ECOLOGY OF A COLONIZING POPULATION OF ROCKY MOUNTAIN ELK (*CERVUS ELAPHUS*)

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ECOLOGY OF A COLONIZING POPULATION OF ROCKY MOUNTAIN ELK (*CERVUS ELAPHUS*)

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CHAPTER I

REINTRODUCTION HISTORY OF ROCKY MOUNTAIN ELK (*CERVUS ELAPHUS*) IN WICHITA MOUNTAINS WILDLIFE REFUGE AND SURROUNDING AREAS

HISTORICAL BACKGROUND

Elk (*Cervus elaphus*) were once widespread in North America and occupied every major natural vegetation type (Bryant and Maser 1982). Merriam's elk (*C. e. merriami*) were believed to be native to Oklahoma prior to the 1900s, but the last known Merriam's elk was harvested on Rainy Mountain, Kiowa County, in 1881 (Halloran 1963, Caire et al. 1989). However, E. F. Morrissey, Wichita Forest and Game Reserve ranger, frequently found elk antlers on his travels through the Reserve after 1881 suggesting that *C. e. merriami* may have persisted (DeSpain 2001).

To preserve the more scenic parts of the Wichita Mountains region, a proclamation by President William McKinley designated 23,116 ha (57,120 acres) as the Wichita Forest Reserve on 4 July 1901 (DeSpain 2001). The Reserve was protected for its aesthetic value but failed to receive status as a national park largely because it lacked comparison to the grandeur of Yellowstone Park or Yosemite Valley. However, to protect the Reserve's resources, President Roosevelt designated it to be "set aside for the protection of game animals and birds and be recognized as a breeding place therefore." The Reserve was renamed the Wichita National Forest and Game Preserve in 1905.

The area's native timber was damaged by fires, cattle grazing, miners, and local woodcutters but was considered important to "preserve" the wilderness of the area. To make the Reserve more aesthetically pleasing, plantings of western yellow pine (*Pinus ponderosa*), eastern red cedar (*Juniperus virginiana*), osage orange (*Maclura pomifera*), black locust (*Robinia pseudoacacia*), honey locust (*Gleditsia triacanthos*), black walnut (*Juglans nigra*), and mulberry (*Morus spp.*) were initiated, and ill-perceived predators such as wolves (*Canis lupus*), coyotes (*Canis latrans*), mountain lions (*Felis concolor*), and black bears (*Ursus americana*) were eradicated (DeSpain 2001). In 1907, a steel-wire fence was erected around 3,237 ha (8,000 acres) of the interior of the Preserve to confine 15 bison (*Bos bison*) from the New York Zoological Society, a wild symbol of the American frontier (DeSpain 2001). Adding to the allure of the Preserve, a male elk of unknown origin was donated by the city of Wichita, Kansas, was released into the bison enclosure in 1908. From 1911 to 1912, 20 elk (4 male, 16 females) were donated from St. Anthony, Idaho, which was a shipping point for elk translocations from Jackson Hole, Wyoming (Halloran and Glass 1959, Bryant and Maser 1982). No additional elk releases in the Preserve have occurred since the early 1900s. In addition, 27 longhorn cattle (*B. taurus*) from Edinburg and Liberty, Texas, were introduced in the bison enclosure in 1927 to conserve a western livestock heritage (Halloran and Glass 1959).

The Preserve became Wichita Mountains Wildlife Refuge (WMWR) under the jurisdiction of U.S. Fish and Wildlife Service in the late 1930s. After 30 years of livestock grazing around the bison enclosure, grazing permits were cancelled, and 12,141 ha (30,000 acres) were enclosed with steel-wire fence, now referred to as the Special Use Area. In November 1939, the north fence of the bison enclosure was removed and the ungulates were free to roam the Special Use Area (DeSpain 2001). To maintain the biological integrity of WMWR, bison, elk, and longhorn cattle were managed through public auctions that were initiated in 1917, 1925, and 1938, respectively (Halloran and Glass 1959, Halloran 1963). Annual elk auctions, which were discontinued in 1956, resulted in 857 elk being removed from WMWR; 15 (1 bull, 14 cows) were sent to the Sierra del Carmen Mountains in Mexico in 1941 (Halloran and Glass 1959). Mortality by natural causes, poaching, and accidents were believed to average 12 elk per year, but mortality was limited in WMWR until 1962. Since 1962, elk have been harvested through annual controlled hunts in association with the Oklahoma Department of Wildlife Conservation (ODWC).

Elk also are found on Fort Sill Military Reservation (FSMR), 38,164 ha of similar habitat and topography that borders WMWR to the south and is also surrounded by a 2.4-m fence. Established in 1869 by General Philip Sheridan and named in memory of a Civil War general, Joshua W. Sill, FSMR is a field artillery and missile base and current home of the U.S. Army Artillery and Missile Center. After FSMR was established, the Wichita, Kiowa, Comanche, and other Native American tribes received homes on the reservation and trained in agriculture. It also is known for Geronimo, leader of the Chiricahua group of the Apaches, who was imprisoned at FSMR and buried there in the Apache cemetery. The reservation was almost abandoned in 1904 but was revitalized in 1911 by the establishment of a school that became the U.S. Army's main field artillery training base.

Twelve Rocky Mountain elk of unknown stock and origin were transported from a captive herd in Ponca City, Oklahoma, and released into FSMR in 1979 to add to the genetic diversity of the elk herd (G. Wampler, Fort Sill Military Reservation Administrator/Game Warden, personal communication). Analysis of genetic data collected from elk harvested on WMWR indicated relatively robust genetic diversity, in contrast to reintroduced elk herds with similar founding histories (i.e., founder herd size, initial population growth; Hicks 2004). Reintroduction of the FSMR elk in 1979 or faster than expected population growth after reintroductions may account for this diversity (Hicks 2004). To further establish elk in eastern Oklahoma, 335–391 elk from WMWR were relocated to Cherokee, Cookson, LeFlore, McCurtain, Pushmataha, and Spavinaw wildlife management areas (WMA) from 1969 to 1971 (Stout et al. 1972, Raskevitz et al. 1991, Walter and Leslie 2002).

Although cattleguards were design to prevent ungulates from leaving WMWR on state highways 49 and 115, elk movements between WMWR, FSMR, and adjacent private lands have been observed. Vandalism, water run-off, and wildlife have caused breaks in the deteriorated fence and permitted emigration from WMWR. To provide a re-entry, WMWR personnel have constructed six ramps that permit elk to return to WMWR but prevent dispersal to private land (S. Waldstein, WMWR manager, personal communication).

SITE DESCRIPTION

The study area was in southwestern Oklahoma, USA (34°47′ to 34°57′N, 98°25′ to 98°50′W) and encompassed some of WMWR. Wichita Mountains Wildlife Refuge was situated along 4 sets of major vertical joints composed of gabbro and granite, igneous material from the Cambrian (Buck 1964, Tyrl et al. 2002). The joints were believed to be important to the vegetational distribution in the area as it controlled rock decomposition and water availability (Buck 1964). The granite is predominantly Lugert, a medium-grained pink granite with some Carlton and Quanah granite (Buck 1964). The mountains of WMWR vary in size from gentle slopes with a minimum elevation of 390 m to the highest elevation in the west at 750 m. The mountainous terrain is bisected by wide grassy valleys with deep soils suitable for a variety of monocotyledonous and dicotyledonous vegetation; the Soil Conservation Service delineated 11 soil types within WMWR (Crockett 1964).

The mean annual temperature at WMWR was 15.7º C (60.3º F) in 1995–2003 with high and low mean temperatures of 29.1º C (84.3º F) and 3.0º C (37.4º F) occurring in July–August and December–January, respectively (National Oceanic and Atmospheric Administration 2003). Mean annual total precipitation was 82.3 cm (32.4 inches) in 1995–2003 with a high of 99.3 cm (39.1 inches) in 1995 and a low of 53.1 cm (20.9 inches) in 2001. Precipitation is greatest in the spring followed by a secondary peak in the autumn and a typical growing season of 203 days (Buck 1964).

Private lands north and west of WMWR comprised a similar granite-derived landscape along the border of WMWR. The private lands were used primarily for cattle grazing interspersed with residential homes and seasonal residences. Forests composed 60% of the area; dominant species were post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), and eastern red cedar (*Juniperus virginiana*), with sugar maple (*Acer saccharum*), pecan (*Carya illinoensis*), and American elm (*Ulmus americana*) in riparian areas (Buck 1964). Dominant tallgrasses included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*). Shortgrasses included buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and sideoats grama (*B. curtipendula*; Tyrl et al. 2002).

Agricultural fields of 1–180 ha and state highways 19 and 115 separate granite-derived private lands bordering WMWR from the limestone-derived private lands to the north. These low to moderate hills range in elevation from 444 to 645 m and are of Ordovician marine limestone and dolomite origin rising above redbed plains (Buck 1964). The limestone-derived hills were classified as mixed-grass eroded plains type that was used primarily for grazing (Tyrl et al. 2002). The rolling hills comprised tallgrass and shortgrass species such as bluestems, gramas, and buffalograss in a mesquite (*Prosopis glandulosa*) grassland (Tyrl et al. 2002). Most bottomlands were composed of ephemeral stream corridors that were forested with pecan, western walnut (*Juglans rupestris*), and eastern red cedar. Residential homes and primary and secondary roads traversed the area separating it into several unbroken tracts of land. The largest tract (about 8,000 ha) contained no primary roads; however, a 2–3 km gravel road and 45 wind-turbines were erected in 2003–2004.

Private lands contain Rocky Mountain elk, white-tailed deer (*Odocoileus virginianus*), feral hog (*Sus scrofa*), Rio Grande turkey (*Meleagris gallopavo intermedia*), bobwhite quail (*Colinus virginianus*), and numerous resident and migratory raptors. Elusive species such as bobcat (*Lynx rufus*), coyote (*Canis latrans*), and porcupine (*Erethizon dorsatum*) also were common. In addition to the elk, white-tailed deer, bison, and longhorn cattle, black-tailed prairie dogs (*Cynomys ludovicianus*) and burrowing owls (*Speotyto cunicularia*) occurred in WMWR.

MANAGEMENT HISTORY

Elk in WMWR are harvested annually through lottery drawings administered by the ODWC. Harvest quotas are set by the WMWR manager based on annual road surveys. Detailed harvest data on WMWR, FSMR, and private lands was compiled for 1987–2001 to document the variability in harvest rates in the southwestern elk herds (Walter and Leslie 2002). Elk harvest on private land was initiated due to crop-damage complaints by farmers and ranchers. From 1987 to 1993, hunters could harvest 1 elk of either sex in lieu of harvesting a deer. In response to several years of recurring crop-damage complaints, ODWC altered the harvest strategy on private land in 1997 (Walter and Leslie 2002). After 2 y of no harvest, crop damage was again a concern of landowners, which prompted the ODWC to re-open the elk harvest in 2000. As the private-land elk harvest developed, regulations on season length and bulls, such As a minimum of 5 points on one side to harvest a bull elk, were imposed to regulate the harvest (Walter and Leslie 2002).

OBJECTIVES

Management agencies are challenged with managing elk as population dynamics and sociological aspects change. Detailed understanding on elk movements and nutrition does not exist for this region, which was the impetus for this work. Our objectives were to:

1) assess movements and grouping behavior of elk occupying 2 distinct habitat types on private lands

2) determine seasonal habitat use incorporating fecal indices of dietary quality of elk on private lands, and

3) determine levels of nutrition with inferences from carbon and nitrogen isotopes in tissues collected from the private-land and WMWR elk herds.

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CHAPTER II

GROUPING AND HOME-RANGE PATTERNS OF COLONIZING ROCKY MOUNTAIN ELK (*CERVUS ELAPHUS*) IN DISTINCT LANDSCAPES

Abstract: Rocky Mountain elk (*Cervus elaphus*) have colonized private lands surrounding Wichita Mountains Wildlife Refuge (WMWR) since reintroductions occurred nearly a century ago. Elk were observed using a closed, forested habitat (Granite Area) and an open, grassland habitat (Slick Hills) on private land and exhibited contrasting grouping patterns although they are from the same founding herd. We studied home range and group size of elk from January 2002 to March 2005. Twenty-one female elk were radiocollared during the study, and elk in the Granite Area had smaller ($P < 0.001$) annual fixed-kernel home-ranges ($\bar{x} = 27.3 \pm 3.05$ km^2) than elk in the Slick Hills ($\bar{x} = 72.5 \pm 5.05$ km^2). Elk in the Granite Area also had smaller annual group sizes ($\bar{x} = 7.1 \pm 0.54$; range: 1.0–30.0; $P < 0.001$) than elk in the Slick Hills ($\bar{x} = 36.8 \pm 2.53$; range: 1–190). Habitat variables were measured at several spatial scales (500, 1,000, 2,000, and 4,000 m) as buffers around elk observations to determine habitat correlates with group size. Several habitat variables were correlated with group size of elk including landowner density, proportion of agricultural habitat, and mean shape and proximity indices of habitat patches. Group size of elk in the Granite Area was smaller resulting from closer proximity of forested and open habitats. Group size of elk in the

Slick Hills was larger with greater distance between like habitat patches. Varying landscape characteristics in the 2 areas caused different foraging behaviors of elk and resulted in differences in elk home-range area and group size.

Key words: aggregation, *Cervus elaphus*, group size, GIS, home-range area, landscape metrics, observations, mean proximity index, mean shape index, radiotelemetry, Rocky Mountain elk

INTRODUCTION

Home-range area is determined by numerous factors such as body size, sex, age, and forage availability (Swihart et al. 1988, Relyea et al. 2000, Kie et al. 2002). Among ungulates, differences in home-range area have been observed between and within populations occupying similar geographic regions (Nicholson et al. 1997, Kie et al. 2002). Foraging habitat, cover habitat, and the landscape configuration of such habitats can influence home-range area of cervids (Schoener 1981, Tufto et al. 1996, Relyea et al. 2000). Elk (*Cervus elaphus*) occupying a forested habitat in Washington had smaller home ranges than elk in more open shrub-steppe habitat (McCorquodale 1991). The spatial scale of study is integral to understanding wildlife use of a landscape, and landscape metrics (i.e., patch shape, size, and interspersion) recently have been used to understand the influence of various habitat characteristics and patch distribution on home-range area (Turner 1989, Wiens 1989, Hewison et al. 2001, Anderson et al. 2005, Kie et al. 2005). Kie et al. (2002) found that spatial heterogeneity accounted for 57% of the variability in the home-range area of mule deer (*Odocoileus hemionus*) in California.

Landscape patterns determined distribution of more productive habitats that, in turn, influenced home-range area in several ungulates (Tufto et al. 1996, Relyea et al. 2000, Kie et al. 2002).

Mechanisms driving differences in group size of ungulates have been debated by researchers (Murie 1951, Geist 1974, Kie and Bowyer 1999). Group size and behavior of gregarious ungulates have been linked to landscape structure, sexual segregation, predator avoidance, and forage availability (Geist 1974, Gross et al. 1995, Main et al. 1996, Weckerly et al. 2001). Geographic Information Systems (GIS) to assess landscape features can assist in understanding long-term ungulate distributions and behavior at the landscape level (Pereira and Itami 1991, Van Deelen et al. 1997, Gross et al. 2002). Using GIS databases, distribution patterns of ungulates have been shown to be influenced by habitat, road density, human disturbance, and conspecifics (Johnson et al. 2000, Roloff et al. 2001, Kie et al. 2002). Generally, the more open an area that a group occupies, the larger the group size (Dasman and Taber 1956, Knight 1970, Franklin et al. 1975). Large groups in open landscapes would be expected because such a landscape is more productive and can sustain heavier grazing pressure (Murie 1951).

Diet, habitat selection, and daily distance moved change as forage availability changes and these factors likely influence the ability of ungulates to maintain internal cohesion, thus influencing group size (Jarman and Jarman 1979). Changes in food availability and distribution rather than predation risk were believed to control group size of resident impala (*Aepyceros melampus*) in Africa, and predation was considered a constant risk (Jarman and Jarman 1979). Unlike African impala that increase group size during seasons of favorable forage availability (i.e., wet season), North American ungulates typically increase herd size during the most forage-scarce seasons (i.e., winter). Moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and black-tailed deer (*O. hemionus columbianus*)—considered relatively solitary species—often form herds during winter (Dasman and Taber 1956, Geist 1974, Hirth 1977). Formation of large herds by solitary individuals or small groups (<5) was observed in Roosevelt elk (*C. e. roosevelti*) and black-tailed deer in response to different cover types (Dasman and Taber 1956, Knight 1970, Franklin et al. 1975). It is difficult to determine if a concentrated food source, landscape-cover type (i.e., open grassland vs. closed forest), or habitat distribution determines herd formation.

I compared annual and seasonal home-range area of reintroduced Rocky Mountain elk (*C. e. nelsoni*) on 2 areas on private land and predicted that the closed, forest habitat would result in smaller home-range areas than in open, grassland habitat. I also predicted that close proximity and smaller patches of like habitat would result in smaller group size of elk occupying the closed, forest habitat than the open, grassland habitat, and would be indicative of behavioral adaptation to contrasting landscapes. I tested this prediction at several spatial scales around elk observations to account for effects that may be detected only at larger spatial scales (Kie et al. 2002).

STUDY AREA

The study occurred on private lands in southwestern Oklahoma, USA (34°47′ to 34°57′N, 98°25′ to 98°50′W) surrounding the 23,879-ha Wichita Mountains Wildlife Refuge (WMWR), which contained elk, bison (*Bos bison*), white-tailed deer, and longhorn cattle (*B. taurus*). Extending northward from WMWR on private land were igneous mountain peaks and slopes >25% with habitat similar to WMWR (Buck 1964;

Fig. 1). Forests composed 24% of the area (= Granite Area) with dominant species of post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), and eastern redcedar (*Juniperus virginiana*); sugar maple (*Acer saccharum*), pecan (*Carya illinoensis*), and American elm (*Ulmus americana*) occurred in riparian areas (Buck 1964). Dominant midgrasses and tallgrasses included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*). Shortgrasses included buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and sideoats grama (*B. curtipendula*). Unlike WMWR, a mixture of permanent and seasonal homes, and primary (i.e., paved) and secondary (i.e., dirt and gravel) roads were dense and scattered throughout the area.

