive nuclei, stable isotopes possess nuclei that do not decay over time. The lightest stable isotope of any given element is typically more common than the heavier isotopes for each element (Fry 2006). For example, average relative abundances of ^{12}C and ^{13}C atoms are about 98.89% and 1.11%, respectively (Ehleringer and Rundel 1989). Mass spectrometers can be used to measure the differences in relative abundances of these isotopes, which are expressed as the ratio of the heavy to light isotopes of each element (Peterson and Fry 1987). These ratios are then standardized against international reference samples called standards and are then reported as parts per mil (‰) with the delta (δ) notation. Increases in δ values of a sample signify increases in the amount of the heavy isotope in the sample, while decreases in a sample's δ value mean there has been an increase in the amount of the light isotope in the sample (Peterson and Fry 1987). A sample is considered to be "enriched" in the heavier isotope when its δ value is higher or more positive than the δ value of a second sample. Samples are considered to be

"depleted" in the heavier isotope when the δ value of that sample is lower or more negative than the δ value of a second sample (Fry 2006). For example, if one performed stable carbon isotope analyses on an animal's muscle tissue and the muscle tissue's δ value for carbon is more positive than the δ value for carbon in samples of its prey, the consumer's muscle tissue sample contains more ^{13}C (the heavier carbon isotope) than the prey items do. Therefore, one would say the muscle tissue is "enriched" relative to the prey items. However, if stable carbon isotope analyses are performed on consumer muscle tissue and the δ value for that tissue sample is lower or more negative than the δ value of its prey, this means the consumer's muscle tissue sample contains less ^{13}C and more of the lighter isotope, ^{12}C, than the prey items do. Therefore, one would say the muscle tissue is "depleted" relative to the prey items.

The stable isotope ratio of a sample provides biologists with two types of information: source information and process information (Peterson and Fry 1987). As organisms take in substances from their environment, the stable isotopes from those source materials become incorporated into those organisms. Various metabolic processes within those organisms change the stable isotope composition of the source material during processing. This event is known as isotopic fractionation (Peterson and Fry 1987, Schimel 1993, Fry 2006). Peterson and Fry (1987) demonstrated how isotope ratios of samples can provide information about both source material and fractionation that occurs during processing by combining results from studies done by Troughton et al. (1974) and Keeling et al. (1963). Keeling et al. (1963) found carbon dioxide in air, the carbon source plants use for photosynthesis, to have a stable carbon isotope composition of -7.4‰. Troughton et al. (1974) showed that terrestrial C_3 plants have an average $\delta^{13}C$ of -27.8‰, which is -20.4‰ more negative than plants' carbon source. Therefore,

-7.4‰-20.4‰ = -27.8‰, demonstrating that the overall plant carbon isotopic composition of -27.8‰ reflects both the source and the fractionation (Peterson and Fry, 1987).

Differences in mass drive isotopic fractionation. Fractionation can occur as a result of either kinetic effects or thermodynamic (equilibrium) effects (Peterson and Fry 1987, Schimel 1993, Fry 2006). Kinetic effects result in lighter isotopes reacting faster because they have lighter mass and therefore require less activation energy to start reacting (Peterson and Fry 1987, Schimel 1993, Fry 2006). Lighter isotopes also have weaker bonds that are easier to break during a reaction. This means the products of a reaction usually contain more of the lighter isotope while more of the heavier isotope tends to stay behind in the organism (Peterson and Fry 1987, Schimel 1993, Fry 2006). Thermodynamic effects result in heavier isotopes concentrating where the bonds are the strongest (Peterson and Fry 1987, Schimel 1993, Fry 2006). Therefore, fractionation processes typically lead to consumer tissues such as muscle tissue becoming enriched with the heavier isotope of an element which in turn leads to waste products produced by that consumer becoming depleted compared to consumer tissue (Olive et al. 2003).

Over the last few decades, stable isotopes have been used as tools in many ecological studies such as research concerning nutrient cycling, water use efficiencies of plants, identifying the various photosynthetic pathways used by plants, trophic level structure of various ecosystems, avian migratory patterns, diet composition determinations, and many more. Here, I will be concerned primarily with using stable isotopes to make determinations about the composition of animal diets.

There are numerous stable isotopic patterns that exist in nature that allow the diets of animals to be reconstructed, particularly with carbon and nitrogen stable isotopes (Hobson 1999). Using

stable isotopes in foraging studies relies on the fact that different food items have different isotopic signatures that are then reflected in consumer tissues as shifts in isotope ratios so that the ratios of dietary items and consumer tissues differ in predictable ways (Inger and Bearhop 2008). Differences in the fractionation of stable carbon isotopes occurring in different photosynthetic pathways, such as C_3, C_4, and CAM, produce distinct isotopic differences in animal tissues, which can be used to infer the composition of avian diets (Hobson 1999). The $\delta^{13}C$ of C_3 plants typically ranges from -22 to -34‰, with an average of -27.8‰ (O'Leary 1988, Ehleringer et al. 1993, Marshall et al. 2007). The $\delta^{13}C$ of C_4 plants typically range between -9 to -16‰, usually averaging around -14‰, while CAM plants typically range from -10 to -20 and usually cluster around -11‰ (O'Leary 1988, Ehleringer et al. 1993, Marshall et al. 2007). Animal tissues tend to be enriched in C^{13} relative to their diet by about 1‰ (DeNiro and Epstein 1978, Fry et al. 1984, Hobson and Clark 1992a, Hobson and Clark 1992b). $\delta^{13}C$ values are known to change very little between trophic levels. Therefore, $\delta^{13}C$ values can be used to determine if a consumer is eating C_3 or C_4 plants (DeNiro and Epstein 1978). Miyake and Wada (1967) were the first researchers to show that enrichment of ^{15}N occurs along food chains. This was later confirmed by DeNiro and Epstein (1981) and Schoeninger et al. (1983). Minagwa and Wada (1984) found ^{15}N enrichment to be 3.4‰ while Wada et al. (1987) determined the enrichment factor was on average 3.3‰. Others have stated that nitrogen (^{15}N) enrichment varies more than ^{13}C and that it ranges from 2‰ to 4‰ and averages about 3‰ (Fry 1988, Inger and Bearhop 2008, Minagawa and Wada 1984, Wada et al. 1987). The $\delta^{13}C$ can be used to determine a consumer's primary food source while the $\delta^{15}N$ of a consumer can be used to determine what trophic level that consumer occupies in a food web (Post 2002).

Traditional methods of reconstructing diets in living animals included field observation, visual examination of fecal material, or examinations of stomach contents that required destroying the animal (Blumenthal et al. 2012). The use of stable isotopes as environmental tracers has provided a way to investigate animal ecology in ways that are much faster and less invasive than traditional methods thus lending to their growing popularity (Blumenthal et al. 2012). By running stable isotope analyses on consumer tissues as well as possible food source samples the resulting isotope ratios can then be used in stable isotope mixing models. These models are commonly used to estimate the relative contribution of assimilated dietary sources to the tissues of animals which in turn helps determine the diet of an animal in a non-invasive manner. These models are based on the idea that if the isotopic signatures of the food items eaten by a consumer as well as the isotopic signature of the consumer itself are known, then estimates can be made about the contributions of different food sources to the diet of a consumer.

Several earlier studies used geometric procedures called Euclidean distance methods to quantify the contributions of three food sources to the diet using ^{13}C and ^{15}N (Kline et al. 1993, Ben-David et al. 1997a, 1997b, Whitledge and Rabeni 1997, Szepanski et al. 1999). In these procedures, Euclidean distances were calculated for three line segments of a triangle and are then used to compute the dietary contributions of the different sources to the diet (Phillips 2001). These procedures assume that all three sources are used and that the partitioning of the three food sources is the same for both elements being used such as carbon and nitrogen. However, none of the formulas that use the Euclidean distances correctly estimate the dietary proportions because they tend to underestimate the proportions for the food sources that are consumed most often and overestimate the proportions of the food sources that are seldom consumed (Phillips 2001). These methods also do not conserve mass balance because they do not return the correct

observed isotopic ratios (Phillips 2001). These methods can calculate unique values for any number of food sources. However, there is not a unique solution when the number of food sources exceeds the number of isotopes by more than 1 (Phillips 2001). Therefore, they give the false impression of a unique solution when using more than three food sources with two isotopes which results in predicted predator isotopic ratios that are usually very different from the observed isotopic ratios (Phillips 2001).