Limestone-derived rolling hills occurred 3–5 km north of WMWR and beyond the Granite Area on private land and were used for cattle grazing. This area (= Slick Hills) was primarily a mixed prairie of tallgrass and shortgrass species such as bluestems, gramas, and buffalograss with some mesquite (*Prosopis glandulosa*) grassland (Tyrl et al. 2002). Forested habitat (i.e., 10% of area) occurred in all bottomlands of ephemeral stream corridors and contained pecan, western walnut (*Juglans rupestris*), and eastern redcedar (Fig. 1). Permanent and seasonal homes along with primary and secondary roads traversed the Slick Hills separating it into 3 unbroken tracts of land. The largest tract (about 8,000 ha) contained no primary roads, but construction of a 2–3 km gravel road was initiated on 1 June 2003 to service a planned wind-power facility. The wind-power facility was completed with 45 NEG Micon 1.65 MW turbines and became active by 31 December 2003; overall effects of the wind-power facility on elk movements were minimal (W.D.Walter, unpublished data). Unlike WMWR, the Granite Area and Slick

Hills had fields of wheat (*Triticum aestivum*), alfalfa (*Medicago sativa*), and sorghum (*Sorghum bicolor*) averaging 10 ha (range: <1–180 ha) and 18 ha (range: <1–251 ha), respectively, used for cropped forages, hunting plots, and cattle grazing.

METHODS

Six free-ranging female elk were immobilized on private lands from January 2002 to April 2002 with a mixture of 500 mg/ml Telazol® (1:1 tiletamine hydrochloride and zolazepam hydrochloride; Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) reconstituted with 2 ml of 100 mg/ml xylazine HCl (Sedazine®, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA; Walter et al. 2005b); 1 male elk was radiocollared but not included in these home-range analyses (Appendix A). An additional 15 female elk were captured on 31 March 2003 from a Bell 206 Series helicopter using net guns (Hawkins and Powers Aviation, Greybull, Wyoming). All elk were fitted with radiocollars that contained an 8-h, time-delayed, mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA) and ear-tagged. Animal care and experimental procedures were approved by Oklahoma State University's Institutional Animal Care and Use Protocol GU-02-01.

Radiotelemetry Error

Because radiotelemetry error often goes unreported (Saltz 1994, Withey et al. 2001) and can lead to false conclusions about home-range area and habitat use (Zimmerman and Powell 1995, Withey et al. 2001, Kernohan et al. 2001), error was evaluated for radiotelemetry locations. Telemetry error was determined by placing test transmitters at known locations throughout the Granite Area and Slick Hills. A GPS unit was used to obtain Universal Transverse Mercator (UTM) coordinates for locations of test transmitters and telemetry receiving stations. Estimated transmitter locations were calculated in the field on a Digital DECpc 433SE personal computer using LOCATE II for calculating telemetry intercepts from ≤10 receiver locations (Nams 1990, Pacer Inc 2001). Bearings that were likely bounced or otherwise had not created a triangulation were not used. Three compass bearings (triangulation) were selected based on the following criteria (censorship-Withey et al. 2001): bearings were collected in ≤30 min, the loudest signal method was used (Springer 1979), and bearings formed a triangle with a confidence ellipse not encompassing either of the 3 receiving locations. Because access to suitable telemetry receiving points was limited by geographic structures, 2 bearings (biangulation) also were used to obtain radiotelemetry locations. Two bearings were used to estimate a location only if their angle of intersection was 45°–135° (Springer 1979) and locations were collected in ≤30 min.

To assess telemetry precision (i.e., bias), bearing error was determined using a Statistical Analysis System (SAS) code to calculate actual bearings from receiving locations to known transmitter locations (White and Garrott 1990, SAS Institute Inc. 2003). Bearing error was tested for normality using a Kolomogorov-Smirnov *D*-statistic (Steel and Torrie 1980). Directional data, such as bearing error, are not expected to be normally distributed because a disproportionately high distribution of angle error around 0° is expected (Zimmerman and Powell 1995). Bias in bearing error may reflect a system or observer bias and allow for *a priori* corrections for bias before estimating locations (Springer 1979, Lee et al. 1985, Zimmerman and Powell 1995). A signed-rank test (Conover 1999) on the means of bearing error indicated there was no bias (Withey et al. 2001) in bearings used for biangulation ($P = 0.349$) and triangulation ($P = 0.1968$).

Most studies report telemetry error as an ellipse or confidence circle that only identifies bearing precision and bias (Zimmerman and Powell 1995, Marzluff et al. 1997, Withey et al. 2001). The location-error method (accuracy—Withey et al. 2001) that determines the linear error distance (ED) between estimated and known locations of a sample of test transmitters is a method for determining accuracy of telemetry locations (Zimmerman and Powell 1995). Mean ED's have been used as confidence distances or confidence areas for overall telemetry error around a telemetry location (Wallingford 1990, Zimmerman and Powell 1995). To assess variables that may affect radiotelemetry locations, I performed a stepwise regression on variables that may influence accuracy of location estimates (Wallingford 1990, Zimmerman and Powell 1995, Withey et al. 2001). Variables were: arithmetic (ARIX) and geometric (GEOX) mean of distance from receiving location to test transmitter, mean bearing error (XBERR), standard deviation of bearing error (SD), absolute values of bearing error prior to determining mean (XBERRABS) and absolute value of bearing error after mean bearing error was determined (BERABSX), maximum angle of intersection (MAXANG), deviation of MAXANG from 90° (DEV90), total of interception angles (SUMINT), and mean of interception angles (XSUMINT). All variables were tested for normality, and non-normal data were cube-root transformed to normalize distributions (Zimmerman and Powell 1995) prior to parametric statistics (i.e., stepwise regression; SAS Institute Inc. 2003).

Home Range

Locations that failed to meet criteria obtained through assessment of telemetry error were censored from home-range analyses. Radiotelemetry was conducted bimonthly with ≥24 h between locations to reduce potential for autocorrelation of radiolocations (Swihart and Slade 1985) by encompassing ≥1 activity shift, defined as a period of high activity followed by a period of low activity (Minta 1992). Radiotelemetry locations were presumed representative of elk movements because they included diurnal (55%) and nocturnal (45%) locations (Beyer and Haufler 1994, Cooper and Millspaugh 2001).

Radiolocations of elk were entered into ArcView GIS 3.2 (ArcView; Environmental Systems Research Institute 2000). As a conservative estimate of home-range area, a 100% Minimum Convex Polygon (MCP; Mohr 1947) was calculated using the Home Range Extension in ArcView (Rodgers and Carr 1998). I also calculated 95% fixed-kernel (fixed-kernel; Worton 1989, Seaman and Powell 1996) estimates of home-range area because that method considered density of locations and was considered most accurate at determining outer boundary areas (i.e., 95% isopleths) compared with adaptive kernel (Seaman et al. 1999). The amount of smoothing was determined by the least-squares cross-validation (h_{LSCV}) method (Worton 1989, Worton 1995). Because kernel-based methods estimate the utilization distribution and underlying densities of locations, selection of the correct amount of smoothing is necessary to obtain accurate kernel estimates of home-range area (Worton 1989, Seaman et al. 1999). An h_{LSCV} determined by large samples (i.e., 150–200 locations), a multimodal distribution of locations, and across seasons would represent more accurately the smoothing parameter for the true distribution (Bowman 1985, Seaman and Powell 1996). Therefore, default h_{LSCV} was determined in the Home Range Extension of ArcView from all elk locations by area, and the resulting h_{LSCV} was entered as the smoothing parameter for each area-season fixed-kernel estimate of home range. Smoothing parameters for the Granite Area and Slick Hills were 793 and 696, respectively.

Group Size

Random bimonthly vehicular excursions throughout the study area from January 2002 to December 2004 permitted observations of elk using 8-x 35-m binoculars or 36-x 50-mm spotting scope. Night visuals of elk groups using a spotlight provided nocturnal observations throughout the study area. Additional observations of elk groups were collected during chemical immobilization efforts at bait sites, an autumn aerial survey, ground-based “homing” on radio signals until the radiocollared elk and its conspecifics were observed (White and Garrott 1990), and random traverses of the study area on foot to collect fecal samples (Chapter III).

Group size and location of elk were recorded, and mean group size was determined as $\Sigma n/N$ where n = number of elk observed in a group and N = number of group observations. To more accurately reflect the group size that the average animal occupied, typical group size (TGS) was calculated as $\Sigma n^2/\Sigma n$ (Jarman 1974, Gross et al. 1995). Observations of elk were considered independent because observations were separated by ≥ 24 h or by ≥ 1 activity shift (Minta 1992).

Two aerial surveys in a Schweizer 333 helicopter were conducted on 7 October and 11 October 2002. A literature review indicated that percent canopy cover and group size were the primary causes of inaccurate counts of elk during aerial surveys in Idaho (Samuel et al. 1987) and Washington (McCorquodale 2001). Percent canopy cover of <25, 25–49, 50–75, and >75 resulted in 8.5, 25.8, 50.3, and 71.8% of elk missed, respectively, during aerial censuses. Group size of 1, 2, 3, 4, 5–15, and >15 resulted in

78.4, 53.5, 27.5, 39.7, 23.2, and 4.0% of elk missed, respectively, during aerial censuses. These associated correction factors for percentage of elk missed due to effects of canopy cover (CC) and group size (GS) were used in the following equation to determine the adjusted number of elk in each group seen during aerial surveys:

$$\text{Adjusted Group Total} = N + (N*CC) + (N*GS) \tag{1}$$

where N = the number of elk observed in a group during each aerial survey. The adjusted group size was summed by area, and the 2-day mean population estimate was used to derive the density of elk in the Granite Area and Slick Hills. Using correction factors from the literature of presumed percentage of elk missed during aerial surveys, elk density was lower in the Granite Area (0.31 elk/km^2) than the Slick Hills (0.62 elk/km^2).

Locational Variables

Characteristics for each group observation were recorded for correlation analyses with group size in SAS (SAS Institute Inc. 2003). To assess effects of home-range area on group size, each group observation was assigned the mean fixed-kernel home-range area by season (AVEHR). To quantify landowner and hunter access as a disturbance factor, numbers of landowners per section were obtained from County Clerk landowner maps for each county. The number of landowners per section were assigned to a GIS layer of sections (1.61 x 1.61 km; 2.6 km^2) resulting in a landowner density/section/county (OWN; landowners/km^2); lower landowner density would result in less access and vulnerability to hunting pressure and disturbance (Brown et al. 2001). Primary vegetation data were determined by the land use-land cover data from 1992 (2001 data were not available for the study area) compiled by the U. S. Geological Survey (USGS) and U. S. Environmental Protection Agency (EPA) based on 30-m

Landsat Thematic Mapper data. To update agricultural fields added to the study site since 1992, agricultural fields were digitized in ArcView from aerial photographs from the U. S. Department of Agriculture's (USDA) 2.0-m National Agriculture Imagery Program (NAIP; http://www2.ocgi.okstate.edu/2003img1). The USGS Gap Analysis Program (GAP) data classified some native grassland as agriculture, but GAP data were more accurate than land use-land cover data in depicting current forested cover based on overlaying GAP data on NAIP. Therefore, GAP-assigned forested vegetation types were combined with land use-land cover data and the digitized agricultural fields, yielding a final vegetation map of the study area in raster format (LULC).

Vegetation in LULC was classified into 4 types considered important for determining elk habitat potential as determined by observations of elk during the study and habitat effectiveness models for western elk (Skovlin 1982, Roloff et al. 2001): 1) *forests* defined as deciduous-coniferous stands with an estimated >50% canopy cover >25 m from a riparian corridor (FOR); 2) *riparian* defined as bottomland forests defined as deciduous-coniferous stands with an estimated canopy cover >50% and ≤25 m from a riparian corridor (RIP); 3) *agriculture* defined as plantings of agricultural crops for production or wildlife management (AGR); and 4) *grassland* defined as tall-, mid-, or short-grass prairies with tree cover <25% (GRA). The resulting habitat layer also included lakes, ponds, and natural springs; rivers and streams were not included because they were deemed seasonally ephemeral and it was not possible to accurately quantify them relative to water availability.

Standard 30-m USGS digital elevation models (DEM) were used to determine elevation, slope, and aspect. Spatial Analyst in ArcGIS 9.0 ArcMap (ArcMap;

Environmental Systems Research Institute 2004) was used to develop a slope (SLO) and aspect (ASP) layer for the Granite Area and Slick Hills. Because elk use different aspects seasonally and forage phenology changes (Skovlin 1982, Unsworth et al. 1998, Roloff et al. 2001), cosine (COS) and sine (SIN) of aspect also were determined to represent the north-south and east-west aspects, respectively (Johnson et al. 2000, Ager et al. 2003). Convexity (CONVEX) was calculated as the difference in elevation of each 30-m x 30-m pixel from the mean of the 3-x-3 pixel neighborhood, with values >0 indicating convex (ridge top) and <0 indicating concave (valley bottom) landforms (Johnson et al. 2000, Ager et al. 2003). Roads were identified with the EPA Topologically Integrated Geographic Encoding and Referencing system files (TIGER/Line® Files 2000). Distances of groups from the nearest road (ROADIS), permanent water source (WATDIS), and forested cover (FORDIS; to determine proximity of escape cover) were calculated with the Spider Distance function in the Animal Movement Extension of ArcView (Hooge and Eichenlaub 1997). In ArcMap, all GIS layers were georeferenced and projected to the same format (i.e., Albers Equal Area Conic, North American Datum–1983) that used 2 standard parallels to minimize distortion of small geographic regions (Environmental Systems Research Institute 2000).

Landscape Variables

Because spatial arrangement of habitats can influence habitat use (Kie et al. 2002, Owen-Smith 2004, Anderson et al. 2005), landscape variables were calculated within a buffer using the Patch Analyst Extension–Fragstats Interface in ArcView (http://flash.lakeheadu.ca/~rrempel/patch/index.html; Elkie et al. 1999). To assess landscape variables at several spatial scales (Wiens 1989, Kie et al. 2002, Johnson et al.

2004), circles with radii of 500, 1,000, 2,000, and 4,000 m were placed around each elk observation, representing areas of 79, 314, 1,256, and 5,024 ha, respectively (Fig. 2). To account for the structural contrasts that occur among different habitat types, I included structural contrast weights for all possible habitat contrasts with forest and crop (0.8) and forest and riparian (0.2) representing the maximum and minimum structural contrast, respectively (Kie et al. 2002). The proportion of vegetation type from LULC (i.e., RIP, FOR, AGR, GRA) within buffers around group observations of elk also was extracted with ArcMap, and proportions were arcsine transformed to ensure normality of proportional data (Gilbert 1989).

Statistical Analysis

For home-range and group-size analysis, 3 seasons were distinguished based on radiotelemetry data, plant phenology, and behavioral changes of elk that were determined during the study: *isolation* (Apr–Jul) defined as isolation by cows for calving and an increase in forage availability; *breeding* (Aug–Nov) defined as harem formation by bulls for breeding; and *aggregation* (Dec–Mar) defined as social grouping behavior and low availability of natural forage. To assess radiotelemetry error by area on private land, differences of ED by area were conducted using a Student's *t*-test (Zar 1996). Differences in annual MCP and fixed-kernel home-range sizes by area were determined using a paired Student's *t*-test (Zar 1996). Differences in seasonal (i.e., isolation, breeding, aggregation) MCP, fixed-kernel home-range areas, and group size by area were determined with separate 2-way analyses of variance (ANOVA; Zar 1996). If a significant area-season interaction was detected ($P < 0.05$), a 1-way ANOVA was conducted on the 6 area-season factors (e.g., Granite Area-Isolation) with Duncan's multiple comparison used as a post-hoc test to identify differences among the 6 factor means (Cody and Smith 1997: pages 163–170). Because group size did not differ by year, I pooled years. Landscape variables measured in Patch Analyst Extension–Fragstats Interface can be grouped into 6 categories: patch, edge, shape, proximity, diversity, and contagion (Li and Reynolds 1994, McGarigal and Marks 1995). Because many locational and landscape variables were highly correlated (Johnson et al. 2000, Kie et al. 2002), separate simple Pearson correlations were conducted in Systat 9.0 (SPSS Inc. 1998) between the log of group size and locational variables and landscape variables using a Bonferroni correction for multiple comparisons to adjust for experiment-wise error rate (Rice 1989); log of group size provided less skew of the data to the outer distribution tails. For each spatial scale independently, differences in landscape variable means between the Granite Area and Slick Hills were assessed with a Student's *t*-test (Zar 1996).

RESULTS

Radiotelemetry Error

Mean ED (±SD) did not differ ($t_{74} = -4.73$, $P = 0.495$) between the Granite Area (548 ± 394 m) and Slick Hills (482 ± 446 m). Triangulation (ED_3; $n = 216$ bearings) and biangulation (ED_2; $n = 244$ bearings) datasets had 95% error arcs of ±11.0° and ±11.2°, respectively. Mean distance from the receiver to test transmitter was 183 m, and the ranges of angles of interception were 25–155° for ED_3 and 45–135° for ED_2.

For the triangulation dataset ($n = 72$ locations), stepwise regression identified 4 variables that contributed 78% ($P < 0.001$) of the error in telemetry locations:

$$[1] \quad ED_3 = -3.72 + 0.001(GEOX) + 0.033(DEV90) + 2.571(BERABSX) + 0.889(XSUMINT)$$

For the biangulation dataset ($n = 122$ locations), stepwise regression identified 2 variables that contributed 82% ($P < 0.001$) of the error in telemetry locations:

$$[2] \quad ED_2 = -5.66 + 0.540(GEOX) + 3.31(XABSBER)$$

Mean, median, and regression confidence circles for ED_3 encompassed 73, 68, and 32% of the test transmitters, respectively. Mean, median, and regression confidence circles for ED_2 encompassed 71, 63, and 71% of the test transmitters, respectively. The upper 75% quartile confidence circles for ED_3 (655 m) and ED_2 (712 m) encompassed 92 and 85% of the test transmitters, respectively. The upper 75th percentile for ED_3 was used for habitat-use analysis and resulted in a confidence area around radiotelemetry locations of 135 ha (Chapter III).