Due to these limitations, Phillips (2001) proposed the linear mass balance mixing model to use as an alternative to these geometric procedures. The linear mass balance mixing model is a system of three equations in three unknowns which can be solved for the values of the three unknowns (Phillips 2001). These equations are for a two element three source situation, but this model can be used for one isotope and two food sources or for two isotopes and three food sources. This model provides mathematically unbiased expected values of the proportion estimates that correctly estimate the proportions for three food sources regardless of how much the sources are used by the animal for its diet (Phillips 2001). It correctly gives the correct observed isotopic ratios because it conserves mass balance (Phillips 2001). As with the Euclidean distance methods, this model assumes that the partitioning of food sources is the same for both elements being used (Phillips 2001). One limitation of this model is that it does not account for how differences among the sources' elemental concentrations might affect the computed source proportions derived from the two elements being investigated. For example, if one source is rich in carbon and poor in nitrogen, this will lead to a proportionate increase in the contribution of carbon to the mixture for that source and a proportionate decrease in the contribution of nitrogen to the mixture for that source (Phillips 2001). The linear mass balance mixing model can be extended to more than three food sources. However, this results in a three

equation system in more than three unknowns, which means that solutions may be found but they will not be unique (Phillips 2001). There are situations under which this model fails to give robust estimates of dietary proportions. This model works best if all the dietary sources have been measured and there are no more than three sources. It also works best when the food sources differ considerably in isotopic composition and show low variance (Phillips and Koch 2002). Another key assumption of this model is that carbon and nitrogen isotopes from all sources are homogenized in the consumer's body prior to the production of tissue (Phillips and Koch 2002). This assumption is valid when the sources provide an element in only one macromolecular form that can be broken down and assimilated in a uniform way. For example, carbon can be from proteins, carbohydrates or lipids each one having a different carbon-13 value while nitrogen comes from one macromolecule, protein, and is digested in a similar way no matter what the diet type happens to be (Phillips and Koch 2002). Proteins in the diet may be routed to produce more body proteins in a process called preferential substrate routing. In this scenario, the carbon isotopes of the body proteins would be labeled by the dietary proteins in an uneven way so that the fraction of protein-rich foods in the diet would be overestimated (Phillips and Koch 2002). Therefore, in this model physiological routing effects are confounded with concentration effects. One other assumption made by this model is that there is independence in this model where the equations are assumed to be linearly independent.

The concentration-weighted linear mixing model is a more complex linear mixing model that assumes that a source's contribution is proportional to the contributed mass multiplied by the elemental concentration in that source for each element involved (Phillips and Koch 2002). Unlike the standard linear mixing model, this model can be generalized to n elements and n+ 1 source. This model can be used whenever the elemental concentrations vary a great deal among

the sources of a mixture in order to obtain accurate dietary proportions. It not only provides information on elemental contributions from each dietary source involved but it also gives biomass proportions very close to the correct biomass proportions (Phillips and Koch 2002). This model is still limited as to the number of sources that can be considered. For example, it cannot be used for finding solutions for >n+1 sources. Phillips and Gregg (2003) developed a procedure that would expand the use of mixing models to more complex systems and that could be used for any number of isotopes and any number of sources. They created a Microsoft Visual Basic program called IsoSource to perform these procedures. Their method along with IsoSource provides a general procedure by which ranges of source proportional contributions to a mixture can be computed when the number of sources is too large to allow unique solutions (> number of isotope systems + 1) from standard linear and concentration-weighted linear mixing models (Phillips and Gregg 2003). This software is designed for situations in which *n* isotopes are being used and more than *n* + 1 sources are likely to be contributing to a mixture that needs to be analyzed (Benstead et al. 2006). IsoSource uses stable isotope data to calculate feasible ranges of source contributions while preserving mass balance unlike earlier Euclidean methods (Hopkins and Ferguson 2012). Examples of when one would need to use IsoSource include determining the sources of pollutants in streams, determining plant water sources, or for determining the variety of food items of which an animal's diet is composed.

The bulk of stable isotope studies in animals have involved analyzing feathers, fur, liver, and muscle tissues for stable isotopic ratios of various stable isotopes such as carbon and nitrogen. Far fewer studies have used fecal samples from animals to reconstruct the diet of those animals. Feces may rarely be used in stable isotope studies because there are little examples of controlled diet experiments with a wide range of species and therefore little is known about the isotopic

differences between diet and feces (Salvarina et al. 2013). Fecal stable isotope analysis has advantages over other stable isotope analysis using other biomaterials. For example, collecting fecal samples for stable isotope analysis is truly non-invasive since it is not required that you capture and restrain an animal to collect samples as one would have to with blood sample collection (Salvarina et al. 2013). Several studies have demonstrated that analyzing stable isotope ratios of fecal material provides a way to detect rapid and recent dietary changes. This could be applied to studies concerning trophic level changes and resource or habitat use changes (Salvarina et al. 2013). Jones et al. (1979) developed a technique for estimating the proportion of C_3 to C_4 plant species selected by sheep and cattle using the ratio of natural carbon isotopes in the feces of these mammals. Jones et al. (1979) found that fecal samples could be dried in ovens and stored indefinitely before analysis. Jones et al. (1979) also noted that this technique would be particularly useful in research conducted in natural grasslands containing mixtures of C_3 and C_4 grasses such as those of the Great Plains of the United States. Coates et al. (1991) conducted a similar study in Australia. They concluded that the changes in the $\delta^{13}C$ ratios of the feces of sheep and cattle from day to day reflected small but real changes in diet selection. It was also concluded that the $\delta^{13}C$ ratio of a single fecal sample reliably reflected the diet of free-grazing ruminants over the previous three to four days (Coates et al. 1991). Podlesak et al. (2005) were able to determine intra-individual changes in diets of various migratory songbirds using the $\delta^{13}C$ isotopic signatures of blood, plasma, feathers, breath, and feces. Feather $\delta^{13}C$ values provide long-term dietary information, whereas fecal $\delta^{13}C$ values reflect the last few days of consumption (Podlesak et al. 2005, Sponheimer et al. 2003a). In addition to stable carbon isotope analyses of diet, analysis of the stable nitrogen isotope ratios of animal tissues can reflect the trophic levels within food chains in which those animals are feeding, which also provides a

means of obtaining valuable information about avian diets (Minami et al. 1995). Nitrogen isotope ratios of animals can reflect trophic levels within food chains, with the animal's tissues becoming enriched relative to food items by about 3 to 4‰ (DeNiro and Epstein 1978). Mituzani and Wada (1988) hypothesized that if avian body tissues are enriched relative to diet that avian fecal matter should show a depletion of the heavy nitrogen isotope, ^{15}N. However, the results of their study showed that the ^{15}N ratio of penguin and gull fecal material was not significantly different than that of their diet (Mituzani and Wada 1988). Mituzani and Wada's study (1988) also demonstrated higher average ^{13}C ratios in feathers than the accepted 1‰ and the ^{13}C ratios in fecal material were not significantly different from that of the diet. Stewart et al. (2003) found that feces of mule deer were significantly depleted in ^{15}N and enriched in ^{13}C compared to elk and cattle. Studies of small mammals by Hwang et al. (2007) showed that fecal ^{15}N was enriched more than diet by about 2.5‰. Sponheimer et al. (2003b) found a similar enrichment pattern between diet and feces of 3‰ in llamas. Reitsema (2012) found there to be nitrogen and carbon enrichment in the feces of nursing primates.

Most of the studies concerned with fecal stable isotope analyses have been carried out using mammals. Few avian studies have been done on fecal stable isotope analysis. In this study, I attempted to determine the dietary composition of Greater Sage-Grouse (*Centrocercus urophasianus*) by comparing carbon and nitrogen stable isotope ratios of various known food items to those ratios present in their droppings. Sage-grouse produce two distinct types of fecal droppings throughout the year: intestinal and cecal. Intestinal droppings are cylindrical, 2-3 centimeters long, and are various shades of light green (Schroeder et al. 1999). Cecal droppings are large, dark, liquid-like feces (Schroeder et al. 1999). Sesquiterpine lactones are digested and

are excreted in the cecal tar. Since they produce two different types of feces, both types were collected and submitted for carbon and nitrogen stable isotope analyses.

The purpose of this study was to estimate the diet of sage-grouse that inhabit both study sites by first performing stable carbon and nitrogen isotope analyses on various plant species present at both locations as well as fresh fecal samples collected from adults sage-grouse and chicks and then using these obtained ratios in a mixing model called IsoSource.

METHODS

Study areas

Both of my study sites, Heart Mountain Ranch and Y U Bench, are located in the Bighorn Basin in Park County, Wyoming. The Bighorn Basin is a 161-kilometer wide plateau and intermontane basin located in north-central Wyoming. It is surrounded by the following mountain ranges: Absarokas to the west, Pryors to the north, Big Horns to the east, and the Owl Creek and Bridger ranges to the south (Figure 1). Since the Bighorn Basin is surrounded by mountains, a rain shadow covers it making it one of the most arid areas in Wyoming. It only receives 15-25 centimeters of precipitation per year. Most of this precipitation falls as snow instead of rain. The Bighorn Basin is characterized by multi-colored badlands and by gravelly arid soils that tend to have sandy subsoils (Dunnewald et al. 1927). Sagebrush, which tends to grow well in locations that have an arid, cold climate as well as this soil type, is the dominant vegetation cover in the Bighorn Basin. Just as the soil type and climatic conditions of the Bighorn Basin determine the distribution of sagebrush, the distribution of a sagebrush-obligate species such as sage-grouse is determined by the distribution of sagebrush.

Heart Mountain Ranch is owned by the Nature Conversancy and is located 18 kilometers north of Cody, Wyoming (44.6667° N, 109.1181° W) (Figure 2). Even though the entire ranch

encompasses 6,070 hectares, my study area was concentrated on the eastern side of the mountain at an elevation of about 1,524 meters while the mountain's summit is at 2,476 meters. Heart Mountain is an untreated site. Y U Bench is owned by the Bureau of Land Management and is located about 48 kilometers east of Cody, Wyoming (44-23'10" N, 108-40'14" W) at an elevation of 1,637 meters (Figure 3).

Sample collection

Fecal samples were collected, prepared, and analyzed using some of the same protocols from Podlesak et al. (2005) and Ben David et al. (1998). Fresh intestinal and cecal droppings were collected from Heart Mountain and Yu Bench study sites during the spring and summer seasons of 2005 and 2006. Some were collected at the lek sites at both study sites around noon to ensure the early morning lekking activities of the birds were not disturbed. Other samples of the intestinal fecal pellets were collected when observing grouse at both sites. However, very few cecal tar specimens were found at the lek areas. Instead cecal tars were usually encountered while out assessing habitat characteristics for both study sites. Whenever cecal tars were encountered, I collected samples because they were no longer seen after early June except for very old (not fresh) samples from winter. Whenever I encountered a hen and her brood, I would collect any feces left behind by the young as this was the only time I witnessed young defecating or encountered pellets left by young birds. Various plants and insects were also collected at both sites. All efforts were made to perform thorough collections of the various plants and insects encountered at both study sites during both field seasons. When any samples was collected, all samples were placed in a small Ziploc sandwich bag along with a note stating the collection date and study site as well as the name of the item collected. When fecal samples were being

collected, fecal samples were picked up with forceps or putty knives held by gloved hands. Surgical masks were also worn over one's nose and mouth whenever collecting fecal matter. Insects were also collected at both study sites. When insects were collected, a butterfly net was used to catch flying/jumping insects such as grasshoppers while forceps were used to pick up crawling insects such as ants and beetles. All samples were frozen in the sandwich bags by placing them in a deep freezer at the end of each field day until they could be brought back to the University of Arkansas to be prepared for analysis. At the end of each field season, the frozen samples were transported on dry ice from Cody, Wyoming, to Fayetteville, Arkansas.

Sample preparation and Stable Isotope Analysis

Upon arrival in Fayetteville, the samples were placed in a drying oven and dried at a temperature of 70° F for 48 hours. The samples were then taken to the Stable Isotope Laboratory at the University of Arkansas (UASIL) to be analyzed. In the lab, each sample was placed in an analytical grinding mill (IKA Works, Model A11) for grinding. The samples were then placed in labeled plastic vials and sealed. The ground samples were then weighed out and placed in 3.5 x 5mm tin capsules. Samples of 1.5 mg for feces, 3mg for insects, and 8 mg for plant samples were used. Carbon and nitrogen stable isotope ratios of prepared samples were determined using a Finnigan Delta+ isotope ratio mass spectrometer under continuous flow. Stable carbon isotope ratios in each sample were determined by comparing the $^{13}C/\ ^{12}C$ ratio of the sample to that of the standard, Vienna-PeeDee Belemnite (VPDB). Stable nitrogen isotope ratios in each sample were determined by comparing the $^{15}N/\ ^{14}N$ ratio of the sample to that of the standard, atmospheric air (AIR). The ratio of carbon and nitrogen stable isotopes was expressed in delta (δ) notation: [(Rsample/Rstandard)-1] x 1,000, where δ is the isotope ratio of the sample relative to a standard as parts per thousand (‰) deviations from all standards used and R represents the

type of isotope being analyzed, which in this case was both $^{13}C/^{12}C$ and $^{15}N/^{14}N$. Multiple samples of each plant species, each insect species and each fecal material type were prepared and analyzed for carbon and nitrogen stable isotope ratios. ANOVAs were used to compare carbon and nitrogen stable isotope ratios of the different fecal materials.

Stable Isotope Mixing Model

To determine the food source contributions to the diet of the grouse that inhabited my two field sites, I used the stable isotope ratios of possible food/prey items and the stable isotope ratios of fecal samples obtained from the stable carbon and nitrogen isotope analyses as input data for a stable isotope mixing model. IsoSource (version 1.3) was chosen as the mixing model. It was chosen primarily because the number of potential food sources contributing to the mixture samples (fecal matter) was greater than $n+1$ (n=number of isotopes being analyzed + 1) making a unique solution unobtainable. Phillips and Gregg (2003) and Caut et al. (2008) recommended using IsoSource when this was the case. IsoSource was used to calculate all feasible solutions of the potential dietary source contributions to the diets of Greater Sage-Grouse at my study sites near Cody, Wyoming. IsoSource was run for all three types of mixtures collected (adult intestinal pellets, adult cecal tars, and chick intestinal pellets). The isotopic signatures for each mixture and each of the possible dietary sources were entered into IsoSource. Source and tolerance increments were set at 1% and 0.1‰ (.01%), respectively. Entering a value of 1% for the source increment directs IsoSource to examine of all possible combinations of source contributions from 0-100% in increments of 1% (Phillips and Gregg 2003). Mass balance tolerance increments of .01% specifies that all source combinations that could result in the predicted mixture signatures within 0.01% of the actual observed signature are considered as feasible solutions (Phillips and Gregg 2003). To simplify the mixing analyses, similar food sources were grouped together a

priori as suggested by Phillips et al. (2005) when potential food sources were very numerous. Hopkins and Ferguson (2012) also recommended combining sources into similar groups because they felt it reduced bias in the mixing model that usually results from too many sources. For the adult intestinal pellet mixing analysis, food sources were grouped into categories because there were so many possible contributing sources to the diets of the adult birds. The adult food source groups were as follows: sagebrush, other shrubs such as greasewood and rabbitbrush, forbs, C_3 grasses, C_4 grasses, CAM plants, and insects. Phillips et al. (2005) and Hopkins and Ferguson (2012) also suggest that this mixing model can be constrained by omitting minor dietary sources that were already known to have not contributed to the diet. It is believed that doing this makes for more accurate results (Hopkins and Ferguson 2012). For example, chicks are not physically able to consume and digest sagebrush until they are older. Therefore, sagebrush and other woody shrubs such as greasewood were not included in the mixing model analysis of the chick intestinal pellets. Adult cecal tar mixing model analysis was constrained to just sagebrush and other shrubs because these birds produce cecal tar only during the winter and very early spring as a result of their almost 100% sagebrush diet during winter and early spring.

IsoSource provides output files which list each feasible solution, descriptive statistics about the distribution of these solutions (number of solutions, mean, standard deviation, minimum, maximum, 1^{st} percentile, median, and 99^{th} percentile for each source), and histograms of these distributions. Mixing model results were reported as the range of feasible solutions instead of focusing on a single value such as the mean as suggested by Phillips and Gregg (2003). Means and standard deviations provided by IsoSource's output were also reported.

RESULTS

Stable isotope analyses

Out of the 24 plant species sampled at both study sites, 22 of them had average stable carbon isotope ratios falling within the range of C_3 plants (-22 to -34‰) (O'Leary 1988, Ehleringer et al. 1993, Marshall et al. 2007) (Table 1, Figures 4, 5, and 6). Out of these 22 different plant species, only 4 species collected at both study sites had average stable carbon isotope ratios that were more depleted than -27.8‰, the demonstrated average $\delta^{13}C$ value for C_3 plants (Troughton et al. 1974, O'Leary 1988, Ehleringer et al. 1993, Marshall et al. 2007) (Table 1). This group of 22 plant species included five species of sagebrush and almost all grass species found at both study sites as well as other plant species (forbs) such as sego lily (*Calochortus nuttallii*) and common dandelion (*Taraxacum officinale*) (Table 1). The average $\delta^{13}C$ values of all C_3 plant species collected ranged from -22.528‰ for Tumble Mustard (*Sisymbrium altissimum*) to -29.350‰ for Goatsbeard *(Tragopogon dubius*) (Table 1). Therefore, Tumble Mustard had the most positive (most enriched) average $\delta^{13}C$ value of the C_3 plants collected at my two study sites while Goatsbeard had the most negative (most depleted) average $\delta^{13}C$ value of the C_3 plants collected (Table 1). Blue grama (*Bouteloua gracilis*) was the only species of C_4 grass that was found at my field sites. Blue grama (*Bouteloua gracilis*) samples had an average $\delta^{13}C$ value of -14.223‰, which is within the typical range of C_4 plants (O'Leary 1988, Marshall et al. 2007, Ehleringer et al. 1993) (Table 2). Yellow prickly pear (*Opuntia engelmannii*) was the only CAM plant present at my field sites. The samples of yellow prickly pear that were collected had an average $\delta^{13}C$ value of -11.695‰, which is consistent with the typical average stable carbon isotope ratio of CAM plants (O'Leary 1988, Marshall et al. 2007, Ehleringer et al. 1993) (Table 2). Nitrogen stable isotope analyses revealed that out of the 22 C_3 plants sampled at both study sites

Greasewood *(Sarcobatus vermiculatus)* had the highest δ^{15}N value and Needle and Thread Grass (*Hesperostipa comate*) had the lowest δ^{15} N value (Table 3). The only C_4 grass, Blue Grama *(Bouteloua gracilis)*, had an average δ^{15} N value of 2.108‰ (Table 4). The only CAM plant, Yellow Prickly Pear *(Opuntia engelmannii)*, had an average δ^{15} N value of 2.893‰ (Table 4).