Home Range

A total of 2,657 radiotelemetry locations of 21 radiocollared female elk was collected to determine home range from April 2002 to March 2005. Two disjunct herds of elk used forested habitat in the Granite Area ($n = 11$ female elk) adjacent to WMWR and the open grassland habitat in the Slick Hills ($n = 10$ female elk) north of the Granite Area and WMWR. Elk in the Granite Area accessed WMWR through fence-breaks as documented by radiotelemetry and automated cameras (Walter et al. 2005a). Six of 11 radiocollared female elk from the Granite Area had >25% (range: 24%–89%) of their radiolocations in WMWR depending on season (Fig. 3), but no female elk from the Slick Hills used WMWR or the Granite Area. All elk remained in the area of capture except 1 female and 1 male elk immobilized on private land (Appendix A).

Mean annual MCP for elk in the Granite Area were smaller than MCP for elk in the Slick Hills ($t_{19} = -4.73$, $P < 0.001$; Table 1). Similarly, mean annual fixed-kernel home ranges for elk in the Granite Area were smaller than fixed-kernel home ranges for elk in the Slick Hills ($t_{19} = 7.83$, $P < 0.001$). Seasonal MCPs of elk in the Granite Area were smaller than seasonal MCPs of elk in the Slick Hills ($F_{5, 47} = 35.13$, $P < 0.001$), but no seasonal differences occurred within areas ($F_{5, 47} = 0.34$, $P < 0.710$). An area-season interaction occurred for fixed-kernel home-range ($F_{5, 47} = 4.65$, $P < 0.014$). Fixed-kernel home-ranges of elk in the Granite Area were smaller during all seasons than the comparable seasonal fixed-kernel home-ranges of elk in the Slick Hills ($P < 0.05$; Table 1). No seasonal differences occurred for fixed-kernel home ranges of elk in the Granite Area. Fixed-kernel home-range area was larger during the breeding season than during isolation and aggregation for elk in the Slick Hills.

Group Size

A total of 405 elk groups was observed in the Granite Area ($n = 150$) and Slick Hills ($n = 255$; Table 2) from January 2002 to March 2005. An area-season interaction occurred for group size ($F_{5, 399} = 26.73$, $P < 0.0001$) with the largest group size during aggregation in the Slick Hills (Table 2). The next largest group sizes occurred during the breeding period in the Slick Hills and the aggregation period in the Granite Area, and both differed from aggregation in the Slick Hills (Table 2). Mean group size during aggregation differed from isolation and breeding in the Granite Area. Mean group sizes in the Slick Hills differed among all 3 periods (Table 2). Typical group size increased from isolation to aggregation for both areas and was larger than mean group size during each period (Table 2).

Locational Variables

The log of group size (hereafter referred to as group size) was correlated negatively with OWN (r = -0.266, $P < 0.001$) and positively correlated with AVEHR (r = 0.486, $P < 0.001$) and CONVEX (r = 0.231, P = 0.003) for all elk observations. Mean OWN was 2.46 in the Granite Area and 1.67 in the Slick Hills. Mean CONVEX was 0.49 in the Granite Area and 0.68 in the Slick Hills. Group size increased with increasing home-range area and with more convex landforms (i.e., ridgetops). Group size was correlated negatively with FOR but positively with RIP and AGR at all spatial scales except at the 500-m spatial scale (Table 3). Mean patch size across all spatial scales was 9.55 ha in the Granite Area and 7.97 ha in the Slick Hills.

Landscape Variables

Landscape variables (n = 9) that were correlated with group size in ≥1 spatial scale included number of patches (NUMP), patch-size coefficient of variation (%; PSCOV), contrast-weighted edge density (m/ha; CWED), mean shape index (MSI), area-weighted mean shape index (AWMSI), mean patch fractal dimension (MPFD), area-weighted mean patch fractal dimension (AWMPFD), mean proximity index (MPI), and interspersion and juxtaposition index (%; IJI; Table 3). Correlation of group size with measurements of patch metrics identified positive correlations for NUMP and PSCOV; strengths of correlations increased as spatial scale increased (Table 3). Shape metrics >1.0 indicated that irregular shapes were present in both areas with no clear trend based on spatial scale. Mean and area-weighted patch fractal dimension suggested comparable complexity in the shapes of patches in the Granite Area and Slick Hills (Table 4).

Contrast-weighted edge density that standardizes edge on a per unit area basis, was correlated negatively with group size (Table 4).

Mean proximity index was correlated negatively with group size, suggesting it increased with increasing distance between habitat types (Table 4). The interspersion and juxtaposition index was correlated positively with group size, and correlations increased in strength as spatial scale increased (Table 4). In the Granite Area and Slick Hills, patch types that were interspersed equally (i.e., forests of similar size adjacent to grassland of similar size) resulted in an increase in group size that became more apparent as spatial scale increased.

DISCUSSION

Elk colonization of 2 disparate landscapes on private lands resulted in different home-range area and herd grouping behavior. Elk that occupied habitat similar to WMWR (i.e., Granite Area), a mosaic of forested and grassland patches, had smaller annual and seasonal home ranges than those occupying the more open grasslands of the Slick Hills. No difference in ED between the Granite Area and Slick Hills suggested that radiotelemetry error did not contribute to differences in home-range area. Home-range has been correlated with forage availability, and ungulates in more productive habitats (i.e., greater edge diversity) tend to have smaller home ranges (Schoener 1981, Tufto et al. 1996, Relyea et al. 2000, Kie et al. 2002). Forested landscapes have more concentrated high-quality forage (i.e., less evenly dispersed patches) due to high interspersion of various plant communities compared with grassland landscapes, which would be expected to have less edge density and more dispersed plant communities (Murie 1951, Skovlin 1982, McCorquodale 1991). This is supported by fixed-kernel home-range area differing during some seasons in the Slick Hills but no seasonal changes in home-range area in the Granite Area. Home-range data suggested that a concentrated food source in a closed forested habitat (i.e., Granite Area) or human-induced agricultural landscapes (i.e., during aggregation in the Slick Hills) resulted in smaller home ranges for elk. Smaller home-range area of native or reintroduced elk populations has been documented in landscapes with concentrated food sources (Eveland et al. 1979, McCorquodale 1991, Tufto et al. 1996, Anderson et al. 2005).

Greater edge density and larger forested patches provide a mosaic of suitable foraging sites and cover and more diverse floral and fauna communities (Whitney and Somerlot 1985, Turner 1989, Milne et al. 1989, Pogue and Schnell 2001). Landscape heterogeneity reflects patch structure and distribution of habitat patches, which in turn, can influence home-range area, group size, and population density of ungulates (Kie et al. 2005, Acevedo et al. 2005, Anderson et al. 2005). Kie et al. (2002) found that spatial heterogeneity contributed to variability in sizes of home ranges of mule deer in 5 herds throughout California. Elk in the Slick Hills used agricultural fields during aggregation (Chapter III) and reduced home-range area during that season. A change in seasonal home-range area in the Slick Hills but not in the Granite Area suggested that native forage was more dispersed throughout the Slick Hills. Pogue and Schnell (2001) documented that agricultural and rangeland landscapes had less edge complexity and adjacent forest and riparian habitats were more elongated and narrow (i.e., lower mean patch shapes) compared with similar habitats in managed grasslands surrounding Fort Sill Military Reservation south of WMWR. Contrast-weighted edge density was higher at the 1,000, 2,000, and 4,000-m spatial scales in the Granite Area compared with the more agricultural-rangeland landscape of the Slick Hills, consistent with Pogue and Schnell (2001).

Areas of high-patch and edge density and proximity that occurred in the Granite Area may have permitted elk to move more easily between forested cover and open foraging areas in contrast to more highly dispersed, open habitats with limited forested cover in the Slick Hills. Shape indices (i.e., mean shape index, mean patch fractal dimension) and CWED showed that irregularly shaped patches occurred in both areas. However, these irregularly shaped patches were more dispersed and had greater distance between like patches in the Slick Hills. Similar to a previous study in WMWR (Waldrip 1977), no seasonal differences in home-range area were documented for elk occupying the closed canopy forest of the Granite Area. The lower MPI and greater IJI in the Slick Hills than in the Granite Area suggested that like patches were in closer proximity in the Granite Area, also leading to decreases in home-range area for elk in the Granite Area. High patch and edge density in close proximity can reduce home-range area of ungulates seeking suitable foraging and cover habitats (Turner 1989, Kie et al. 2002, Anderson et al. 2005). Without corridors, use of suitable patches should decline with increasing isolation in the landscape (Turner 1989, Milne et al. 1989).

Group formation has been considered an anti-predator strategy in numerous ungulate species (Roberts 1996, Wisdom and Cook 2001, Hebblewhite and Pletscher 2002). Geist (1974) suggested that the anti-predator behavior of an ungulate species is a function of habitat concealment. An increase in home-range area during forage-limited winter months is common among ungulates (Tufto et al. 1996, Mysterud et al. 1999, Relyea et al. 2000), but the smallest home ranges and largest group sizes occurred in the

Slick Hills during the forage-limited winter months (Dec–Mar) when elk traveled to and from large agricultural fields. Unlike the Granite Area where small groups of elk (5–10) congregated on small agricultural fields in winter and never exceeded 30 animals, elk in the Slick Hills traveled to and from agricultural fields in group sizes typically exceeding 80–100 elk in December–March. Ungulates spend more time scanning for predators in closed habitats and reduce foraging rates than elk in open habitats, which decreases vigilance by occurring in larger groups (Underwood 1982, Risenhoover and Bailey 1985).

Elk in the Granite Area did not occur in large groups and vocalized infrequently, but elk in the Slick Hills vocalized routinely apparently to maintain group cohesion. Elk remain quiet in small groups to reduce detection by predators in dense forested habitat but vocalize routinely in an open landscape because predator detection is primarily through sight rather than sound (Geist 1974, Jarman 1974). Similar grouping behaviors were observed in elk in Banff National Park, Alberta, Canada, to minimize predation by wolves (*Canis lupus*). Elk congregated in small herds that were rarely encountered by wolves or in large herds that reduced predation risk through dilution (Hebblewhite and Pletscher 2002). Unlike many elk populations in the western U.S. that have large predators such as wolves, mountain lions (*Felis concolor*), and grizzly bear (*Ursus arctos*), predator avoidance in my study area could not be the sole reason for grouping behavior. Coyotes (*C. latrans*), the only natural predator in both areas, presumably exerted minimal predation pressure on elk; <1% of coyote scats included elk in WMWR (Litvaitis 1978).

Increases in human disturbance (i.e., distance to roads, landowner access) were believed to decrease available habitat and carrying capacity in several western elk populations (Lyon 1983, Johnson et al. 2000, Rowland et al. 2000, Brown et al. 2001). Large tracts of land owned by a few landowners resulted in lower vehicular traffic, less hunting pressure, and less access for ranching operations (Lyon and Ward 1982, Brown et al. 2001). Therefore, smaller group sizes of elk would be expected to occur on tracts of land with lower landowner densities if they formed large groups in response to disturbance (i.e., human or predator). Landowner density was correlated negatively ($r = -0.267$) with group size, suggesting larger groups of elk occurred in the landscape with less human disturbance, contrary to expected. However, group size also increased with more ridgetop landforms (i.e., CONVEX > 0; $r = 0.231$) but not concave landforms occurring at lower elevations (i.e., valleys, riparian areas) near roads. Lower elevations and concave landforms typically have higher soil moisture and nutrient loads resulting in better forage (Swanson et al. 1988). Radiocollared elk in small groups (i.e., 1–5) vacated mountainous terrain during isolation for lower-elevation, riparian areas that were in close proximity to roads but typically remained in forested cover or foraged in the adjacent agricultural fields after sunset. Radiocollared elk in large groups (i.e., 80–100) used agricultural fields diurnally and did not frequent forested and riparian habitat.

Group size of ungulates has been correlated with landscape variables because group size relates to forage distribution, human disturbance, and predator-avoidance (Hewison et al. 2001, Brashares and Arcese 2002, Acevedo et al. 2005). Group size was correlated negatively with percent forested habitat and that relationship strengthened as spatial scale increased (Table 3). The tendency of group size of elk to increase with increasing distance from forested habitat (i.e., escape cover) has been documented in other ungulates (Geist 1974, Hebblewhite and Pletscher 2002, Wei-Dong et al. 2005). Lower MPI and only 10% forested cover suggested elk in the Slick Hills occupied larger group sizes seasonally because of an uneven distribution of forested habitat with low proximity between forested patches. Because IJI was high and similar at each spatial scale in the Granite Area, elk occupied smaller group sizes in response to a larger quantity and more even distribution of forested patches. An increase in group size with habitat openness has been considered an adaptation to open grasslands with minimal security cover of forest and foraging efficiency in a more visible landscape (Geist 1974, Jarman 1974, White 1983, Hewison et al. 2001).

Unlike security cover provided by the closed-canopy forests in the Granite Area, elk in the Slick Hills likely used expansive rolling hills as escape terrain in the presence of disturbance as previously proposed for ungulates (Edge and Marcum 1991, Roloff et al. 2001, Hewison et al. 2001). Perceiving humans as a threat, formation of large groups during aggregation in the Slick Hills may be a predator-adaptation to the open landscape; large groups decrease individual vigilance and increase foraging potential (Jarman 1974, Senft et al. 1987, Roberts 1996). However, differences in group size also have been considered "behavioral plasticity" to an uneven distribution of seasonally available resources (Gerard and Loisel 1995, Jepsen and Topping 2004) and not an adaptive response to predation pressure. In adapting to unfamiliar environments, the tradeoff between seeking suitable forage to increase fitness or finding security cover to potentially reduce predation pressure has been debated (Geist 1974, Barten et al. 2001, Krause and Ruxton 2002). Ungulates have a flexible social organization and can adapt to changes in landscape characteristics (Geist 1974, Franklin et al. 1975, Hirth 1977). Elk exhibited inter and intra-seasonal flexibility in behavior to exploit high-quality resources available in natural and human-impacted landscapes nearly a century after reintroductions into WMWR.

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Table 1. Annual and seasonal mean (±SE) Minimum Convex Polygon (MCP) and 95% fixed-kernel (fixed-kernel) estimates of home-range area (km^2) for radiocollared female elk during isolation, breeding, and aggregation seasons in southwestern Oklahoma, April 2002–March 2005.

Area	Season	Sample size[a]	MCP[b]	Fixed-kernel[b]
Granite	Annual[c]	11	42.9 (8.67)	27.3 (3.05)
	Isolation	9	29.0 (9.25)a	23.2 (2.23)a
	Breeding	9	24.2 (7.31)a	23.5 (3.05)a
	Aggregation	8	20.2 (6.05)a	25.4 (2.67)a
Slick Hills	Annual	10	99.7 (8.26)	72.5 (5.05)
	Isolation	9	52.0 (4.83)b	41.4 (4.23)b
	Breeding	9	53.9 (7.54)b	53.8 (3.51)c
	Aggregation	9	69.2 (5.94)b	36.6 (2.75)b

[a] Sample sizes differed seasonally due to mortality of radiocollared females and only elk with >25 location/season were used.

[b] Seasonal means within a column with different letters differed at $P < 0.05$ (Duncan's post-hoc).

[c] Annual MCP and fixed-kernel means differed between Granite and Slick Hills at $P < 0.05$.

Table 2. Mean group size (±SD) and typical group size (TGS) of elk by season in the Granite Area and Slick Hills on private lands in southwestern Oklahoma, 2002–2005.

Area	Season[a]	*N*[b]	Mean[c]	TGS
Granite	Isolation	37	3.6 (3.0)a	6.0
	Breeding	22	5.2(5.6)a	11.3
	Aggregation	91	8.8(7.3)b	14.7
Slick Hills	Isolation	69	6.3(9.8)a	21.3
	Breeding	58	18.0(22.5)c	58.9
	Aggregation	128	53.9(38.2)d	90.1

[a] Isolation = April–July; breeding = August–November; aggregation = December – March.

[b] N = number of groups observed.

[c] Seasonal means with different letters differed at $P < 0.05$ (Duncan's post-hoc).

Table 3. Pearson correlation coefficients (*r*) between log(group size) and landscape variables at the 500, 1,000, 2,000, and 4,000-m spatial scale in the Granite Area and Slick Hills on private lands in southwestern Oklahoma. Correlation coefficients with an asterisk within a column were significant at $P < 0.05$.

		Spatial scale (m)			
Variable	Description	500	1,000	2,000	4,000
RIP	Riparian habitat	0.138	0.246*	0.398*	0.402*
FOR	Forested habitat	-0.305*	-0.341*	-0.370*	-0.400*
AGR	Agricultural habitat	0.189	0.206*	0.297*	0.243*
NUMP	Number of patches	0.100	0.170	0.331*	0.328*
PSCV	Patch size coefficient of variation	0.166	0.144	0.142	0.324*
CWED	Contrast-weighted edge density	-0.068	-0.088	-0.086	-0.256*
MSI	Mean shape index	-0.252*	-0.260*	-0.299*	-0.406*
AWMSI	Area-weighted MSI	-0.242*	-0.202*	-0.169	0.040
MPFD	Mean patch fractal dimension	-0.183	-0.283*	-0.283*	-0.398*
AWMPFD	Area-weighted MPFD	-0.230*	-0.189	-0.187	-0.058
MPI	Mean proximity index	-0.173	-0.268*	-0.282*	-0.215*
IJI	Interspersion-juxtaposition index	0.224*	0.278*	0.366*	0.382*

Table 4. Means (±SE) for landscape variables used in correlation analysis at the 500, 1,000, 2,000, and 4,000-m spatial scale in the Granite Area and Slick Hills on private lands in southwestern Oklahoma. Vegetation types (LULC) refer to the total hectares of that habitat (RIP, FOR, GRA, AGR) occurring within each spatial scale. Variable means were all different at $P < 0.05$ at each spatial scale between the Granite Area and Slick Hills except CWED at the 500-m scale ($P = 0.680$).

Landscape	Granite Area				Slick Hills			
Variables [a]	500	1,000	2,000	4,000	500	1,000	2,000	4,000
LULC								
RIP	3 (0.26)	14 (0.51)	57 (0.84)	226 (1.41)	7 (0.21)	26 (0.55)	98 (1.42)	377 (3.27)
FOR	25 (1.58)	86 (4.44)	293 (11.05)	879 (32.77)	3 (0.14)	11 (0.35)	42 (0.80)	165 (1.62)
GRA	40 (1.18)	189 (3.52)	798 (10.72)	3,395 (35.78)	53 (1.29)	224 (3.73)	916 (10.26)	3,759 (22.53)
AGR	9 (1.04)	23 (2.92)	99 (11.80)	486 (47.52)	15 (1.10)	50 (3.25)	191 (9.06)	690 (20.94)
NUMP	12 (0.52)	39 (0.85)	132 (1.73)	475 (5.37)	17 (0.51)	51 (1.14)	173 (2.59)	630 (5.57)
PSCV	170 (5.19)	312 (6.16)	486 (11.06)	840 (23.40)	213 (3.88)	362 (4.86)	654 (13.24)	1445 (18.64)
IJI	52.9 (1.83)	51.3 (1.12)	49.5 (0.91)	51.5 (0.76)	77.1 (1.51)	73.3 (0.65)	64.1 (0.44)	61.8 (0.17)

Table 4. Continued

Landscape Variables[a]	Granite Area 500	Granite Area 1,000	Granite Area 2,000	Granite Area 4,000	Slick Hills 500	Slick Hills 1,000	Slick Hills 2,000	Slick Hills 4,000
CWED	86.4 (1.43)	63.9 (0.84)	51.5 (0.46)	42.4 (0.24)	85.5 (1.07)	58.0 (0.68)	43.6 (0.45)	36.9 (0.22)
MPI	63 (3.77)	212 (8.91)	585 (22.91)	1292 (34.47)	44 (2.14)	110 (4.35)	228 (6.14)	762 (15.87)
MSI	1.55 (0.12)	1.52 (0.01)	1.51 (0.01)	1.45 (0.003)	1.40 (0.01)	1.40 (0.004)	1.36 (0.002)	1.33 (0.001)
AWMSI	2.01 (0.04)	2.74 (0.06)	3.82 (0.08)	5.62 (0.10)	1.67 (0.02)	2.11 (0.02)	3.12 (0.04)	5.60 (0.05)
MPFD	1.07 (0.001)	1.07 (0.001)	1.06 (0.001)	1.06 (0.000)	1.06 (0.001)	1.06 (0.001)	1.05 (0.0003)	1.04 (0.000)
AWMPFD	1.11 (0.003)	1.14 (0.003)	1.17 (0.002)	1.20 (0.002)	1.08 (0.002)	1.10 (0.001)	1.14 (0.002)	1.19 (0.001)

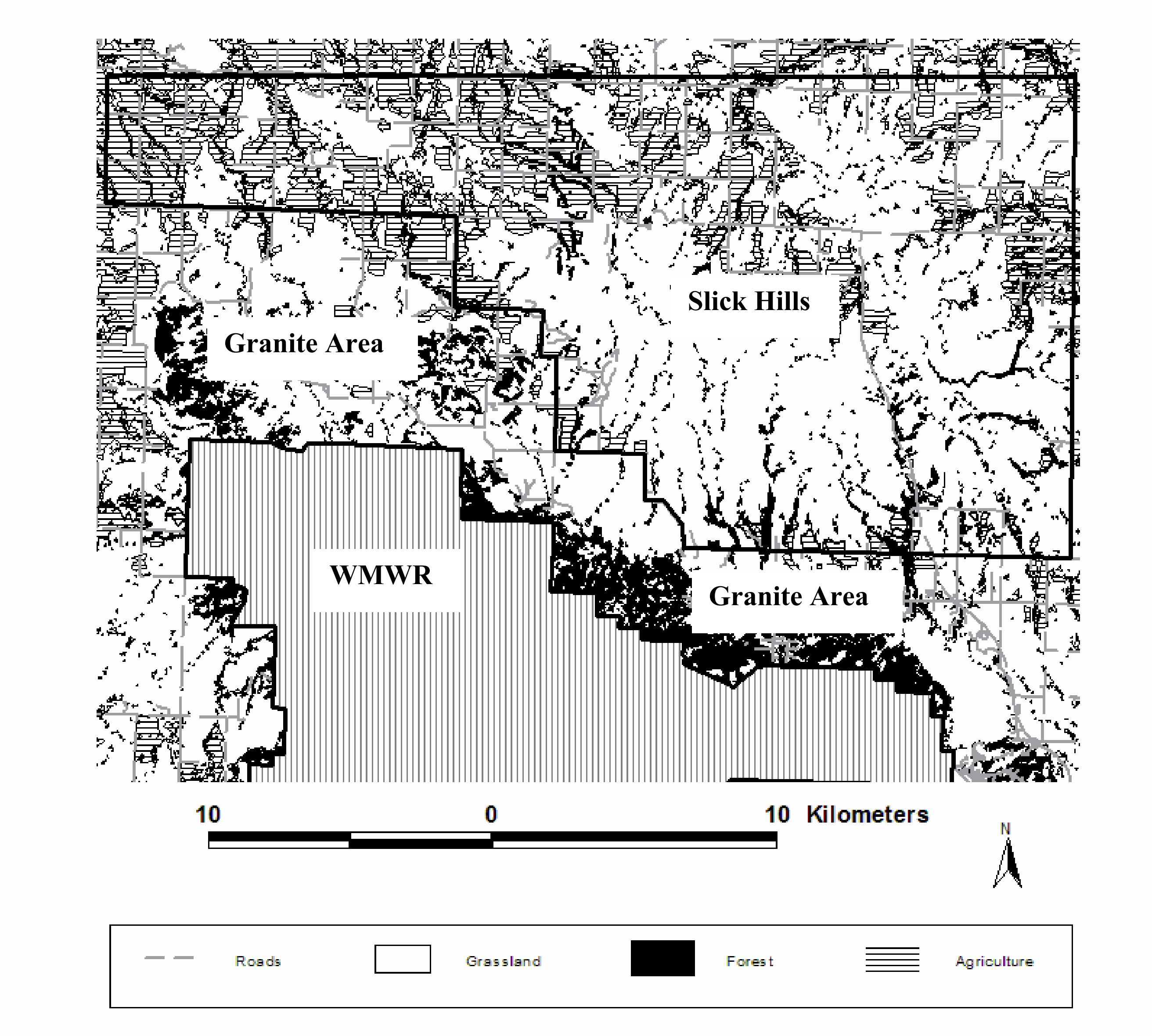
[a] Landscape variables include number of patches (NUMP), patch size coefficient of variation (PSCV; %), interspersion juxtaposition index (IJI; %), contrast-weighted edge density (CWED; m/ha), mean proximity index (MPI), mean shape index (MSI), area-

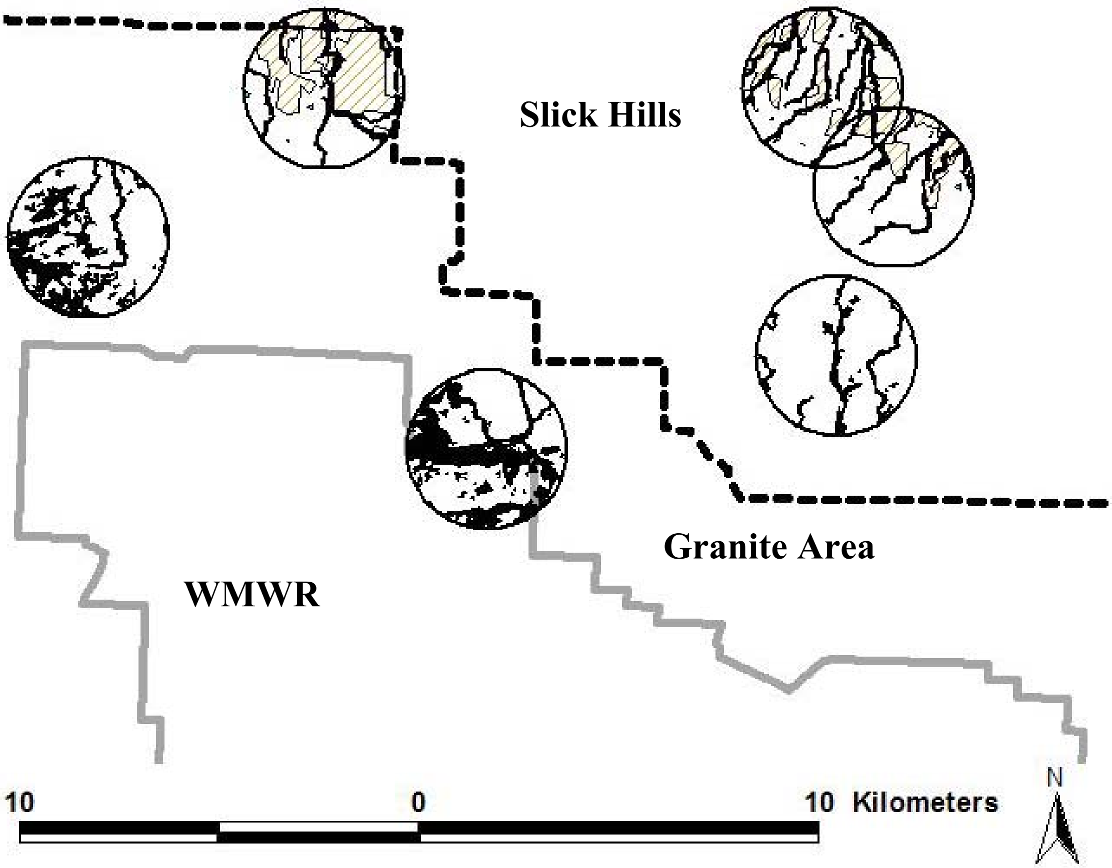
weighted mean shape index (AWMSI), mean patch fractal dimension (MPFD), area-weighted mean patch fractal dimension (AWMPFD).

Figure 1. Study area north of the Wichita Mountains Wildlife Refuge (WMWR) in the Granite Area and Slick Hills on private lands in southwestern Oklahoma.

Figure 2. Representative buffers of elk observations at the 2,000-m spatial scale showing landscape characteristics computed in ArcView 3.2–Fragstats Interface for the Granite Area and Slick Hills north of Wichita Mountains Wildlife Refuge (WMWR). Note that more forested patches are present in the Granite Area, south of the dashed line, compared with the Slick Hills.

Figure 3. Percentage of radiolocations of the 6 elk that used the Wichita Mountains Wildlife Refuge (WMWR) during isolation, breeding, and aggregation. All elk were considered private-land elk because they were radiocollared in the Granite Area in January–April 2002.


Granite Area
Slick Hills
WMWR
Granite Area
10
0
10 Kilometers
N
Roads
Grassland
Forest
Agriculture


Slick Hills
Granite Area
WMWR
10
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10 Kilometers
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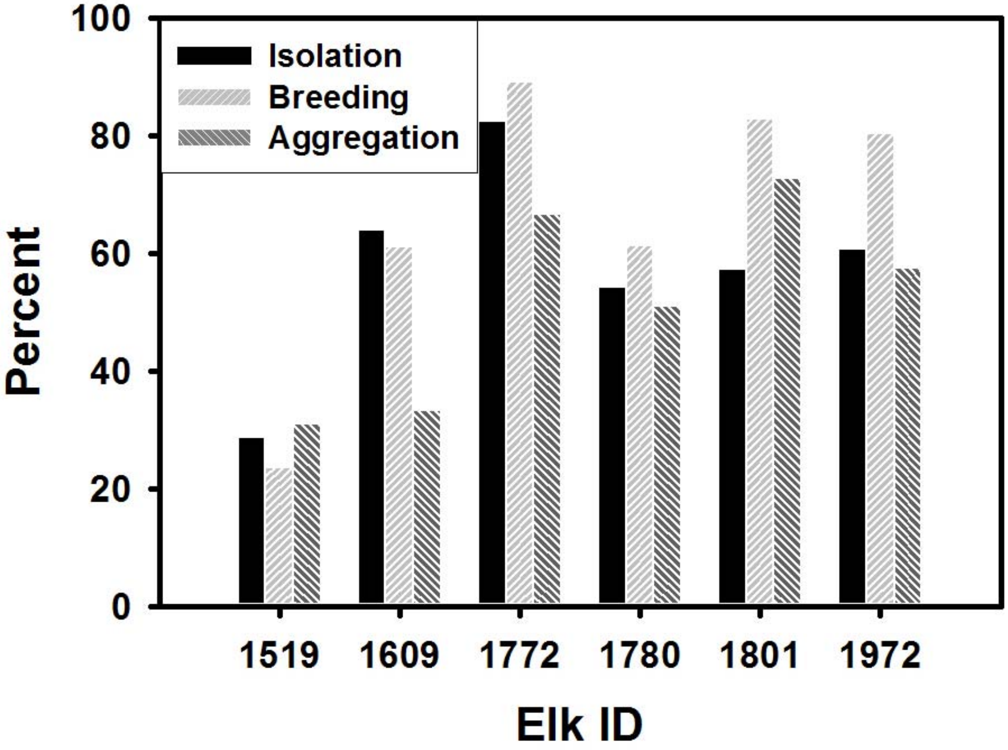
Isolation
Breeding
Aggregation
Percent
0
20
40
60
80
100
1519
1609
1772
1780
1801
1972
Elk ID

CHAPTER III

FECAL CARBON AND NITROGEN ISOTOPES: IMPLICATIONS TO FOURTH-ORDER HABITAT SELECTION IN ROCKY MOUNTAIN ELK (*CERVUS ELAPHUS*)

Abstract: Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes in feces can be used to identify the photosynthetic pathways (C_3 vs. C_4) of plants consumed and infer nutritional condition of consumers. We assessed habitat use and stable isotopes in feces of free-ranging elk (*Cervus elaphus*) on private land in southwestern Oklahoma occupying distinct habitats of mature oak savannah (Granite Area) and C_4-dominated grasslands (Slick Hills). Radiotelemetry of 21 female elk was conducted from January 2002 to March 2005 in the Granite Area ($n = 11$) and the Slick Hills ($n = 10$). Fecal samples were collected at random from elk on private land and the Wichita Mountains Wildlife Refuge (WMWR) from May to August, 2002–2003 and January to March, 2003–2004 representing summer and winter periods, respectively. Elk in the Granite Area used primarily forested habitat (third-order selection) whereas elk in the Slick Hills preferred agricultural habitat; elk in both areas preferred agriculture during winter. Low fecal δ^{13}C and high δ^{15}N during forage-limited months (Jan–Mar) suggested that elk in the Slick Hills consumed more C_3 forage (i.e., winter wheat of high nutritional value) than elk in the Granite Area and WMWR. Fecal δ^{13}C and δ^{15}N provided an index of fourth-order

selection of diet that would be more informative than current methods to describe resource selection.

Key words: carbon isotopes, *Cervus elaphus*, compositional analysis, microhistological, nitrogen isotopes, Oklahoma, Rocky Mountain elk, fourth-order selection

INTRODUCTION

Home range can be defined as an area with a defined probability of an animal's occurrence during a specified time period (Kernohan et al. 2001). Home range determined through radiotelemetry can provide valuable information on resource selection such as use of vegetation types and topographic features (i.e., elevation, slope, aspect) and proximity to water sources or other critical habitats (Johnson 1980, Roloff et al. 2001, Cooper and Millspaugh 2001). Considerable literature has described home-range area and resource selection of various species, but only recently have studies moved beyond where animals occur to understand why animals choose a particular resource or habitat (Barten et al. 2001, Cooper and Millspaugh 2001, Boyce et al. 2002). Most studies on resource selection are challenged with defining resource availability that changes temporally, spatially, and behaviorally and can often be difficult to quantify (Porter and Church 1987, Arthur et al. 1996, Erickson et al. 2001).

Johnson (1980) suggested that analysis of habitat selection should occur at several spatial scales (referred to as *stages* in Johnson 1980) to address arbitrary definition of resource availability and termed them orders-of-selection (Porter and Church 1987). Scales of study can be defined as first-order (geographical range), second-order (study site), third-order (home range), and fourth-order selection (food items selected) using compositional analysis of proportions of used and available habitat (Aebischer et al. 1993). Compositional analysis uses locations of individual animals as the experimental unit and relies on defining used and available habitat in some non-arbitrary fashion (i.e., within a defined home-range; Aebischer et al. 1993, Erickson et al. 2001). Although various technological advances (i.e., Geographic Information Systems) have increased our ability to identify and manage important wildlife habitat, understanding the nutritional benefit of resource selection (i.e., dietary quality) is poorly understood using only assessment of home range and resource selection. Previous studies have documented fourth-order selection of habitat use but its relationship to nutrition is often lacking (Mace et al. 1996, Lariviere and Messier 2000).

Therefore, a logical step to improve assessments of resource selection is to unify information on resources used by and available to an animal with the potential nutritional benefits from such resources. Previous research has measured dietary quality of wildlife using feeding trials, percent fecal nitrogen, microhistology, and gut contents (Vavra and Holechek 1980, Leslie and Starkey 1985, Osborn et al. 1997, Servello et al. 2005). Concerns regarding differential digestibility of forages, influence of protein-precipitating compounds on nitrogen excretion, and relating captive wildlife research to free-ranging wildlife nutrition have been expressed (Leslie et al. 1983, Hobbs 1987, Shahkhalili et al. 1990, Servello et al. 2005). Fecal indices have been used to identify spatial and temporal differences in diets of sympatric ungulates (Leslie and Starkey 1985, Gogan and Barrett 1995, Stewart et al. 2003). Although microhistological techniques may underestimate highly digestible forages (Leslie 1983, Hobbs 1987, McDonald et al. 2005), they provide an additional tool to understand seasonal diet selection in cervids when combined with other methods (Stewart et al. 2003, Kie and Bowyer 1999).

Diets composed primarily of C_3 plants are higher in nitrogen and dry matter digestibility than C_4 plants and, therefore, should contain more available energy (Wilson and Hacker 1987, Wilson and Hattersley 1989). Alfalfa (*Medicago sativa*) and winter wheat (*Triticum aestivum*), both C_3 plants, had higher levels of crude protein (CP) than native grassland forages in several studies (Mould and Robbins 1981, Griffin 1991, Sponheimer et al. 2003a). Fecal nitrogen has been correlated positively with forage intake, dietary protein, and seasonal dietary quality (Cordova et al. 1978, Leslie and Starkey 1985, 1987). Ungulates grazing on greater proportions of C_3 plants at particular times of year would be expected to be on a higher nutritional plane (Wilson and Hattersley 1989, Post et al. 2001). By comparison, levels of nutrition would be lower for elk consuming predominantly C_4 grass with < 10% crude protein, which is considered a minimum for maintaining nitrogen balance (Mould and Robbins 1981, Sponheimer et al. 2003c). For example, Post et al. (2001) found that fecal nitrogen content of bison (*Bos bison*) peaked in May and June, which coincided with a peak in C_3 production. Fecal nitrogen values also showed that male bison consumed a lower-quality diet than females (Post et al. 2001).