Stable isotope analyses of various insects seen at both study sites showed that the insects sampled had average δ^{13} C and δ^{15} N values that ranged from -18.564‰ to -27.466‰ and 6.551‰-13.582‰, respectively (Table 5). Scarab beetles had the highest or most enriched average δ^{13} C and δ^{15} N values at -18.564 and 13.582, respectively (Table 5). These same analyses showed that harvester ants and sagebrush grasshoppers possessed carbon ratios within the range of C_3 plants and higher nitrogen ratios that showed a stepwise enrichment for their trophic level (Table 5).

Adult intestinal fecal samples had an average carbon stable isotope ratio of -25.981‰ (Table 6). This average is consistent with an animal that is eating C_3 plants because it falls within the C_3 plant stable carbon isotope range and it is known that δ^{13}C values are known to change very little between trophic levels (DeNiro and Epstein 1978). This average was most similar to that of Wyoming Big Sagebrush (-25.631‰, Table 1) and Squirreltail Grass (-25.776‰, Table 1). The average nitrogen stable isotope ratio of adult intestinal fecal pellets was 2.447‰ (Table 6). Adult cecal tar had an average carbon stable isotope ratio of -27.694‰ and an average nitrogen stable isotope ratio of 1.288‰ (Table 7). Adult cecal tar specimens were found by ANOVA analyses to be significantly depleted in both ^{13}C and ^{15}N when compared to adult intestinal fecal samples (*$F=12.5987$, $df=46$, $p<.0001$* and *$F=4.2741$, $df=46$, $p<.0001$, respectively*). Chick intestinal pellets had average carbon and nitrogen stable isotope ratios of -18.675‰ and 11.25‰, respectively (Table 8). ANOVA results show a statistically significant difference between chick

and adult intestinal pellet carbon stable isotope ratios as well as between chick and adult intestinal pellet nitrogen stable isotope ratios (F=*31.2085, df=34, p<.0001* and *F=18.4175, df=34, p<.0001, respectively*). Therefore, chick fecal material is more enriched in both ^{13}C and ^{15}N than adult intestinal fecal pellets and cecal tars. No cecal tar samples existed for sage-grouse chicks because they do not produce cecal tar at that age. Figures 4-6 show the average carbon to nitrogen isotope ratios for adult grouse intestinal fecal pellets, adult grouse cecal tars, and grouse chick intestinal pellets compared to the various food sources that were available at both field sites.

Mixing model analyses

Mixing model output for adult intestinal fecal pellets indicates that C_3 grasses were the most important food source contributing between 80-92% (average=85.6%) of the late spring/summer (May-July) diet of the grouse that inhibit my field sites (Table 9). Forbs had a surprisingly low feasible solution range of only 0-14% with an average of about 4.1% (Table 9). Sagebrush and other shrubs had similar feasible solution ranges to one another at 0-11% (average= 3.7%) and 0-12% (average=3.8%), respectively (Table 9). Insects, C_4 grasses, and CAM plants contributed the least to the adult diet with feasible solution ranges of 0-5 % (mean=1.4%), 0-2% (mean=.9%), and 0-2% (mean=.5%), respectively (Table 9).

Mixing model output for adult cecal tar samples indicate the following feasible solution ranges and means: sagebrush 47-74% (mean=60.3%), rabbitbrush 1-53% (mean=27.4%), and greasewood 0-25% (mean=12.3%) (Table 10). Mixing model results for grouse chick intestinal fecal samples indicate insects are the most important food source for young birds with a feasible solution range of 78-79% (mean=78.5%) (Table 11). Forbs were the second highest contributor to diet with a feasible solution range of 2-11% (mean=7%) (Table 11). Grasses were the third

highest contributor to chick diets with a feasible solution ranges of 5-9% (mean=6.3%) and 1-8% (mean=4%) for C_4 and C_3 grasses, respectively (Table 11). CAM plants had a feasible solution range of 2-6% (mean=4.2%) (Table 11).

DISCUSSION

Stable carbon isotope results showed that adult sage-grouse at Heart Mountain and Y U Bench were eating primarily C_3 plants because the average $\delta^{13}C$ value of the adult intestinal fecal pellets was -25.981‰ (Table 6) which falls within the well documented range for C_3 plants which is -22 to -34‰ (O'Leary 1988, Ehleringer et al. 1993, Marshall et al. 2007). Stable isotope ratios for nitrogen in adult intestinal fecal pellets were depleted relative to diet and did not exhibit the stepwise enrichment of 3.4‰ that is often seen with animal tissues (Minagwa and Wada 1984). If enrichment of animal tissues occurs with nitrogen, one would assume animal wastes such as fecal material would be depleted in nitrogen as my results showed. Mixing model results from all three fecal types made it possible to rank food sources in terms of their trophic importance to sage-grouse. Adult intestinal fecal pellet mixing model results clearly backed up the initial stable carbon isotope analyses that suggested the adult birds were consuming primarily C_3 plants. These mixing model results for adult intestinal fecal pellets revealed that summer food sources could be ranked in this order of importance: C_3 grasses> forbs> sagebrush and other shrubs>insects>C4 grasses>CAM plants (Table 9). Many studies have documented the year-round consumption of sagebrush by sage-grouse and its huge importance to sage-grouse not only as a dietary component but also for nesting and brooding as well as shelter in the colder months (Girard 1937, Patterson 1952, Schneegas 1967, Martin 1970, Klebenow 1973, Wallestad 1975, Call 1979, and Call and Maser 1985). Many of these same studies have also stated that even though adult birds would eat sagebrush year-round they would

decrease their intake of sagebrush from almost all sagebrush in the winter and early spring to less sagebrush during the summer months in order to partake of succulent forbs and grasses as well as insects that were available during the summer months (Martin 1970). Martin (1970) found that sagebrush comprised 34% of sage-grouse summer diets. Griner (1939) found stomach contents were comprised of 77% sagebrush in the summer months. Therefore, my results for adult intestinal fecal pellets were somewhat surprising because sagebrush contributed much less to the diet of these birds than expected especially considering what information is found in the vast literature base about this matter. For example, my results show that sagebrush contributed anywhere from 0% to 11% of the adult diet with a mean contribution of about 3.7% (Table 9) whereas other studies such as those mentioned above show that sagebrush is a much bigger contributor to adult summer diets even though they do not eat 100% sagebrush in the summer as they do in winter. Martin (1970) found that forbs such as dandelion comprised 45% of Greater Sage-Grouse summer dietary intake. Trueblood (1954) stated that the adult summer diet was composed of 39-47% forbs. However, my results indicate that forbs were actually of minor importance to birds at my field sites in terms of summer diet contributing anywhere from 0-14% with an average of 4.1% (Table 9). Martin et al. (1951) reported insects were only a minor dietary item for adults making up only 2% of the adult Greater Sage-Grouse diet in spring and fall and only 9% of the diet in the summer. My results indicated insects were also of minor importance with a contribution of only 0-5% (mean=1.4%) (Table 9).

Fresh adult cecal tars were not found after the first week in May so it was expected they would contain information about the late winter/early spring diet of adult birds before the birds had made the switch to summer dietary items. Stable carbon isotope ratios of adult cecal tar samples indicated that the birds were ingesting plants that used the C_3 pathway such as

sagebrush. However, carbon and nitrogen isotope ratios of cecal tars were even more depleted in carbon and nitrogen stable isotopes than adult intestinal fecal pellets were. Once again, trophic level enrichment was not seen in the results of the stable nitrogen isotope analysis on cecal tar samples. Unlike my results, Mituzani and Wada (1988) found carbon and nitrogen isotope ratios in bird feces were not significantly enriched, depleted, or different from their diet. Also, although the cecal tar samples exhibited average $\delta^{13}C$ values typical of C_3 plants, these values were even more depleted than those of the adult intestinal fecal pellets as mentioned in the results section of this chapter. Mixing model results of adult cecal tar samples confirmed the conclusion made from stable carbon isotope analysis results in that the primary food item was a C_3 plant, sagebrush. Mixing model results for adult cecal tar samples indicated that food sources could be ranked in this order of importance: sagebrush>rabbitbrush>greasewood. Values for other possible food items such as forbs, grasses, and insects had zero percent contributions across the board in an initial run of adult cecal tar stable carbon and nitrogen isotope ratios in IsoSource. The cecal tar stable carbon and nitrogen isotope values were run through the mixing model a second time with only the values for sagebrush, rabbitbrush, and greasewood which returned the same results in terms of percent contributions to the late winter/early spring diets of adult birds. As expected, my results did indicate that sagebrush was the major contributor to the late winter/early spring diets of adult birds (Table 10). However, it was found to comprise anywhere from 47-74% of the adult diet (mean=60.3%) at a time of the year the literature states their diet is made up of almost 100% sagebrush. For example, Wallestad (1975) found only sagebrush in adult crops around that time of the year and he stated that around June sagebrush started to make up slightly less than 60% of the adult diet. Rabbitbrush and greasewood have both been documented as food sources for adult grouse (Judd

1905, Girard 1937). According to the existing literature, the contribution of these two plants to the adult diet is a small one (Girard 1937) and they are mentioned most often as serving as nesting plants for the hens instead of food items. However, my mixing model results for adult cecal tar indicates that before making the switch to a summer diet the adult birds at my field sites were utilizing rabbitbrush and greasewood as food sources in higher than expected amounts. Rabbitbrush was found to contribute 1-53% (mean=27.4%) to the diet and greasewood was found to contribute 0-25% to the diet (mean=12.3%) (Table 10).