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes have been used to identify the photosynthetic pathway (i.e., C_3 or C_4) of plants consumed by herbivores (Tieszen et al. 1983, Kelly 2000, Sponheimer et al. 2003b). Tieszen et al. (1983) indicated that different tissues turn over carbon and nitrogen at different rates, which was critical to making nutritional inferences. Although variation exists by source, more metabolically active sources (i.e., feces, liver, muscle) can reflect a dietary shift in a shorter time period than less metabolically active sources (i.e., hair, bone, connective tissue; Tieszen et al. 1983, Sponheimer et al. 2003a, Sare et al. 2005). Tieszen et al. (1983) documented that a change in diets of gerbils (*Meriones unguienlatus*) from corn (C_4) to wheat (C_3) caused tissue $\delta^{13}C$ to be similar to $\delta^{13}C$ in wheat. Carbon and nitrogen isotopes can be used to identify and compare diets of ungulates occupying different habitat types at the time of sample collection (Tieszen and Imbamba 1980, Tieszen et al. 1989). Carbon and nitrogen isotopes measured in feces would be indicative of ungulate diets consumed within 2–3 days (Tieszen et al. 1983, Coates et al. 1991).

Differences in habitat use by subpopulations, combined with the nutritional outcome of resource selection, can provide greater insight on the factors that contribute to landscape-level population dynamics. Subpopulations may experience different levels of nutrition because habitat productivity varies by location within the landscape. I determined seasonal habitat use by Rocky Mountain elk (*Cervus elaphus*) in distinct landscapes in a C_4-dominated native grassland. I predicted second-order selection of habitat would identify forested (Granite Area) and grassland (Slick Hills) habitat as the most preferred or that habitat use would not differ from random. I predicted third-order selection of habitat would identify agricultural crops as the most preferred habitat on private lands during the forage-limited aggregation period. I used fecal $\delta^{13}C$, $\delta^{15}N$, and percent nitrogen as indices of fourth-order selection by elk. I predicted that elk consuming forage from landscapes with C_3 agricultural crops would benefit nutritionally compared with elk consuming forages dominated by native C_4 grasses.

STUDY AREA

The study was conducted on private lands in southwestern Oklahoma, USA (34°47′–34°57′N, 98°25′–98°50′W) north of the 23,879-ha Wichita Mountains Wildlife Refuge (WMWR) that contained elk, bison, white-tailed deer (*Odocoileus virginianus*), and longhorn cattle (*B. taurus*). Igneous mountain peaks with slopes >25% (Buck 1964) and habitat similar to WMWR extended northward from WMWR on private land and was referred to as the Granite Area (Chapter II; Fig. 1). Forests composed 24% of the Granite Area, and dominant tree species were post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), and eastern redcedar (*Juniperus virginiana*); sugar maple (*Acer saccharum*), pecan (*Carya illinoensis*), and American elm (*Ulmus americana*) occurred in riparian areas (Buck 1964). Dominant tallgrasses included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*). Shortgrasses included buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and sideoats grama (*B. curtipendula*). A mixture of permanent and seasonal homes and primary (i.e., paved) and secondary (i.e., dirt and gravel) roads were dense and scattered throughout the Granite Area than in WMWR.

Limestone-derived rolling hills occurred 3–5 km north of WMWR on private land with habitat in contrast to the Granite Area and WMWR and was referred to as the Slick Hills (Chapter II; Fig. 1). This area was used for cattle grazing and was dominated (>78%) by tallgrass and shortgrass species such as bluestems, gramas, and buffalograss with some in a mesquite (*Prosopis glandulosa*) grassland (Tyrl et al. 2002). Forested habitat (10% of area) occurred in all bottomlands of ephemeral stream corridors and contained pecan, western walnut (*Juglans rupestris*), and eastern redcedar (Fig. 1). Residential homes and primary and secondary roads traversed the Slick Hills separating it into 3 unbroken tracts of land. The largest tract (about 8,000 ha) contained no primary roads, but construction of a 2–3 km gravel road was initiated on 1 June 2003 to service a planned wind-power facility. The wind-power facility was completed with 45 NEG Micon 1.65 MW turbines constructed and active by 31 December 2003; overall effects of the wind-power facility on elk movements were minimal (W.D.Walter, unpublished data). Unlike WMWR, the Granite Area and Slick Hills had fields of wheat (*Triticum aestivum*), alfalfa (*Medicago sativa*), and sorghum (*Sorghum bicolor*) averaging 10 ha (range: <1–180) and 18 ha (range: <1–251 ha), respectively, used for cropped forages, hunting plots, and cattle grazing.

METHODS

Six free-ranging female elk were immobilized on private lands from January to April 2002 with a mixture of 500 mg/ml Telazol® (1:1 tiletamine hydrochloride and zolazepam hydrochloride; Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) reconstituted with 2 ml of 100 mg/ml xylazine HCl (Sedazine®, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA; Walter et al. 2005). An additional 15 elk were captured on 31 March 2003 from a Bell 206 Series helicopter using net guns (Hawkins and Powers Aviation, Greybull, Wyoming). All elk were fitted with radiocollars that contained an 8-h, time-delayed, mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA) and ear-tagged. Animal care and experimental procedures were approved under Oklahoma State University's Institutional Animal Care and Use Protocol GU-02-01.

Habitat Use

Three seasons were delineated based on radiotelemetry data, plant phenology, and behavioral changes of elk in the study area: *isolation* (Apr–Jul) defined as an increase in forage availability and isolation of cows for calving; *breeding* (Aug–Nov) defined as extended harem formation by bulls for breeding; and *aggregation* (Dec–Mar) defined as social grouping behavior (Chapter II) and low availability of natural forage.

I determined second-order (i.e., within each study area) and third-order (within individual home range) selection of habitat using radiotelemetry locations of elk with compositional analysis in the Resource Selection for Windows program (Aebischer et al. 1993, Leban 1999). Used habitat for second-order selection was delimited in an elk's home range as determined by the Minimum Convex Polygon method (MCP; Aebischer et al. 1993, Erickson et al. 2001) and available habitat as the MCP encompassing all elk locations for each study area (i.e., Granite Area and Slick Hills). Used habitat for third-order selection was delimited in a 655-m radius around each elk location (135 ha), and available habitat was the MCP home range for each elk. The 135-ha buffer around each elk location was used to minimize the inherent bias in characterization of habitat use resulting from radiotelemetry error (Zimmerman and Powell 1995, Erickson et al. 2001; Chapter II) and mean patch size (Rettie and McLoughlin 1999). The 75th quartile of error distance around estimated locations was 655 m and encompassed >85% of the test transmitter locations. Mean, median, and regression error distances can be used to correct for error (Wallingford and Lancia 1991, Zimmerman and Powell 1995, Marzluff et al. 1997) but were considered unsatisfactory because they encompassed 73, 68, and

32% of the test transmitter locations, respectively, as determined by radiotelemetry error of known transmitter locations (Chapter II).

Fourth-order Selection

Fourth-order selection of elk habitat use was determined from fecal samples of elk collected from May to August 2002–2003 and January to March 2003–2004, representing periods of high and low natural forage availability, respectively. Fresh pellets (*n* = 5−10), free of insects, were collected opportunistically from individual elk pellet groups (*n* = 14−23 per month) in all 3 areas where elk were known to occur or were located with radiotelemetry. To prevent over-representation of diet by a single group of elk, samples were collected from ≥3 disjunct locations during each month in the Granite Area, Slick Hills, and WMWR. Fecal samples were placed in a paper bag and allowed to air dry to a constant weight before grinding to uniform consistency in a Wiley Mill. Subsequently, 2–3 mg were loaded into 5 x 8-mm tin capsules for carbon and nitrogen isotope analysis in an isotope ratio mass spectrometer (IRMS; Stable Isotopes Facility, University of California, Davis, California). Nitrogen content for each fecal sample was determined by gas chromatography prior to admission to the IRMS (Tieszen et al. 1998).

Carbon isotopes from C_3 plants average about –27% (range: −35 to −21%) while $\delta^{13}C$ from C_4 plants average –13% (range: −14 to −10%; Kelly 2000, Peterson and Fry 1987). Plants can have mean $\delta^{15}N$ ranging from -7 to 7‰ due to differential fractionation of nitrogen by N_2-fixing and non-N_2-fixing plants (Hoering 1955, Virginia and Delwiche 1982, Hobbie et al. 2000). Isotope values in feces were expressed in delta (δ) notation where δ was the ratio of the heavy to light isotope of the sample compared with δ of known standards. Standards for $\delta^{13}C$ and $\delta^{15}N$ were the Peedee Belemnite marine fossil limestone formation from South Carolina ($^{13}C/^{12}C = 0.01124$) and atmospheric nitrogen ($^{15}N/^{14}N = 0$), respectively; $\delta^{13}C$ and $\delta^{15}N$ were reported in per mil notation (‰; Peterson and Fry 1987). Because heavy isotopes of carbon and nitrogen were most limited in organic matter, enrichment of the heavy isotope (i.e., ^{13}C and ^{15}N) would result in more positive values for $\delta^{13}C$ and $\delta^{15}N$ (Schroeder and Ben-Ghedalia 1986, Sponheimer et al. 2003c).

Dietary components

Fecal samples of 8–10 individual pellet groups were composited (Jenks et al. 1989) to assess diets of elk in the Granite Area, Slick Hills, and WMWR from May to August 2003 and January to March 2004. Fecal samples were analyzed for dietary components by the Wildlife Habitat Nutrition Laboratory (Washington State University, Pullman, Washington, USA) to species level using relative cover of plant epidermal fragments in 100 microscopic views.

Data Analysis

To test second- and third-order selection of habitat, I used compositional analysis; a MANOVA tested for nonrandom habitat use, and use of habitat types was contrasted with a paired *t*-test (Aebischer et al. 1993, Erickson et al. 2001). To test for differences in fecal indices as an index to fourth-order selection of habitat, $\delta^{13}C$, $\delta^{15}N$, and percent nitrogen in feces were rank transformed because of heteroscedasticity of data (Conover and Iman 1981); standard deviations for replicated internal standards for $\delta^{13}C$ and $\delta^{15}N$ were 0.08 and 0.22 ‰, respectively. Differences in mean ranked $\delta^{13}C$, $\delta^{15}N$, and percent nitrogen in feces between area and month were analyzed using 2-way analysis of variance (ANOVA; Conover and Iman 1981, Zar 1996). If a significant area-month interaction was detected (P < 0.05), a one-way ANOVA was conducted on area-month factors with Tukey's multiple comparison used as a post-hoc test to identify differences between factor means (Cody and Smith 1997: pages 163–170). Means ± SE for non-transformed data are reported. To determine separation of elk diets between the 3 areas, plants that composed ≥10% of the diet in any month and area from microhistological analysis were used in Principal Component Analysis (PCA; McGarigal et al. 2002); plants composing ≥10% in the diet explained more variation in PCA axes than plants composing 5% in the diet or raw data. Remaining plants that made up <10% in the diet were placed into the following categories prior to inclusion in the PCA: grasses, forbs, woody, shrubs, and other. Percentage data were transformed with arcsine square-root to ensure additivity of treatment effects prior to PCA (Kie and Bowyer 1999, McGarigal et al. 2000, Stewart et al. 2003). Principal Component Analysis was conducted in SAS (SAS Institute Inc. 2003) and loading of each variable was used to interpret dietary separation of elk among the 3 areas.

RESULTS

A total of 2,657 radiotelemetry locations of 21 radiocollared female elk were collected to assess habitat use from April 2002 to March 2005. Nocturnal and diurnal habitat use by elk (Beyer and Haufler 1994, Cooper and Millspaugh 2001) was considered adequately documented because elk locations after sunset constituted 45% of all locations. Second-order selection of habitat for elk in the Granite Area ranked habitat preference as forest > grassland > riparian > agriculture during the isolation ($\chi^2_3 = 12.72$, $P < 0.05$), breeding ($\chi^2_3 = 16.64$, $P < 0.001$), and aggregation ($\chi^2_3 = 9.56$, $P < 0.05$) periods (Table 1). Habitat selection for elk in the Slick Hills ranked habitat preference as grassland > riparian > forest > agriculture during the breeding period ($\chi^2_3 = 19.64$, $P < 0.001$), but no habitat preference was found during the isolation ($\chi^2_3 = 6.16$, $P = 0.10$) and aggregation periods ($\chi^2_3 = 2.73$, $P = 0.44$).

Third-order selection within the home range of elk in the Granite Area ranked habitat preference as forest > riparian > grassland > agriculture during isolation ($\chi^2_3 = 16.10$, $P < 0.05$) and breeding ($\chi^2_3 = 8.49$, $P < 0.05$) but ranked preference during aggregation ($\chi^2_3 = 14.39$, $P < 0.05$) as agriculture > forest > grassland > riparian (Table 1). Habitat selection within the home range of elk in the Slick Hills ranked agriculture as most preferred and grassland as least preferred during breeding ($\chi^2_3 = 8.21$, $P < 0.05$) and aggregation ($\chi^2_3 = 33.28$, $P < 0.0001$) but forest > agriculture > riparian > grassland during isolation ($\chi^2_3 = 12.35$, $P < 0.05$; Table 1).

Because annual differences of fecal isotopes were minimal (i.e., ≤ 1 month/area significant at $P < 0.05$), years were combined for analysis. There was an area-month interaction for elk fecal $\delta^{13}C$ ($F_{12, 375} = 12.51$, $P < 0.001$). Fecal $\delta^{13}C$ of elk in the Granite Area and Slick Hills differed from elk in WMWR in January–March. June and July fecal $\delta^{13}C$ were lower in the Slick Hills and Granite Area than WMWR, but no differences in fecal $\delta^{13}C$ between the 3 areas occurred in May and August (Table 2, Fig. 2a). There was an area-month interaction for fecal $\delta^{15}N$ ($F_{12, 375} = 15.50$, $P = 0.0115$) with differences in all 3 areas in January, February, and August. Fecal $\delta^{15}N$ for elk in the Granite Area and WMWR differed from the Slick Hills but not each other in June–August (Fig. 2b). Fecal $\delta^{15}N$ for elk in the Granite Area and Slick Hills differed from those in WMWR but not each other in March and May (Fig. 2b). There was an area-month interaction for percent fecal nitrogen ($F_{12, 375} = 12.58$, $P < 0.0001$) with the Granite Area and Slick Hills differing from WMWR in January and March but not in February and May–August (Fig. 2c). Percent fecal nitrogen for elk in the Granite Area and Slick Hills differed in January and February.

To assess potential seasonal differences in fecal indices by year, May–August (summer) and January–March (winter) were combined for analysis. There was a season-area interaction ($F_{6, 384} = 42.30$, $P < 0.0001$) for fecal $\delta^{13}C$. No difference in fecal $\delta^{13}C$ occurred among the 3 areas in summer 2002; elk in the Granite Area and WMWR had higher fecal $\delta^{13}C$ than elk in the Slick Hills, but they did not differ from each other in summer 2003 (Fig. 3a). Fecal $\delta^{13}C$ of elk in the Granite Area and Slick Hills differed from WMWR during both winters but not from each other. There was a season-area interaction for fecal $\delta^{15}N$ ($F_{6, 384} = 63.27$, $P < 0.0001$) with differences among all 3 areas during all seasons except summer 2002 when elk from the Granite Area and WMWR were similar. There was a season-area interaction for percent fecal nitrogen ($F_{6, 384} = 45.91$, $P < 0.0001$). No differences in percent fecal nitrogen occurred by area for either summer, but it differed for all possible area comparisons in winter 2004 (Fig. 3c). Percent fecal nitrogen in the Granite Area and Slick Hills was higher than WMWR during winter 2003 but not from each other.

Mean annual percentages of C_3 plants in diets of elk were 60.8, 37.6, and 35.5% for the Slick Hills, Granite Area, and WMWR, respectively. Mean annual percentages of C_4 plants in diets of elk were 39.2, 62.4, and 65.5% for the Slick Hills, Granite Area, and WMWR, respectively. Mean percentage of C_3 plants in diets of elk during summer were 51.0, 16.6, and 32.4% for the Slick Hills, Granite Area, and WMWR, respectively (Fig.

4). A seasonal shift occurred in diets of elk in winter with mean percentage of C_3 plants of 74.0, 65.7, and 37.3% for the Slick Hills, Granite Area, and WMWR, respectively (Fig. 4). Composite fecal samples contained 13 grass, 10 forb, 7 woody, 5 shrub, and 3 agricultural species in May–August and January–March (Table 3). Flowers of an unknown species were present in feces of elk from the Granite Area in large quantities (i.e., 30%) in June and July. Principal Component Analysis yielded 3 primary axes that explained 68% of the variation in diets between the 3 areas. Principal component 1 (30%) was identified as a forage-class axis ranging from C_3 forage (i.e., winter wheat, browse) with negative loadings to C_4 grasses with positive loadings (Fig. 5a and 5b). Principal component 2 (24%) was a seasonal forage axis from summer forage (i.e., wheat grain, flower, alfalfa) with negative loadings to winter forages (i.e., C_4 grasses, shrubs, woody) with positive loadings (Fig. 5a). Principal component 3 (14%) was an area-forage axis ranging from forested habitat in WMWR (i.e., C_4 grasses, shrubs, woody) with negative loadings to grassland habitat in the Slick Hills (i.e., C_4 grasses, wheat grain, winter wheat, alfalfa) with positive loadings (Fig. 5b).

DISCUSSION

Habitat use by elk differed between the Granite Area and Slick Hills as predicted in contrasting habitat types (i.e., closed forest versus open grassland; Chapter II). Within the study area (i.e., second-order selection), elk in the Slick Hills used predominantly grassland habitats but elk in the Granite Area used forested habitats. That result was to be expected for mixed-feeders (Hofmann 1988), such as elk, because the Slick Hills were composed primarily of grassland (i.e., 10% forested) and the Granite Area had a greater proportion of forested habitat within a mosaic of grasslands (i.e., 25% forested; Chapter

II). Although elk are classified as mixed-feeders, elk select grasses over trees and shrubs when suitable amounts are available (Nelson and Leege 1982). Selection of contrasting habitat types by ungulates has been related to forage quality and distribution, reproductive strategies, predator avoidance, and human disturbance (Lyon 1983, Barten et al. 2001, Kie et al. 2002, Krause and Ruxton 2002).

Third-order selection of habitat by elk in the Slick Hills showed that agricultural areas were ranked highest during all periods except isolation when forests and agricultural areas were preferred habitats. Direct observations and radiotelemetry documented that elk in the Slick Hills and Granite Area used forested habitat during isolation apparently for thermal and security cover or improved foraging (Chapter II). Forests provide thermal and security cover, a concentrated food source, and delayed plant phenology (Nelson and Leege 1982, Irwin and Peek 1983, McCorquodale 1991, Millspaugh et al. 1998). Elk in the Granite Area occupied habitat similar to WMWR, a mosaic of forests and open grassland, and often selected for habitats within WMWR. Forested habitats along riparian corridors were used by individual elk or elk with calves likely to avoid summer temperatures >38º C (100º F; National Oceanic and Atmospheric Administration 2003) and as secure calving habitat (Waldrip 1977). Nocturnal activity exhibited by cow elk during summer may decrease energetic costs of thermoregulation and reduce human disturbance at preferred foraging sites (Lyon 1983, McCorquodale et al. 1986, Millspaugh et al. 1998). These special habitat requirements have been documented for elk adjusting to climatic variables, behavioral changes, and decreasing forage availability (McCorquodale et al. 1986, Millspaugh 1999, Roloff et al. 2001).

Selection of agricultural areas by elk was apparent during the forage-limited months (i.e., aggregation) in the Granite Area and Slick Hills. That result was consistent with the tendency of elk to forage in the most productive habitats (Irwin and Peek 1983, McCorquodale 1991, Unsworth et al. 1998). Elk in the Slick Hills reduced their home-range area in December–February around fields of concentrated winter wheat (Chapter II). Elk used fields of winter wheat that were visible from primary roads diurnally and nocturnally in November–March in large groups (i.e., ≥30 elk) in both areas, highlighting the importance of agricultural areas during forage-limited winter months. Selection for agricultural crops by elk has been well documented during periods of limited natural forage availability, high elk densities, or in refuges (Lyon and Ward 1982, Boyce 1989, Brelsford et al. 1998, Burcham et al. 1999).

Because habitats were similar in the Granite Area and WMWR, second and third-order selection for elk would be similar except during aggregation because agricultural crops were not available to elk in WMWR. However, for fecal indices of fourth-order selection in all elk herds, May–August represented a period of high (i.e., May–June) and moderate (i.e., July–August) natural forage availability because mean precipitation totals in a typical year were higher and temperatures lower in May–June than in July–August (National Oceanic and Atmospheric Administration 2003). Monthly fecal $\delta^{13}C$ among the 3 areas differed because of the variability in the proportion of C_3 and C_4 plants in the diet of elk in the 3 areas. However, higher fecal $\delta^{13}C$ suggested a shift from C_3 to C_4 plants in diets of elk in all 3 areas as the growing season progressed from May to August, but the shift was most pronounced for elk in WMWR. Dietary crude protein decreases through summer as plants mature (Huston et al. 1981, Nelson and Leege 1982, Canon et al. 1987). Microhistological results showed that alfalfa and wheat grain, both C_3 plants, increased in the summer diets of elk in the Slick Hills whereas elk in the Granite Area and WMWR relied on C_4 grasses and woody vegetation as native forage senesced. Thus, feces of elk in the Slick Hills reflected a diet of alfalfa and wheat grain with lower fecal $\delta^{13}C$ than elk in the Granite Area and WMWR foraging on C_4 grasses. Similarly, PCA documented a greater overlap in dietary components between elk from the Granite Area and WMWR during summer than elk in the Slick Hills.

Similar percent fecal nitrogen for elk in all 3 areas in May–August suggested that any variability in diets by area resulted in similar overall nutrition. Elk in WMWR used habitat similar to elk in the Granite Area during summer (Waldrip 1977; Table 4 Fig. 5), and it provided similar nutrition between the 2 areas as indicated by percent fecal nitrogen. Leaves of forbs, non-deciduous trees, and shrubs maintain comparatively high nitrogen levels at all times and have low $\delta^{15}N$, but grasses have low nitrogen levels and greater $\delta^{15}N$ during the dry season (Tolsma et al. 1987, Boutton et al. 1988, Van Soest 1994). Although absolute amounts of forage consumed and effects of density of sympatric ungulates (i.e., cattle, bison) were not quantified, it appears that consuming a combination of natural forage and agricultural crops by elk in the Slick Hills as the summer progressed (i.e., alfalfa, sorghum) provided comparable nutrition to the native vegetation consumed by elk in the Granite Area and WMWR.

Higher fecal $\delta^{15}N$ and percent nitrogen for elk on private land in forage-limited winter months of January and March suggested that dietary nitrogen obtained by elk on private lands could be comparable to nitrogen obtained during months of high natural forage availability (i.e., summer). Fecal nitrogen has been correlated with dietary quality of ruminants (Leslie and Starkey 1985, Wehausen 1995, Robinson et al. 2005). Fecal $\delta^{13}C$ suggested that elk from WMWR had a greater proportion of C_4 plants in their diets during winter compared with elk on private land. Microhistology confirmed results of fecal $\delta^{13}C$ indicating that >50% of elk diets in January–March in WMWR were C_4 grasses (e.g., *Andropogon gerardii*, *A. scoparius*, and *Bouteloua gracilis*), which was 20–40% higher than both private land herds. Plants that follow the C_4 photosynthetic pathway have lower nitrogen levels during winter than winter wheat because protein is bound up in highly vascularized bundle sheath cells (Wilson and Hacker 1987, Hanley et al. 1992, Robinson et al. 2005). As $\delta^{13}C$ increased and $\delta^{15}N$ decreased in plants in the study area, percent nitrogen in plants also decreased reflecting the greater nitrogen content of C_3 plants compared with C_4 plants (Chapter IV; Table 2). Elk foraging on winter wheat would have higher nitrogen intake because wheat is more digestible than senesced C_4 grass and has 25% CP (Hanley et al. 1992, Robbins 1993).

Plant phenology and numerous interrelated factors that affect phenology influence elk forage quality and hence, elk movements to foraging areas. Elk in our study varied their choice of foraging areas depending on season and experienced different diet quality from those choices as reflected in their fecal $\delta^{13}C$ and $\delta^{15}N$. Natural forage was preferred during spring green-up but readily decreased with plant phenology as summer progressed. Fecal $\delta^{13}C$ provided a method to index fourth-order selection and assess primary diet components and dietary shifts in a mixed-feeder such as elk. Based on previous work with $\delta^{13}C$, a pure diet of C_3 forage would have resulted in fecal $\delta^{13}C$ for elk of $< -27.0‰$ whereas a pure C_4 diet would result in values $> -12.0‰$ (Vogel 1978). Fecal $\delta^{13}C$ between the extremes, such as those found in this study, indicated a mixture of

C_3 and C_4 plants in the diets of elk. Availability of agricultural crops provided an alternate food source during late summer or winter when climatic conditions caused forages to senesce. For elk on private lands, alternate food sources could provide enough dietary nitrogen and digestible energy for body maintenance during forage limited periods (i.e., dry summers and harsh winters). Nutrition has been thoroughly linked with survival, fertility, and population growth (Nelson and Leege 1982, Clutton-Brock and Lonergan 1994, Benton et al. 1995, Taper and Gogan 2002), and population dynamics would be expected to change in response to this nutritional advantage. Fourth-order selection as indexed with fecal indices was unique to my study and provided valuable insight into resource selection of ungulates.

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Table 1. Second and third-order selection using compositional analysis for seasonal habitat use by elk in the Granite Area and Slick Hills in southwestern Oklahoma. The most preferred habitats received the highest rank (i.e., 3), and ranks with different letters within a row differed at $P < 0.05$.

		Habitat			
Area	Season[a]	Riparian	Forest	Grass	Crop
Second-order (within area)					
Slick Hills	Isolation	NP	NP	NP	NP
	Breeding	2a	1bc	3a	0c
	Aggregation	NP	NP	NP	NP
Granite Area	Isolation	1a	3b	2a	0c
	Breeding	1a	3a	2a	0b
	Aggregation	1a	3b	2ab	0c
Third-order (within home range)					
Slick Hills	Isolation	1a	3b	0c	2abc
	Breeding	1a	2ab	0c	3b
	Aggregation	2a	1b	0c	3abc
Granite Area	Isolation	2a	3b	1a	0c
	Breeding	2ab	3a	1b	0c
	Aggregation	0a	2b	1a	3ab

[a] Isolation = April–July, Breeding = August–November, Aggregation = December–January

Table 2. Mean (±SE) fecal $\delta^{13}C$, $\delta^{15}N$, and percent nitrogen in the Slick Hills, Granite Area, and Wichita Mountains Wildlife Refuge (WMWR) during summer (May–August) and winter (January–March), 2002–2005.

Month	n	$\delta^{13}C$	$\delta^{15}N$	Percent nitrogen
Slick Hills				
Summer				
May	14	-26.21 (0.270)	2.77 (0.342)	2.87 (0.120)
June	18	-25.56 (0.342)	3.12 (0.485)	2.06 (0.131)
July	20	-24.07 (0.362)	3.30 (0.355)	1.85 (0.94)
August	19	-24.34 (0.263)	3.61 (0.215)	1.96 (0.063)
Winter				
January	20	-27.11 (0.199)	4.97 (0.170)	2.77 (0.084)
February	20	-26.07 (0.185)	3.85 (0.147)	2.23 (0.073)
March	18	-26.91 (0.192)	3.49 (0.239)	2.22 (0.072)
Granite Area				
Summer				
May	19	-23.58 (0.797)	1.60 (0.338)	2.62 (0.151)
June	21	-22.66 (0.481)	0.31 (0.332)	2.00 (0.057)
July	20	-23.11 (0.717)	0.18 (0.305)	1.92 (0.060)
August	20	-23.32 (0.395)	0.23 (0.215)	1.84 (0.053)
Winter				
January	16	-27.02 (0.171)	1.47 (0.353)	2.08 (0.125)

Table 2. Continued.

Month	n	$\delta^{13}C$	$\delta^{15}N$	Percent nitrogen
February	20	-26.78 (0.152)	2.07 (0.293)	1.83 (0.099)
March	17	-26.47 (0.438)	3.24 (0.430)	2.25 (0.137)
WMWR				
Summer				
May	20	-25.95 (0.232)	0.14 (0.228)	3.03 (0.155)
June	22	-23.64 (0.301)	0.23 (0.181)	2.24 (0.107)
July	23	-20.17 (0.525)	-0.52 (0.255)	1.85 (0.078)
August	19	-21.99 (0.747)	-0.33 (0.236)	1.77 (0.059)
Winter				
January	10	-20.28 (0.838)	-1.22 (0.189)	1.13 (0.073)
February	20	-22.59 (0.813)	-2.17 (0.198)	1.41 (0.069)
March	20	-21.28 (0.759)	-1.89 (0.119)	1.36 (0.052)

Table 3. Percentage of species or major forage classes (i.e., grass, forbs, shrubs, woody) identified in microhistological analysis of composite fecal samples of elk collected in May–August 2003 and January–March 2004 in the Slick Hills, Granite Area, and Wichita Mountains Wildlife Refuge (WMWR) in southwestern Oklahoma.

Scientific name	May	June	July	August	January	February	March
Slick Hills							
Grasses							
Andropogon gerardii	18.4	13.2	10.6	4.5	2.7	6.6	13.2
Andropogon scoparius	15.9	8.9	4.3	3.6	0.0	1.2	2.6
Bouteloua curtipendula	0.0	1.2	0.0	0.0	0.0	0.0	0.0
Bouteloua gracilis	0.8	1.2	0.0	2.2	0.0	1.2	0.8
Bouteloua hirsute	0.0	0.0	0.0	1.8	0.0	0.0	1.9
Bouteloua spp.	4.6	5.4	0.4	9.4	0.8	1.7	1.5
Bromus tectorum	0.4	3.5	0.0	0.0	0.0	0.0	0.0
Buchloe dactyloides	0.0	1.9	0.0	2.2	0.0	0.0	0.0
Panicum virgatum	5.4	0.8	0.0	0.0	0.8	2.1	7.2
Setaria geniculatus	0.8	1.6	0.0	2.2	1.9	0.8	1.9
Sorghastrum nutans	9.2	10.1	3.9	0.0	2.7	0.8	3.4
Sporobolus asper	5.9	0.8	3.1	1.4	1.6	7.8	0.8
Tridens flavus	0.0	0.0	2.4	10.3	0.0	0.0	0.0
Unknown Grass #1	0.0	3.1	0.0	0.0	0.0	0.0	0.0
Other Grass	5.9	5.1	6.7	2.2	1.9	3.3	3.4
Carex	0.8	0.0	0.0	0.0	1.2	0.4	1.9
Forbs							
Ambrosia spp.	0.0	0.0	0.0	0.0	0.0	0.8	0.0
Aster ericoides	2.3	0.0	0.0	0.0	0.4	0.4	0.4
Chenopod family	0.0	0.0	0.0	0.0	0.0	0.0	1.1
Coreopsis tinctoria	0.0	0.0	0.0	0.0	0.0	1.7	0.0
Croton spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lesquerella (probable)	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Psoralea tenuiflora	2.5	0.8	0.0	0.0	0.6	0.4	1.1
Yucca	1.7	0.0	0.0	0.0	6.3	23.8	5.3
Legume	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Legume pod	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Forbs	8.8	6.6	5.5	2.2	3.1	2.1	3.0
Woody							
Acer saccharum leaf	0.0	1.9	0.0	0.0	0.0	0.0	0.0
Acer saccharum stem	1.7	1.2	0.0	0.0	0.0	0.0	0.0
Acer saccharum seed	0.0	0.0	0.0	0.0	0.0	0.0	2.3
Bumelia lanuginose	0.0	0.0	0.0	0.0	0.0	0.0	0.7

Table 3. Continued.

Scientific name	May	June	July	August	January	February	March
Juglans rupestris leaf	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Juglans nut	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Juniperus virginiana	0.0	0.0	0.0	0.0	0.0	0.8	2.6
Parkinsonia	0.0	4.7	0.0	0.0	0.0	0.0	0.0
Quercus spp. leaf	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Quercus spp. stem	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acorn	0.0	1.5	0.0	0.0	0.0	0.0	0.0
Sida/Abutilon	0.0	0.4	0.4	0.0	0.0	0.0	0.0
Cornus drummondii leaf	1.7	1.5	0.0	0.9	0.0	0.0	0.0
Cornus drummondii stem	3.8	0.8	0.0	0.0	0.0	0.0	0.0
Rhus glabra leaf	0.0	0.0	0.0	0.0	0.0	1.2	3.4
Rhus glabra stem	1.7	0.0	0.0	0.0	0.0	0.0	0.0
Smilax spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Symphoricarpos orbiculatus leaf	2.1	0.8	0.0	0.0	0.0	1.2	3.4
Symphoricarpos orbiculatus stem	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown shrub leaf	1.3	1.6	0.0	0.0	0.0	0.8	1.9
Unknown shrub stem	1.7	2.3	0.0	0.9	0.8	1.6	3.8
Cultivated crop							
Medicago sativa	1.3	4.7	4.3	21.3	0.0	0.0	0.0
Triticum aestivum grain	0.0	10.5	46.6	28.5	0.0	0.0	0.0
Sorghum bicolor	0.0	0.0	0.0	0.0	1.2	1.2	1.1
Triticum aestivum leaf	0.0	0.0	3.5	3.1	73.6	37.3	29.8
Other							
Nut	0.0	0.0	0.0	1.4	0.0	0.0	0.0
Seed	0.0	0.0	7.5	1.4	0.0	0.8	0.4
Flower	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Insect	0.0	3.9	0.0	0.5	0.4	0.0	0.7
Granite Area							
Grasses							
Andropogon gerardii	19.1	22.3	21.2	12.1	10.8	5.7	5.9
Andropogon scoparius	8.9	18.9	10.4	11.3	7.0	7.5	3.9
Bouteloua curtipendula	0.0	0.0	2.6	7.0	1.5	1.9	2.7
Bouteloua gracilis	0.0	0.0	6.0	11.3	1.1	4.1	2.4
Bouteloua hirsute	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Bouteloua spp.	2.5	1.1	0.0	5.1	3.7	2.3	1.6
Bromus tectorum	1.7	8.3	1.5	0.0	0.0	0.0	0.0
Buchloe dactyloides	0.0	0.0	0.4	1.2	0.4	0.8	2.0
Panicum virgatum	4.7	4.5	1.5	5.1	5.2	3.0	2.7
Setaria geniculatus	7.2	6.4	1.9	2.7	2.2	0.4	0.0
Sorghastrum nutans	11.0	6.1	4.5	7.8	3.7	0.8	1.2

Table 3. Continued.

Scientific name	May	June	July	August	January	February	March
Sporobolus asper	9.8	1.9	5.2	2.3	4.8	2.6	3.9
Tridens flavus	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Unknown Grass #1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Grass	3.0	2.6	4.1	3.5	1.9	1.9	1.2
Carex	8.5	2.3	0.7	2.0	0.0	0.0	0.8
Forbs							
Ambrosia spp.	1.7	0.4	0.0	0.0	0.7	0.0	0.0
Aster ericoides	4.0	1.1	0.9	0.4	0.0	0.0	0.0
Chenopod family	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coreopsis tinctoria	0.0	0.8	0.8	0.0	0.0	0.0	0.0
Croton spp.	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Lesquerella (probable)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Psoralea tenuiflora	0.2	0.0	1.1	1.0	0.0	0.0	0.0
Yucca	0.0	0.0	0.0	0.0	6.7	4.5	7.1
Legume	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Legume pod	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Forbs	3.4	3.0	1.9	2.2	1.9	0.4	0.4
Woody							
Acer saccharum leaf	0.0	0.8	0.0	2.0	0.7	1.1	2.0
Acer saccharum stem	0.0	0.0	1.1	3.1	0.0	0.7	0.8
Acer saccharum seed	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Bumelia lanuginose	0.0	0.0	0.0	0.0	2.2	3.8	0.8
Juglans rupestris leaf	0.0	0.0	0.0	0.0	0.0	0.4	0.8
Juglans nut	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Juniperus virginiana	0.0	0.0	0.0	0.0	0.0	0.0	0.8
Parkinsonia	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quercus spp. leaf	9.6	0.6	0.0	9.2	11.5	21.9	33.5
Quercus spp. stem	0.0	0.0	0.0	0.8	0.0	0.0	1.6
Acorn	0.0	0.0	0.0	0.0	7.0	3.8	0.0
Sida/Abutilon	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Cornus drummondii Leaf	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cornus drummondii Stem	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhus glabra leaf	0.0	0.0	0.0	2.3	4.8	7.5	5.5
Rhus glabra stem	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Smilax spp.	0.9	0.0	0.7	0.0	0.0	0.0	0.0
Symphoricarpos orbiculatus leaf	0.4	0.0	0.0	2.0	2.2	2.3	3.5
Symphoricarpos orbiculatus stem	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown shrub leaf	0.0	0.0	0.0	2.0	0.0	0.0	0.8
Unknown shrub stem	0.0	0.0	1.9	2.0	0.0	0.0	0.0

Table 3. Continued.