Young chicks consume mostly insects during the first three weeks of life (Patterson 1952). Patterson (1952) stated that chicks primarily consumed ants and beetles of various species during the first few weeks of life. Klebenow and Gray (1968) found that the diet of one week old chicks was 52% insects. Klebenow and Gray (1968) also found that the majority of insects being consumed by chicks during the first week of life were beetles from family Scarabaeidae . Between the first and third week of life insects make up a large part of their diet but they gradually start to eat more and more forb species after the first three weeks of life (Girard 1937). Trueblood (1954) found that juvenile chicks in Utah had diets composed of 54-60% of various forb species. In my study, stable carbon isotope analyses revealed that chicks were not eating C_3 plant types and the stable carbon isotope values were very enriched compared to those of C_3 plants. This indicated a completely different food source was being consumed by chicks. The average stable carbon isotope values from chick intestinal pellets closely matched those of scarab beetles (Tables 5 and 8). The average stable nitrogen isotope values for chick intestinal pellets did show some mixed results (Table 8). The mixing model results for chick intestinal pellets did confirm that insects composed 78-79% of the diet (mean=78.5%) (Table 11). Insects were followed by forbs in terms of dietary importance with 2-11% of the diet comprised of forbs with

an average of 7% (Table 11). These results match the information found in the existing literature. The lower number for forbs obtained from IsoSource was probably the result of young chicks just starting to incorporate forbs into their diets as they gradually began the process of moving away from eating mostly insects. The results for insects and forb consumption also match my actual field observations of hens with broods at my field sites during which I witnessed young chicks eating scarab beetles and ants that were exiting ant hills. I also took the opportunity to examine the fecal pellets left by the young around the ant hills at my sites and I could make out pieces of insect exoskeletons in the fresh fecal samples of the chicks. I would also like to note that the intestinal fecal pellets of the chicks had a much looser construction to them than those of the adult birds which was probably due to the lack of plant fiber. The mixing model analysis of stable carbon and nitrogen isotope ratios for chick intestinal pellets also indicated other food items were being eaten that I have not seen mentioned in the literature as food items normally taken by extremely young chicks. C_4 grasses comprised anywhere from 5-9% (mean=6.3%) (Table 11). CAM plants and C_3 grasses comprised 2-6% (mean=4.3%) and 1-8% (mean=4%) of the diet, respectively (Table 11).

Stable isotope studies involving the analyses of feather, fur, or tissue have reported only slight enrichments in those items over diet for carbon at an average of about 1‰ (DeNiro and Epstein 1978, Fry et al. 1984, Hobson and Clark 1992a, Hobson and Clark 1992b). These same types of studies have also shown that nitrogen is enriched in tissues at an average of about 3-4‰ over diet (DeNiro and Epstein 1978). Previous studies that have looked at stable carbon and nitrogen ratios for fecal matter have varied much more than those of various tissues. Stable isotope studies done on fecal material of some mammal species have shown that both carbon and nitrogen are enriched and not depleted relative to diet (Stewart et al. 2003, Sponheimer et al.

2003b, Hwang et al. 2007, Reitsema 2012). Salvarina et al. (2013) found no significant difference between bat feces and diet in terms of carbon, nitrogen, and sulfur isotopic signatures. Mituzani and Wada (1988) showed that avian feces were neither enriched nor depleted relative to diet as the studies in some mammals have shown. Instead, they found that the carbon and nitrogen stable isotope ratios of avian feces were not significantly different from that of their diet. Bird et al. (2008) also found no significant difference between carbon and nitrogen isotopic signatures of bird guano and diet. In my study, I found that carbon isotope ratios of adult intestinal pellets were not that much different from their C_3 plant diets, the nitrogen stable isotope ratios of adult intestinal pellets showed much depletion in nitrogen relative to food items, the adult cecal tars showed even more depletion in carbon and nitrogen, and chick pellets were enriched in carbon compared to the possible grasshoppers and ants making up a portion of their diets but also not significantly different from the scarab beetles they were seen eating most of the time. Nitrogen isotope values of chick intestinal pellets indicate an average nitrogen ratio that is enriched relative to ants and grasshoppers sampled at my study sites but depleted relative to scarab beetles collected at both study sites.

More studies need to be done using fecal material to determine the diet of animals to add to the body of literature that currently exists because there seems to be such varied results even within the same taxonomic classes. Examining the stable carbon and nitrogen isotope ratios of avian feces is much easier and less stressful for birds. It provides a less invasive option to examining stomach contents. My results seem to suggest that carbon isotope analyses are a good way to determine diet especially if teamed up with mixing model analyses. However, according to my results, nitrogen stable isotope analyses alone on avian feces do not appear to be a very

reliable way to determine diet composition or trophic level by the typical stepwise enrichment factor of 3.4‰.

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APPENDIX B: TABLES AND FIGURES

Figure 1. Topographic map of the Bighorn Basin, Wyoming, USA. Map provided by Google Earth (2009).

Figure 2. Topographic map of Heart Mountain Ranch study site located in Park County, WY, USA. Map provided by the Bureau of Land Management (2005).

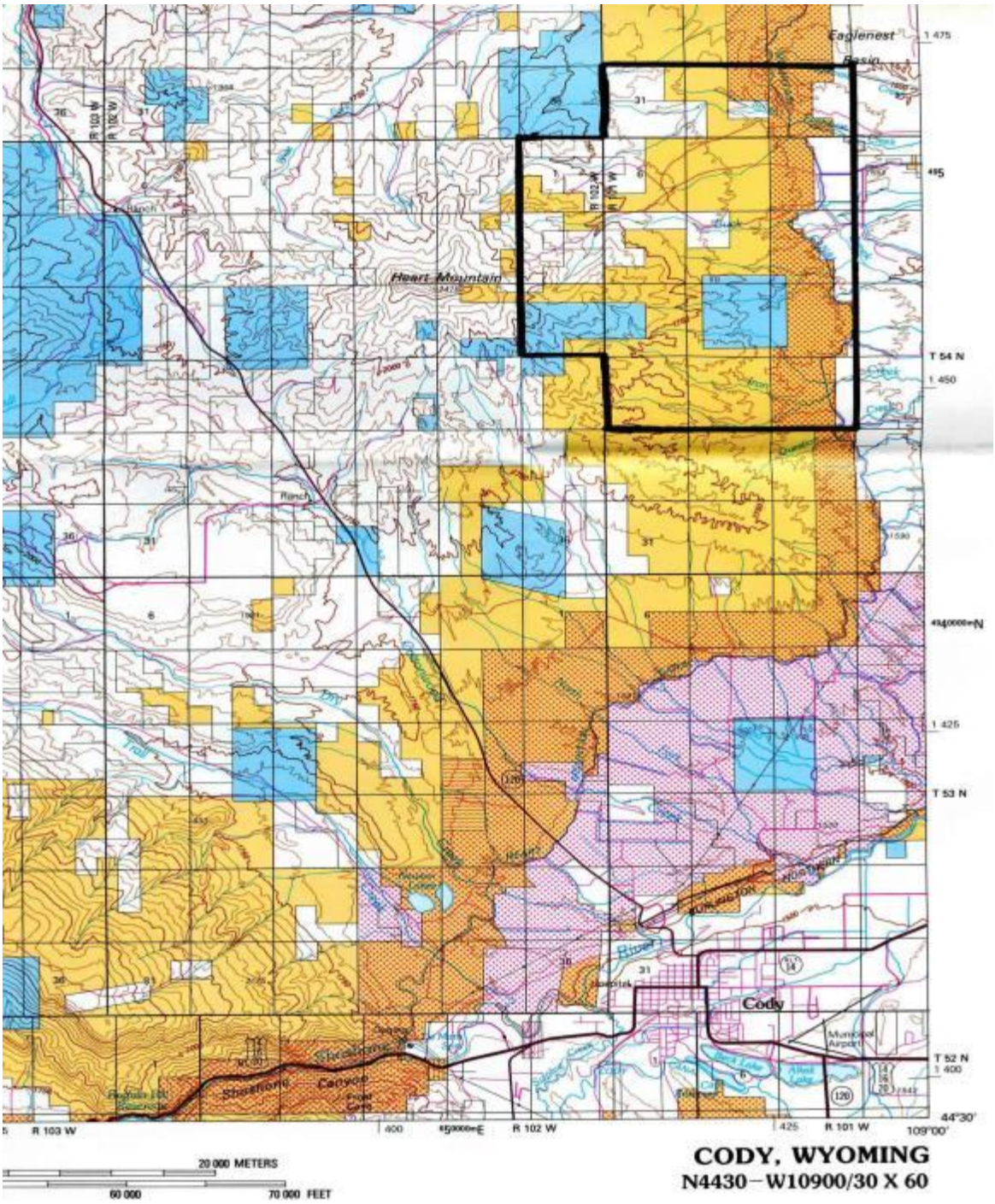

Figure 3. Topographic map of Y U Bench study site located in Park County, WY, USA. Map provided by the Bureau of Land Management (2005).

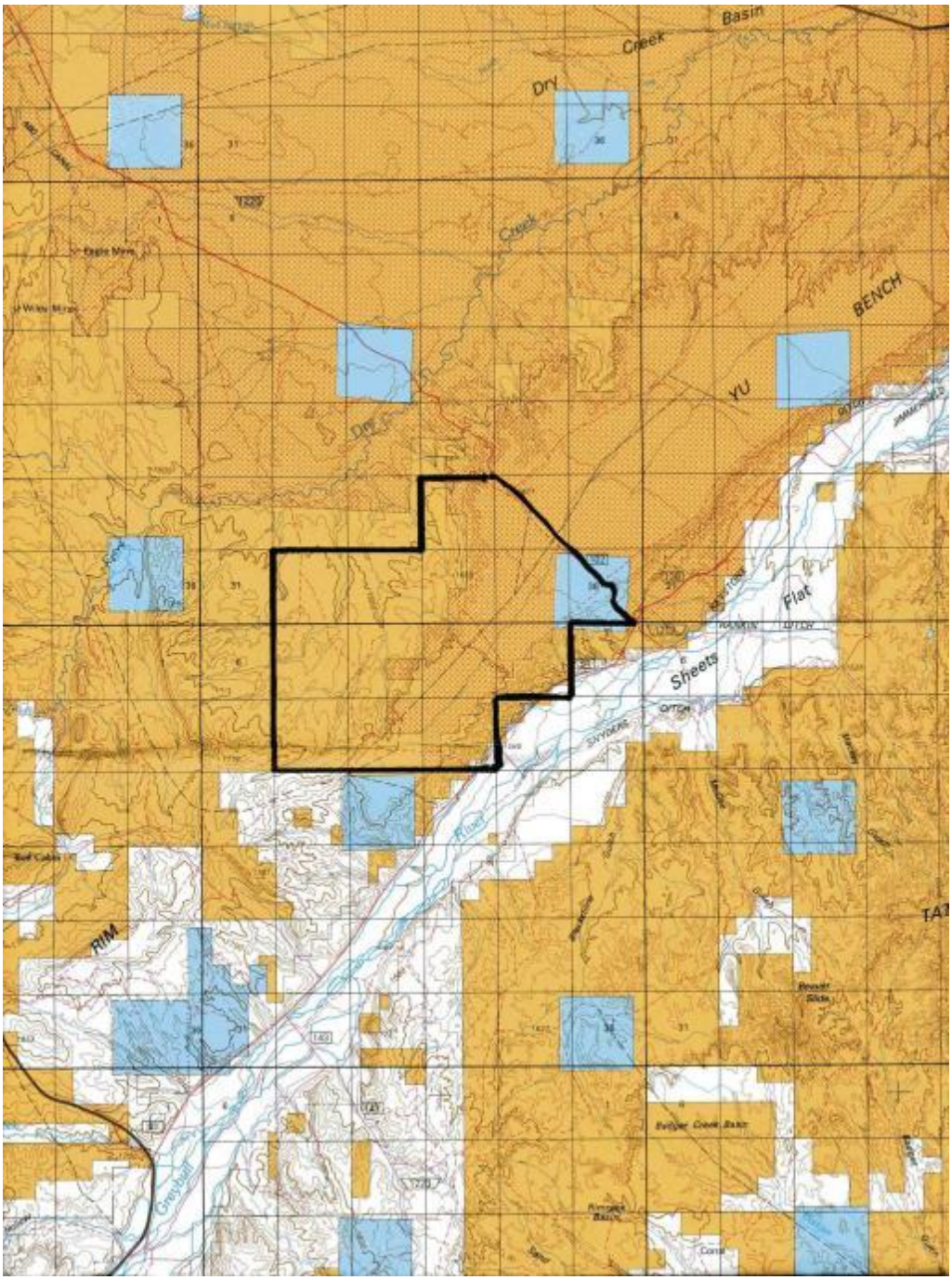

TABLE 1. Summary of average carbon stable isotope ratios of C_3 plants found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006.

C_3 Plants	**$\delta^{13}C‰$ ($\bar{x}$ ± SE)**	**95% CI**
Sagebrush species		
Wyoming Big Sagebrush *(Artemisia tridentate Nutt ssp. wyomingensis)*	-25.631 ± .173	.374
Black Sagebrush *(Artemisia nova)*	-24.508 ± .121	.384
Fringed Sagebrush *(Artemisia frigida)*	-27.930 ± .196	.624
Silver Sagebrush *(Artemisia cana)*	-28.675 ± .136	.432
Basin Sagebrush *(Artemisia tridentata ssp. tridentata)*	-26.736 ± .165	.374
Other Shrubs		
Rabbitbrush *(Chrysothamnus viscidiflorus)*	-26.825 ± .493	.569
Greasewood *(Sarcobatus vermiculatus)*	-24.825 ± .212	.676
Forbs		
Wild Onion *(Allium spp.)*	-26.820 ± .310	.985
Tumble Mustard (*Sisymbrium altissimum)*	-22.528 ± .155	.492
Plains Daisy (*Melampodium leucanthum)*	-28.555 ± .187	.596
Orange Globe Mallow *(Sphaeralcea munroana)*	-27.528 ± .194	.618
Bitterroot *(Lewisia rediviva)*	-24.540 ± .138	.438
Sego Lily *(Calochortus nuttallii)*	-27.258 ± .084	.266
Western Vetch *(Hedysarum occidentale)*	-28.590 ± .138	.438
Common Dandelion (*Taraxacum officinale)*	-23.675 ± .074	.234
Goatsbeard (*Tragopogon dubius*)	-29.350 ± .169	.538

TABLE 1. (continued) Summary of average carbon stable isotope ratios of C_3 plants found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006.

C_3 Plants	**$\delta^{13}C‰$ ($\bar{x}$ ± SE)**	**95% CI**
C_3 Grasses		
Western Wheatgrass (*Pascopyrum smithii)*	-26.498 ± .126	.401
Indian Rice Grass (*Achnatherum hymenoides)*	-23.085 ± .351	.118
Junegrass *(Koeleria macrantha)*	-26.418 ± .077	.198
Cheat Grass *(Bromus tectorum)*	-27.258 ± .084	.266
Needle and Thread Grass *(Hesperostipa comata)*	-26.433 ± .152	.483
Squirreltail Grass (*Elymus elymoides)*	-25.776 ± .183	.509

TABLE 2. Summary of average carbon stable isotope ratios of C_4 and CAM plants found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006.

Plant Species	**$\delta^{13}C$‰ ($\bar{x}$ ± SE)**	**95% CI**
Blue Grama Grass *(Bouteloua gracilis)* (C4)	-14.223 ± .317	1.010
Prickly Pear Cactus *(Opuntia engelmannii)* (CAM)	-11.695 ± .091	0.290

TABLE 3. Summary of average nitrogen stable isotope ratios of C_3 plants found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006.

C_3 Plants	**δ^{15}N‰ ($\bar{x}$ ± SE)**	**95% CI**
Sagebrush species		
Wyoming Big Sagebrush *(Artemisia tridentata Nutt ssp. wyomingensis)*	5.396 ± .213	.459
Black Sagebrush *(Artemisia nova)*	4.305 ± .197	.627
Fringed Sagebrush *(Artemisia frigida)*	3.498 ± .338	.074
Silver Sagebrush *(Artemisia cana)*	4.098 ± .059	.188
Basin Sagebrush *(Artemisia tridentata ssp. tridentata)*	3.313 ± .149	.336
Other Shrubs		
Rabbitbrush *(Chrysothamnus viscidiflorus)*	3.215 ± .153	.486
Greasewood *(Sarcobatus vermiculatus)*	5.583 ± .161	.512
Forbs		
Wild Onion *(Allium spp.)*	2.343 ± .092	.293
Tumble Mustard (*Sisymbrium altissimum)*	4.558 ± .140	.445
Plains Daisy (*Melampodium leucanthum)*	2.335 ± .072	.229
Orange Globe Mallow (*Sphaeralcea munroana*)	3.603 ± .074	.237
Bitterroot *(Lewisia rediviva)*	3.528 ± .097	.309
Sego Lily *(Calochortus nuttallii)*	2.245 ± .074	.234
Western Vetch *(Hedysarum occidentale)*	4.240 ± .106	.338
Common Dandelion (*Taraxacum officinale)*	3.613 ± .138	.438
Goatsbeard *(Tragopogon dubius)*	3.725 ± .089	.282

TABLE 3. (continued) Summary of average nitrogen stable isotope ratios of C_3 plants found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006.