Scientific name	May	June	July	August	January	February	March
Cultivated crop							
Medicago sativa	2.1	0.0	0.0	0.0	0.0	0.0	0.0
Triticum aestivum grain	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sorghum bicolor	0.0	0.0	0.0	0.0	0.0	0.8	2.3
Triticum aestivum leaf	0.0	0.0	0.0	0.0	19.3	20.7	9.4
Other							
Nut	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Seed	0.0	0.4	1.1	0.0	0.7	0.0	0.0
Flower	0.9	18.5	30.5	0.8	0.0	0.0	0.0
Insect	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WMWR							
Grasses							
Andropogon gerardii	8.1	27.3	28.3	17.2	13.3	11.1	15.6
Andropogon scoparius	3.0	7.5	11.0	13.0	3.3	7.4	8.6
Bouteloua curtipendula	1.7		4.1	5.5	7.1	5.2	1.7
Bouteloua gracilis	0.9	3.7	1.8	10.1	9.2	12.2	8.2
Bouteloua hirsute	0.0	0.0	0.0	0.0	1.7	1.9	0.0
Bouteloua spp.	0.8	3.3	2.9	4.2	6.7	2.2	4.8
Bromus tectorum	0.4	1.2	0.0	0.8	0.0	0.0	0.0
Buchloe dactyloides	0.0	0.0	2.2	0.0	1.3	0.0	0.0
Panicum virgatum	6.4	2.1	5.9	2.1	4.2	3.3	2.2
Setaria geniculatus	3.0	4.1	1.8	1.3	1.3	2.2	3.5
Sorghastrum nutans	5.1	5.8	13.6	3.8	5.8	0.0	4.3
Sporobolus asper	0.9	5.0	3.3	3.4	5.8	4.1	7.3
Tridens flavus	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown Grass #1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Grass	2.6	7.9	4.4	1.7	1.7	2.6	2.6
Carex	0.0	2.9	3.7	1.3	3.3	5.9	6.1
Forbs							
Ambrosia spp.	0.9	0.8	0.0	0.0	0.0	1.5	0.0
Aster ericoides	0.0	1.5	1.5	1.3	0.0	0.8	0.0
Chenopod family	0.0	0.0	0.0	0.0	0.0	0.7	2.2
Coreopsis tinctoria	1.7	0.0	0.0	0.0	0.8	0.0	1.7
Croton spp.	1.7	0.0	1.1	0.0	0.4	0.7	
Lesquerella (probable)	0.0	0.0	0.0	0.0	0.0	0.7	0.9
Psoralea tenuiflora	0.6	1.2	0.4	0.0	0.0	0.4	0.9
Yucca	0.0	0.0	0.7	0.8	3.3	3.3	1.3
Legume	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Legume pod	4.3	0.0	0.0	0.0	0.0	0.0	0.0
Other Forbs	2.1	1.3	3.0	0.8	0.0	1.5	1.3
Woody							
Acer saccharum leaf	0.4	2.1	0.0	0.0	2.5	1.5	1.3
Acer saccharum stem	0.0	0.4	0.0	0.0	0.4	0.0	1.7

Table 3. Continued.

Scientific name	May	June	July	August	January	February	March
Acer saccharum seed	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Bumelia lanuginose	0.0	0.0	0.0	1.7	0.8	0.4	2.2
Juglans rupestris leaf	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Juglans nut	0.0	0.0	0.0	0.0	1.3	0.7	3.0
Juniperus virginiana	0.0	0.0	0.0	0.0	1.7	0.7	0.0
Parkinsonia	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quercus spp. leaf	40.8	2.5	0.0	13.5	4.6	7.4	3.0
Quercus spp. stem	5.6	0.0	0.0	0.0	0.8	0.0	1.7
Acorn	0.0	0.0	0.0	0.0	3.8	5.2	2.2
Sida/Abutilon	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cornus drummondii leaf	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cornus drummondii Stem	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhus glabra leaf	0.0	0.0	0.0	5.5	2.5	1.9	2.6
Rhus glabra stem	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Smilax spp.	0.0	0.8	0.7	2.1	0.0	0.0	0.0
Symphoricarpos Orbiculatus leaf	0.0	0.8	1.5	5.0	6.3	1.5	0.9
Symphoricarpos Orbiculatus stem	4.3	0.0	1.1	0.0	1.2	2.6	0.0
Unknown shrub leaf	0.0	0.4	0.0	2.1	0.8	1.1	0.0
Unknown shrub stem	3.4	0.4	0.0	0.8	0.0	2.6	1.3
Cultivated crops							
Medicago sativa	0.0	2.1	0.0	0.0	0.0	0.0	0.0
Triticum aestivum grain	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sorghum bicolor	0.0	0.0	0.0	0.0	0.8	0.0	2.2
Triticum aestivum leaf	0.0	0.0	0.0	0.0	1.7	3.0	2.6
Other							
Nut	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Seed	1.3	2.9	0.4	0.8	1.2	2.2	1.7
Flower	0.0	12.0	6.6	0.8	0.0	0.0	0.0
Insect	0.0	0.0	0.0	0.4	0.0	0.4	0.0

Table 4. Eigenvectors and eigenvalues from Principal Component Analysis of plant variables from fecal microhistological analysis in the Slick Hills, Granite Area, and Wichita Mountains Wildlife Refuge (WMWR) during winter (January–March) and summer (May–August), 2003–2004.

Variable	PC 1	PC 2	PC 3
Andropogon gerardii	0.465	-0.066	0.118
Andropogon scoparius	0.417	0.054	-0.103
Bouteloua spp.	0.148	0.285	-0.489
Panicum virgatum	0.213	0.372	0.335
Setaria geniculatus	0.299	-0.092	0.155
Sorghastrum nutans	0.334	-0.004	0.294
Sporobolus asper	0.128	0.068	0.265
Grasses	0.243	-0.318	-0.189
Forbs	-0.187	0.101	0.600
Woody	-0.023	0.453	-0.126
Shrubs	-0.273	0.510	-0.137
Cropped forages	-0.429	-0.241	0.031
Other	0.214	-0.355	-0.111
Eigenvalue	3.928	3.073	1.760
% of variance	30.2	23.6	13.5

Figure 1. Study area north of the Wichita Mountains Wildlife Refuge (WMWR) in the Granite Area and Slick Hills on private land in southwestern Oklahoma.

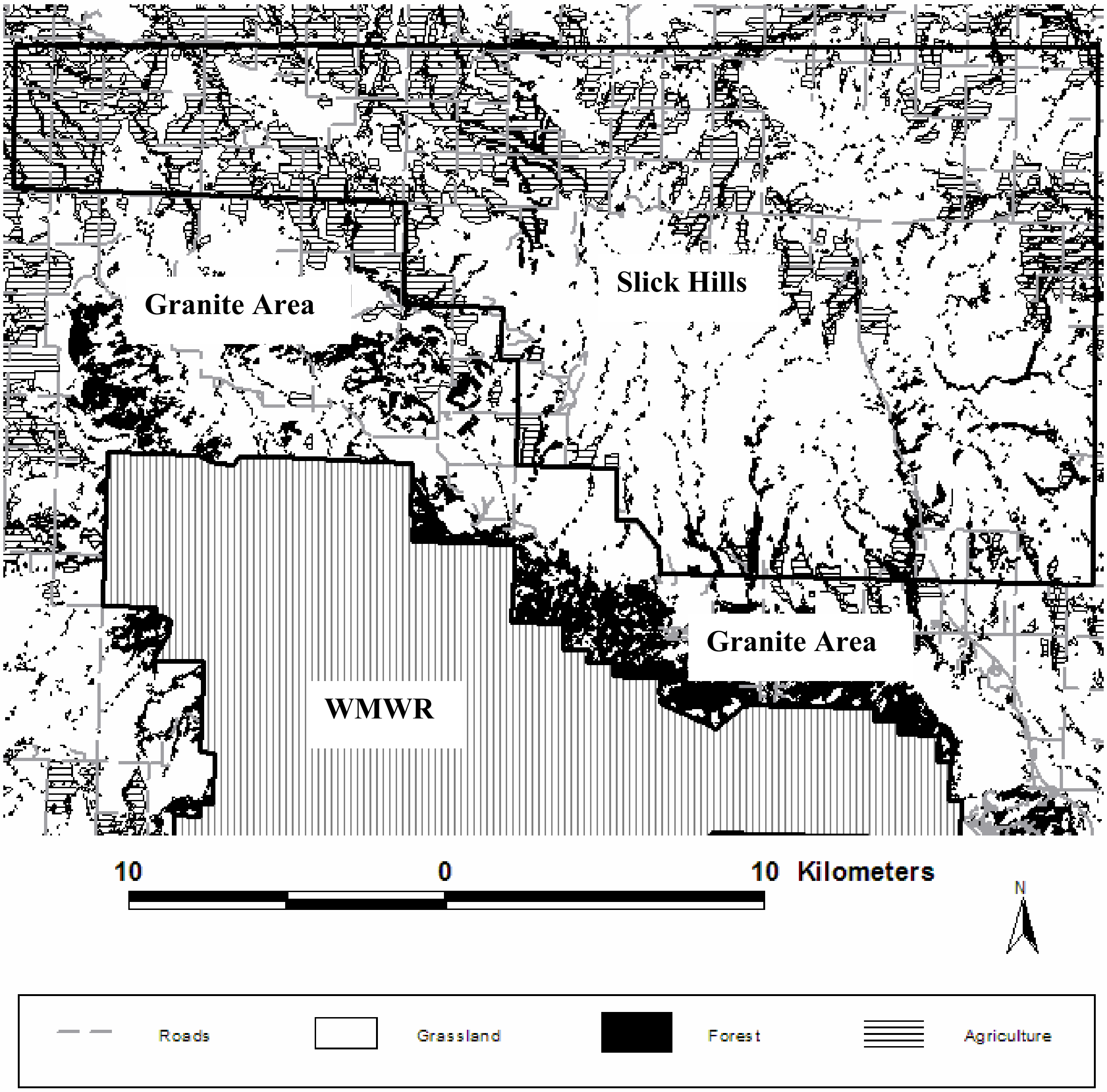
Figure 2. Monthly mean (±SE) fecal a) δ^{13}C, b) δ^{15}N, and c) percent nitrogen in the Slick Hills, Granite Area, and Wichita Mountains Wildlife Refuge (WMWR) in May–August and January–March, 2002–2004. Differences in monthly means among areas are indicated by different letters at $P < 0.05$; no letters indicate no differences.

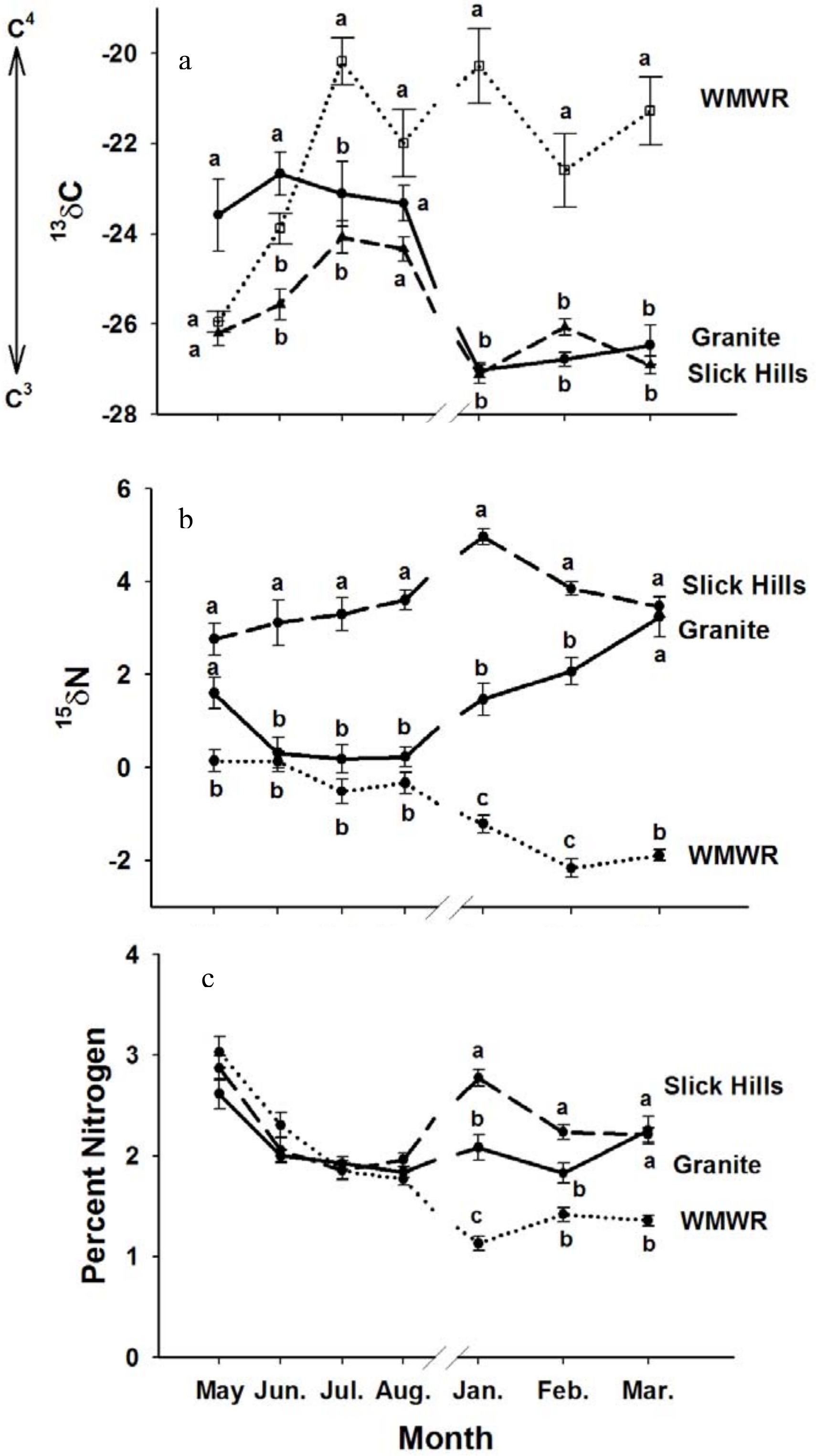
Figure 3. Seasonal mean (±SE) fecal a) δ^{13}C, b) δ^{15}N, and c) percent nitrogen in the Slick Hills, Granite Area, and Wichita Mountains Wildlife Refuge (WMWR) in summer (May–August) and winter (January–March), 2002–2004. Differences in seasonal means among areas are indicated by different letters at $P < 0.05$; no letters indicate no differences.

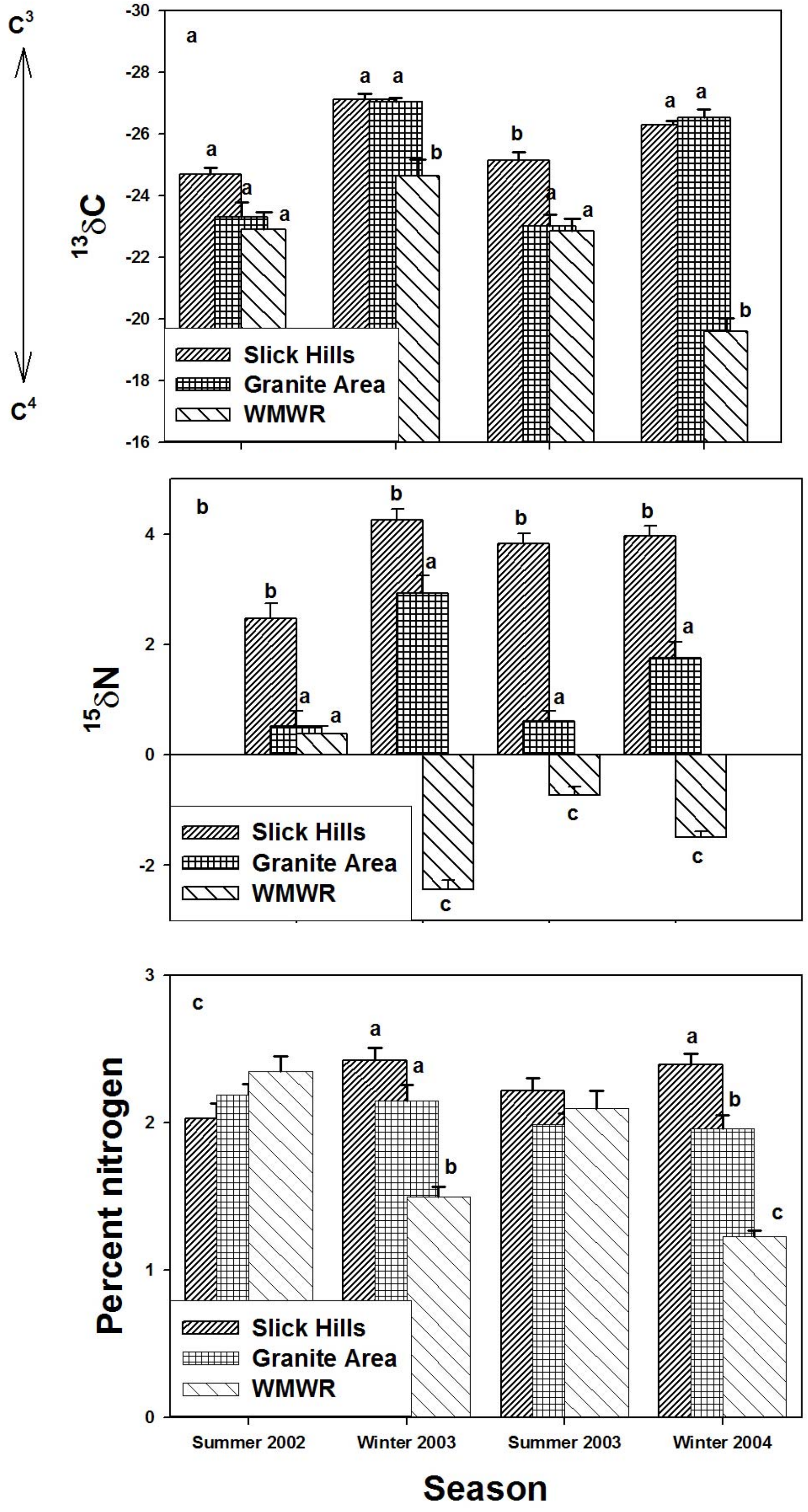
Figure 4. Mean percentage of C_3 and C_4 plants from microhistological analysis of feces of elk for a) summer and b) winter in the Slick Hills, Granite Area, and Wichita Mountains Wildlife Refuge (WMWR).