C_3 Plants	**δ^{13}N‰ ($\bar{x}$ ± SE)**	**95% CI**
C_3 Grasses		
Western Wheatgrass *(Pascopyrum smithii)*	3.828 ± .183	.583
Indian Rice Grass *(Achnatherum hymenoides)*	3.193 ± .194	.617
Junegrass *(Koeleria macrantha)*	2.008 ± .048	.124
Cheat Grass *(Bromus tectorum)*	2.355 ± .148	.471
Needle and Thread Grass *(Hesperostipa comata)*	1.758 ± .163	.519
Squirreltail Grass *(Elymus elymoides)*	3.418 ± .106	.294

TABLE 4. Summary of average nitrogen stable isotope ratios of C_4 and CAM plants found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006.

Plant Species	**δ^{13}N‰ ($\bar{x}$ ± SE)**	**95% CI**
Blue Grama Grass *(Bouteloua gracilis)* (C4)	2.108 ± .239	.759
Prickly Pear Cactus *(Opuntia engelmannii)* (CAM)	2.893 ± .057	.182

TABLE 5. Summary of average carbon and nitrogen stable isotope ratios of various insects found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006.

Species	**δ^{13}C‰ ($\bar{x}$ ± SE)**	**95 % CI**	**$\delta^{15/14}$N ($\bar{x}$ ± SE)**	**95% CI**
Harvester Ants *(Pogonomyrmex spp.)*	-27.466 ± .107	.242	9.466 ± .076	.172
Scarab Beetles (Scarabaeidae)	-18.564 ± .087	.196	13.582 ± .244	.244
Sagebrush Grasshoppers *(Melanoplus spp.)*	-24.487 ± .125	.283	6.551 ± .108	.245

TABLE 6. Summary of carbon and nitrogen stable isotope ratios of adult intestinal fecal pellets found at Heart Mountain and Y U Bench study sites during spring/summer seasons of 2005-2006 with mean and standard error calculations.

Fecal type	**$\delta^{13/12}C$**	**$\delta^{15/14}N$**
Intestinal	-25.96	2.50
Intestinal	-25.71	2.81
Intestinal	-26.14	2.51
Intestinal	-26.93	3.47
Intestinal	-25.46	3.40
Intestinal	-25.49	2.52
Intestinal	-26.32	1.89
Intestinal	-25.77	4.07
Intestinal	-26.56	1.88
Intestinal	-25.95	1.19
Intestinal	-26.37	5.34
Intestinal	-25.65	2.26
Intestinal	-25.41	1.13
Intestinal	-25.61	1.53
Intestinal	-25.23	2.82
Intestinal	-25.99	0.34
Intestinal	-25.51	3.11
Intestinal	-26.00	2.93
Intestinal	-25.70	1.84
Intestinal	-25.68	2.29
Intestinal	-25.96	2.50
Intestinal	-26.38	1.09
Intestinal	-26.89	2.68
Intestinal	-26.98	2.72
Intestinal	-25.84	2.60
Intestinal	-26.02	2.56
Intestinal	-26.56	2.34
Intestinal	-25.92	2.38
Intestinal	-26.06	1.58
Intestinal	-25.78	2.67
Intestinal	-25.81	2.75
Intestinal	-25.74	2.59
n	32	32
Mean ± SE	-25.981 ± .079	2.447 ± .164

TABLE 7. Summary of carbon and nitrogen stable isotope ratios of adult cecal tar found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006 with mean and standard error calculations.

Fecal type	**$\delta^{13/12}C$**	**$\delta^{15/14}N$**
Cecal	-27.14	1.58
Cecal	-27.74	0.24
Cecal	-27.86	0.28
Cecal	-27.19	2.90
Cecal	-27.92	1.54
Cecal	-27.22	2.44
Cecal	-27.33	0.85
Cecal	-27.56	0.46
Cecal	-27.40	1.64
Cecal	-27.63	1.24
Cecal	-28.38	0.84
Cecal	-27.32	1.06
Cecal	-27.66	0.83
Cecal	-27.89	0.56
Cecal	-28.61	2.36
Cecal	-28.25	1.78
n	16	16
Mean ± SE	-27.694 ± 0.11	1.288 ± 0.200

TABLE 8. Summary of carbon and nitrogen stable isotope ratios of chick intestinal fecal pellets found at Heart Mountain and Y U Bench study sites during the spring/summer seasons of 2005-2006 with mean and standard error calculations.

Fecal type	**$\delta^{13/12}C$**	**$\delta^{15/14}N$**
Intestinal	-18.46	11.84
Intestinal	-18.31	10.89
Intestinal	-19.20	11.52
Intestinal	-18.73	10.75
n	4	4
Mean ± SE	-18.675 ± .195	11.25 ± .258

FIGURE 4. Average stable isotope values (δ^{13}C and δ^{15}N) of adult grouse intestinal fecal pellets compared to average stable isotope values for food source samples.

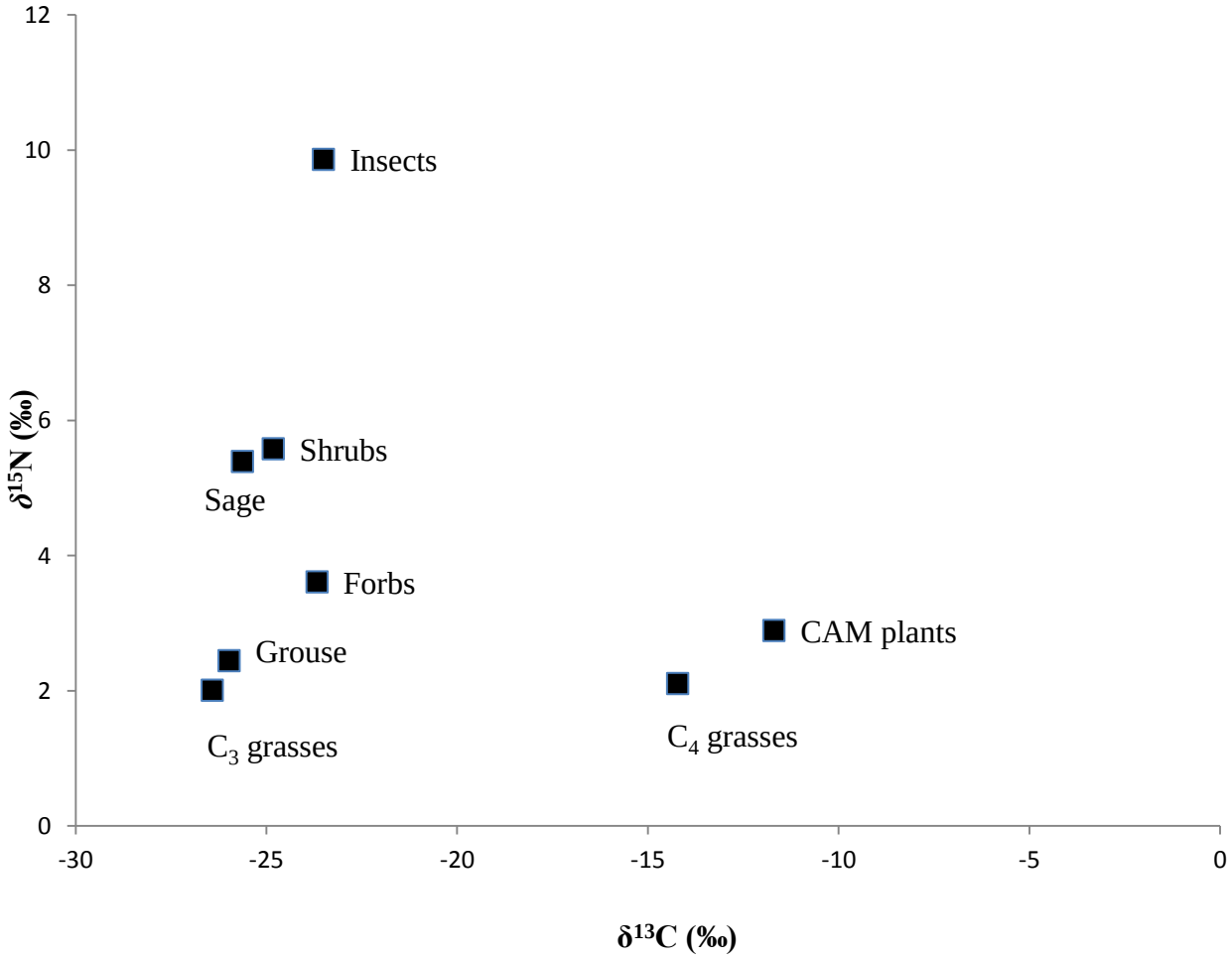

FIGURE 5. Average stable isotope values (δ^{13}C and δ^{15}N) of adult cecal tar samples compared to average stable isotope values for food source samples.

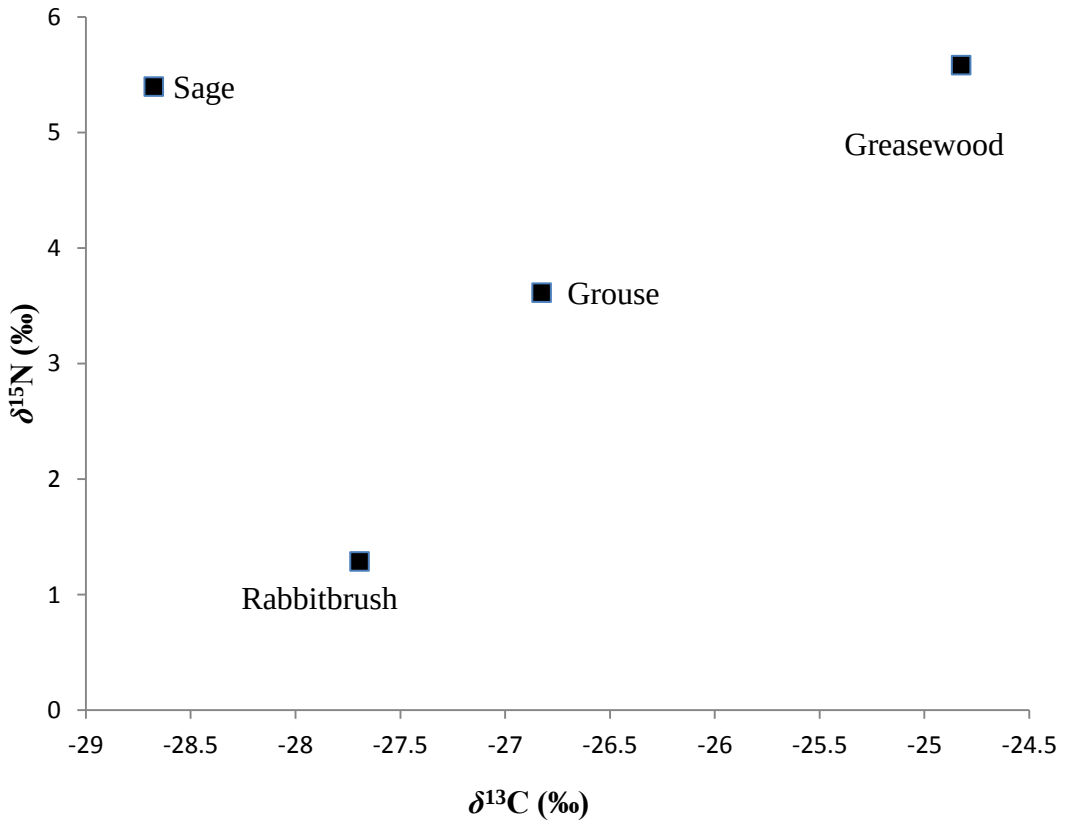

FIGURE 6. Average stable isotope values (δ^{13}C and δ^{15}N) of chick intestinal fecal pellets compared to average stable isotope values for food source samples.

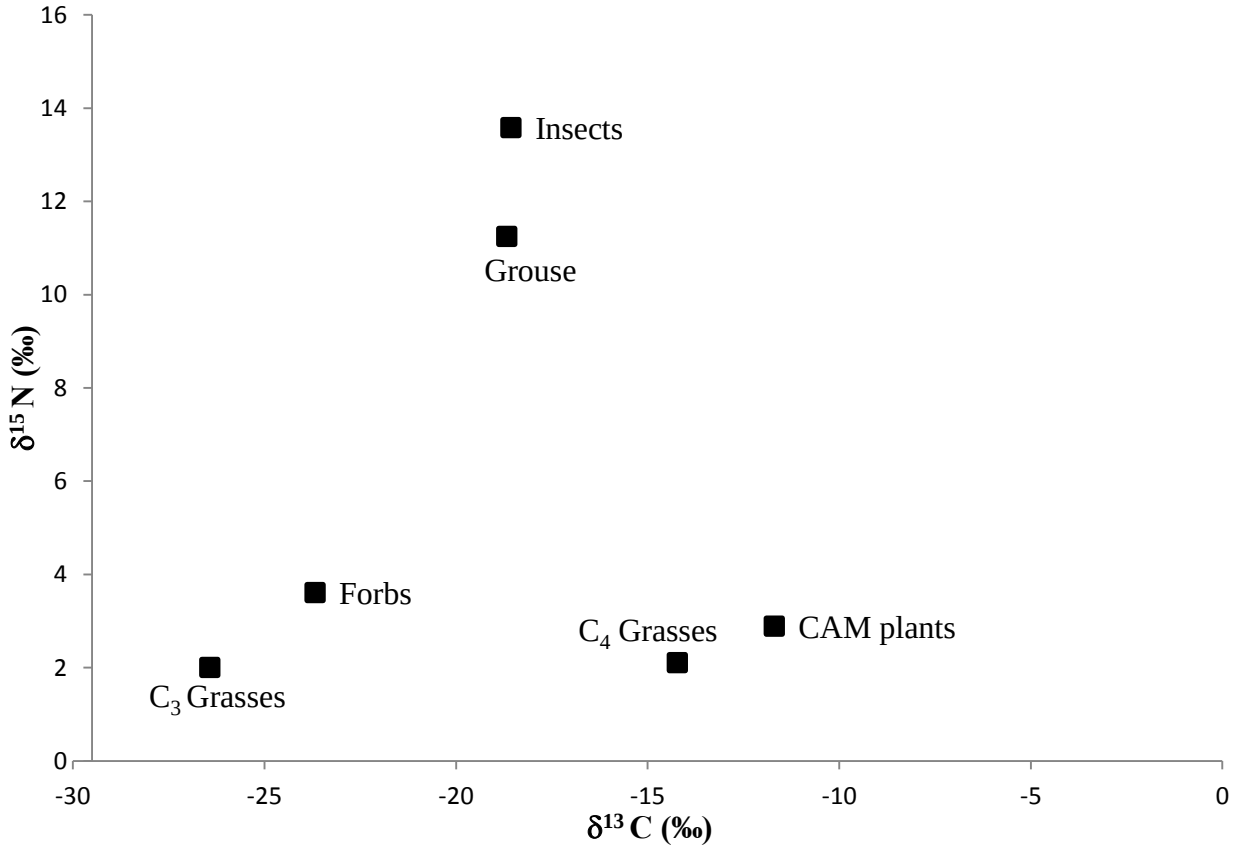

TABLE 9. Mixing model output of food source percent contributions to the diets of Greater Sage-Grouse based on adult intestinal fecal pellet stable carbon and nitrogen isotope analyses. Minimum and maximum values below are the range of feasible solutions. Means and standard deviations were also given by IsoSource.

Food Source	**Mean% (%)**	**Minimum (%)**	**Maximum (%)**	**Standard Deviation**
Sagebrush	3.7	0.00	11	0.028
Other Shrubs	3.8	0.00	12	0.031
Forbs	4.1	0.00	14	0.040
C_3 Grasses	85.6	80.00	92	0.026
C_4 Grasses	0.90	0.00	2	0.008
CAM Plants	0.50	0.00	2	0.007
Insects	1.4	0.00	5	0.014

TABLE 10. Mixing model output of food source percent contributions to the diets of Greater Sage-Grouse based on adult cecal tar stable carbon and nitrogen isotope analyses. Minimum and maximum values below are the range of feasible solutions. Means and standard deviations were also given by IsoSource.

Food Source	**Mean (%)**	**Minimum (%)**	**Maximum (%)**	**Standard Deviation**
Sagebrush	60.3	47	74	0.082
Rabbitbrush	27.4	1	53	0.157
Greasewood	12.3	0	25	0.075

TABLE 11. Mixing model output of food source percent contributions to the diets of Greater Sage-Grouse based on chick intestinal fecal pellet stable carbon and nitrogen isotope analyses. Minimum and maximum values below are the range of feasible solutions. Means and standard deviations were also given by IsoSource.

Food Source	**Mean (%)**	**Minimum (%)**	**Maximum (%)**	**Standard Deviation**
Forbs	7.0	2	11	0.042
C_3 Grasses	4.0	1	8	0.032
C_4 Grasses	6.3	5	9	0.019
CAM Plants	4.3	2	6	0.017
Insects	78.5	78	79	0.006

CHAPTER 5. CONCLUSION

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Data were collected on a variety of habitat variables in spots selected by sage-grouse for foraging, nesting, and brood-rearing activities. These variables were compared to the same variables measured at random points at both study sites. Significant differences existed between foraging/nesting habitat plots selected by sage-grouse and random habitat plots at both sites. Data analyses indicated sage-grouse at Heart Mountain were choosing foraging and nesting areas dominated by junegrass while sage-grouse at YU Bench were choosing foraging sites dominated by junegrass and nesting sites dominated by needle and thread grass. Areas used most by sage-grouse for lekking, nesting, and brood-rearing were identified at both study locations in an effort to help habitat managers at both study sites target certain areas of both large study sites for conservation efforts.

Stable carbon and nitrogen isotope ratios were used to determine diet compositions of adults and chicks using avian fecal matter instead of tissue. Sage-grouse produce two different kinds of fecal material: intestinal droppings and cecal tars. Both types of fecal matter as well as various insect and plant species were collected at both field sites. Isotope analyses combined with mixing model analyses indicated that adult grouse at both sites were relying more on C_3 grasses than either forbs or sagebrush in the summer months compared to what has been previously reported. Mixing model results of adult cecal tars indicate that while sagebrush made up the majority of their late winter/early spring diets, greasewood and rabbitbrush were also being consumed in higher than expected amounts. Mixing model results confirmed that insects were the main food item for chicks at these two locations but these results also indicated that chicks

were consuming more C_3, C_4 and CAM plants than has been previously reported for young of this species.