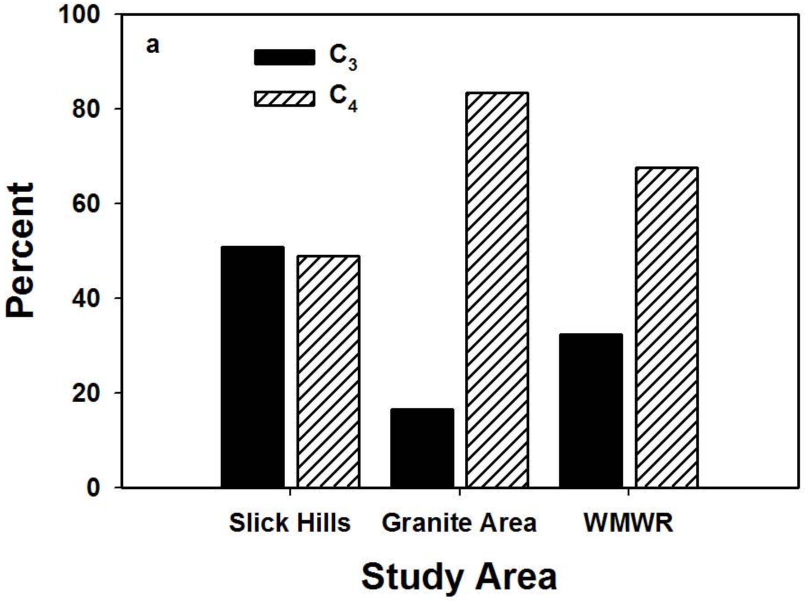
Figure 5. Principal component analyses by area determined from microhistological analysis of feces of elk in the Slick Hills, Granite Area, and Wichita Mountains Wildlife Refuge (WMWR) for a) components 1 and 2 (54% of variation

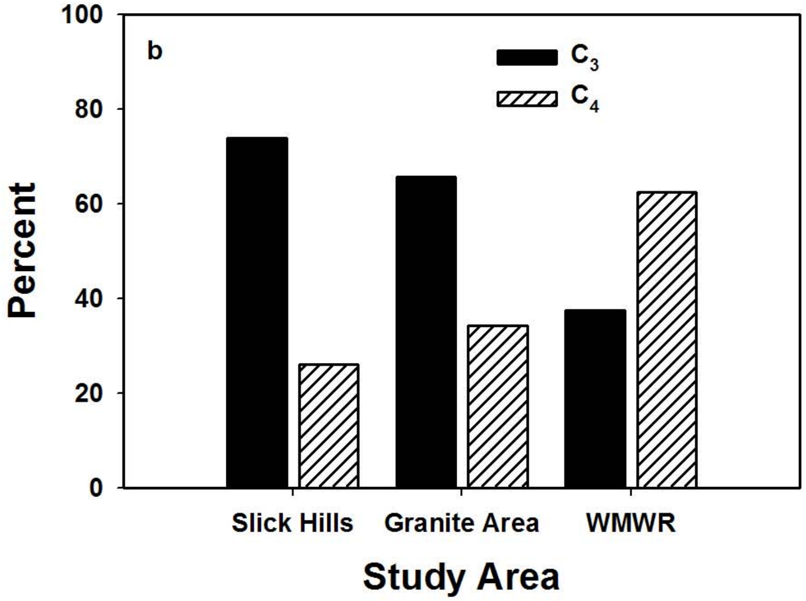
explained) and b) components 1 and 3 (44% of variation explained) during summer 2003 (May–August) and winter 2004 (January–March).

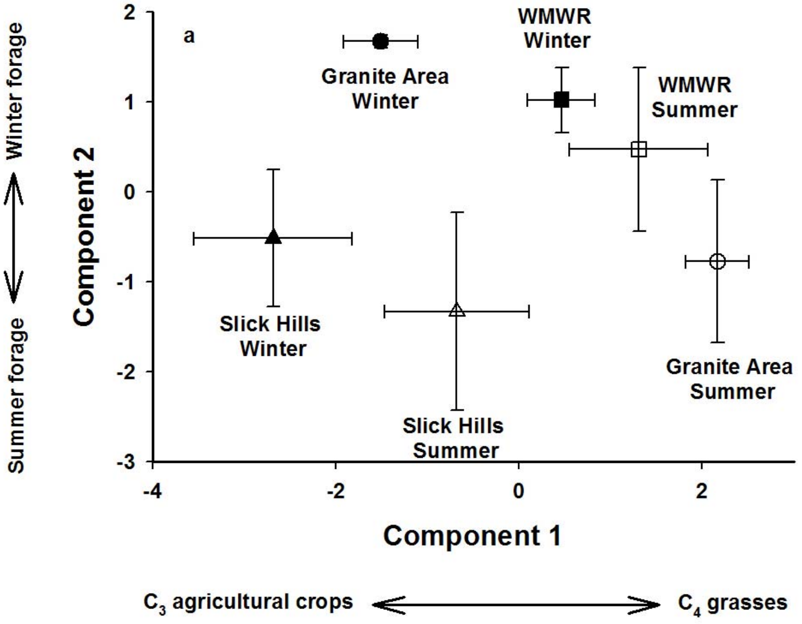

Granite Area
Slick Hills
Granite Area
WMWR
10
0
10 Kilometers
N
Roads
Grassland
Forest
Agriculture

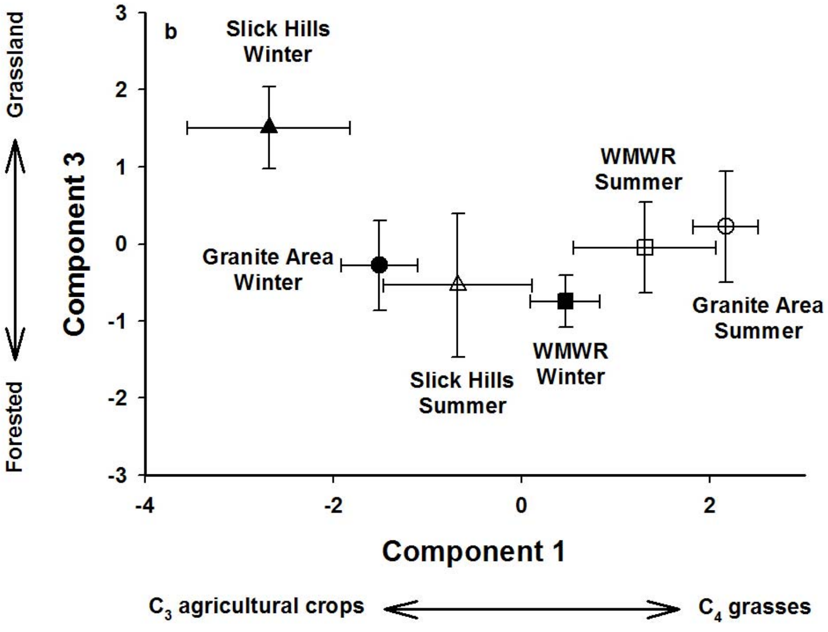

C4
C3
$^{13}\delta$C
a
-20
-22
-24
-26
-28
WMWR
Granite
Slick Hills
$^{15}\delta$N
b
6
4
2
0
-2
Slick Hills
Granite
WMWR
Percent Nitrogen
c
4
3
2
1
0
Slick Hills
Granite
WMWR
May
Jun.
Jul.
Aug.
Jan.
Feb.
Mar.
Month


C3
C4
13δC
-30
-28
-26
-24
-22
-20
-18
-16
a
a a a b a a
b a a
a a b
Slick Hills
Granite Area
WMWR
15δN
4
2
0
-2
b
b a a
b a c
b a c
b a c
Slick Hills
Granite Area
WMWR
Percent nitrogen
3
2
1
0
c
a a b
a b c
Slick Hills
Granite Area
WMWR
Summer 2002
Winter 2003
Summer 2003
Winter 2004
Season


a
C$_3$
C$_4$
Percent
0
20
40
60
80
100
Slick Hills
Granite Area
WMWR
Study Area


b
C$_3$
C$_4$
Percent
0
20
40
60
80
100
Slick Hills
Granite Area
WMWR
Study Area


a
Winter forage
Summer forage
Component 2
Component 1
C₃ agricultural crops
C₄ grasses
2
1
0
-1
-2
-3
-4
-2
0
2
Granite Area Winter
WMWR Winter
WMWR Summer
Slick Hills Winter
Slick Hills Summer
Granite Area Summer


b
Grassland
Forested
Component 3
Component 1
C₃ agricultural crops
C₄ grasses
3
2
1
0
-1
-2
-3
-4
-2
0
2
Slick Hills Winter
Granite Area Winter
Slick Hills Summer
WMWR Winter
WMWR Summer
Granite Area Summer

CHAPTER IV

ECOLOGY OF A COLONIZING HERBIVORE: INFERENCES FROM TISSUE CARBON AND NITROGEN ISOTOPES

Abstract: Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in tissues can be used to identify photosynthetic pathways (C_3 vs. C_4) of plants consumed by various taxa and to infer nutritional condition of consumers. We assessed $\delta^{13}C$ and $\delta^{15}N$ in free-ranging elk (*Cervus elaphus*) in southwestern Oklahoma occupying disparate habitats of mixed prairie-oak savannah and private-land agriculture in a C_4-dominated landscape. Muscle (index of short-term nutrition, ~ 1 mo.) and hoof (index of long-term nutrition, ~6 mos.) samples were collected from elk harvested on private land and the Wichita Mountains Wildlife Refuge (WMWR) in 2001–2004. Mean $\delta^{13}C$ in hoof (-20.83‰ ± 0.63 *SE*) of elk on private-land were lower than hoof $\delta^{13}C$ from elk in WMWR (-18.96 ± 0.61‰) indicating greater long-term consumption of C_3 plants by elk on private land. The $\delta^{15}N$ in hoof (4.84 ± 0.38‰) also were greater for elk on private land than hoof $\delta^{15}N$ for elk in WMWR (1.71 ± 0.36‰). An area-sex interaction occurred in elk with muscle $\delta^{13}C$ (P = 0.031) of private-land females ($\bar{x}$ = -23.18 ± 0.34‰) and males ($\bar{x}$ = -22.86 ± 0.35‰) being lower than those of females ($\bar{x}$ = -21.64 ± 0.32‰) and males ($\bar{x}$ = -20.55 ± 0.32‰) in WMWR. Mean $\delta^{15}N$ in muscle samples differed between elk on private land ($\bar{x}$ = 4.77 ± 0.34‰) and in WMWR ($\bar{x}$ = 1.41 ± 0.32‰, $P < 0.001$) but not between sexes for $\delta^{15}N$

(*P* = 0.191). Availability of protein-rich C_3 agriculture on a nearly annual basis in a C_4-dominated landscape resulted in greater nutrition for elk on private land than WMWR. My data suggests that tissue $\delta^{15}N$ increases as protein intake increases but the confounding effects of plant type and their $\delta^{15}N$ signatures need to be examined.

Key words: carbon isotopes, *Cervus elaphus*, hoof, isotopic fractionation, muscle, nitrogen isotopes, Rocky Mountain elk, sexual segregation

INTRODUCTION

Stable isotopes have been used to identify and compare spatial and temporal variation in diets across many taxonomic groups (Tieszen and Imbamba 1980, Webb et al. 1998, Hobson and Schell 1998, Rubenstein and Hobson 2004) and to investigate diets of African ungulates (Tieszen et al. 1989), populations of living and extinct American black bear (*Ursus americanus*; Hilderbrand et al. 1996), trophic-level studies of marine mammals (Abend and Smith 1997), and migration of avian species (Kelly 2000, Hobson 2005). The premise for using stable isotopes of carbon in ecological studies is that sources of dietary carbon have distinct, measurable carbon-isotope signatures ($\delta^{13}C$), and those signatures are incorporated into the consumer's tissues with minimal fractionation between diet and tissue (Tieszen et al. 1983, Kelly 2000). Along with $\delta^{13}C$, nitrogen-isotope signatures ($\delta^{15}N$) have been used to understand nutritional gain in herbivores from diets of plants following the C_3 or C_4 photosynthetic pathway (Sponheimer et al. 2003b, Barboza and Reynolds 2004, Sare et al. 2005). Previous research suggested that percent fecal nitrogen was a good indicator of dietary nitrogen in ungulates (Leslie and

Starkey 1985), but the influence of protein-precipitating compounds was difficult to overcome in seasonal comparisons (Homb and Breirem 1952, Hobbs 1987, Leslie and Starkey 1987). Microhistological analysis of gut contents or feces have been considered unreliable because differential digestibility can lead to over- or underestimation of forages consumed (Leslie et al. 1983, Osborn et al. 1997, Servello et al. 2005). Conclusions based on tissue $\delta^{13}C$ and $\delta^{15}N$ may address the confounding factors that make percent fecal nitrogen and microhistology questionable because dietary carbon and nitrogen is incorporated and measured in tissue and not predicted as with gut or fecal content indices.

The relationship between tissue isotopes and dietary $\delta^{13}C$ and $\delta^{15}N$ depends on what tissue is analyzed and the composition of the diet (DeNiro and Epstein 1981, Martinez del Rio and Wolf 2005). To understand isotopic turn-over rate, ecological studies of nutrition should rely on analysis of several tissue types (DeNiro and Epstein 1981, Dalerum and Angerbjorn 2005). Positive correlations of $\delta^{13}C$ and $\delta^{15}N$ among tissue types of varying metabolic activity have been documented in common cormorants (*Phalacrocorax carbo*; Mizutani et al. 1991), Arctic bowhead whale (*Balaena mysticetus*; Hobson and Schell 1998), and rats (Yoneyama et al. 1983). Tieszen et al. (1983) indicated that different tissues turn over carbon and nitrogen at different rates which was critical to making dietary inferences. Although variation exists among tissue types, more metabolically active tissues (i.e., liver, muscle) can reflect a dietary shift in a shorter time period than less metabolically active tissues (i.e., hair, bone, connective tissue; Tieszen et al. 1983, Sponheimer et al. 2003a, Sare et al. 2005). Tieszen et al. (1983) documented that a change in diets of gerbils (*Meriones unguienlatus*) from corn (C_4) to wheat (C_3)

caused tissue $\delta^{13}C$ to be similar to $\delta^{13}C$ of wheat. Metabolically active tissues, such as liver (6.4 days) and muscle (27.6 days), had shorter turnover rates of tissue $\delta^{13}C$ and detected changes in gerbil diets before less metabolically active tissues (i.e., hair = 47.5 days; Tieszen et al. 1983). Because larger ungulates have lower mass-specific metabolic rates than small mammals, diet-hair nitrogen isotope equilibration was about 24 weeks for captive ungulates (Sponheimer et al. 2003b). Isotope equilibration in hooves was longer because they are among the least metabolically active tissues (Miller et al. 1986) and reflected about a 1-year dietary history from proximal to distal end (Barnett 1994).

Correlation of $\delta^{13}C$ and $\delta^{15}N$ in bone collagen of African ungulates was negative for grazers which was related to an increase in C_3-browse consumption by grazers during the dry season (Thackeray et al. 1993, Thackeray et al. 1996). Decrease of $\delta^{15}N$ in bone collagen of grazers was associated with an increase in C_4-plants (i.e., greater $\delta^{13}C$) in their diets because of the lower nitrogen content of C_4 plants. Typically, $\delta^{15}N$ increases by about 3‰ (range: 1–6‰) from diet to tissue and variation depends on the anatomy of the organism and its ability to catabolize and route protein from dietary sources to various tissues (Yoneyama et al. 1983, Mizutani et al. 1991, Gannes et al. 1998). The $\delta^{15}N$ of several foregut- and hindgut-fermenting herbivores show strong support for Ambrose's "urinary nitrogen excretion" hypothesis for water-independent species (Ambrose and DeNiro 1986, Ambrose 1991, Sponheimer et al. 2003c). The "urinary nitrogen excretion" hypothesis posits that dietary protein levels influence tissue $\delta^{15}N$ values. It follows that urea recyclers that never excrete much nitrogen through physiological processes (i.e., urine, feces) cannot create tissues significantly enriched in ^{15}N (Ambrose 1991). Studies on ungulates suggested that tissue $\delta^{15}N$ increases as dietary protein increases with differential routing of endogenous or exogenous protein to various endpoints (Peltier and Barboza 2003, Sponheimer et al. 2003b, Sponheimer et al. 2003c, Barboza and Reynolds 2004).

Variation in tissue $\delta^{15}N$ has been linked to differences in plant $\delta^{15}N$ and the tissue-diet relationship that varies considerably due to physiologic and abiotic factors (Virginia and Delwiche 1982, Evans 2001). Plants can have $\delta^{15}N$ values ranging from -7 to 7‰ due to differential fractionation of nitrogen by N_2-fixing and non-N_2-fixing plants (Hoering 1955, Virginia and Delwiche 1982, Hobbie et al. 2000). Plants that fix N_2 typically have lower ^{15}N enrichment than non-N_2-fixing plants resulting in lower $\delta^{15}N$ than non-N_2-fixing plants (Hoering 1955, Peterson and Fry 1987). Cool, moist forest soils also have lower $\delta^{15}N$ than hot, dry open-grassland soils because of higher nitrogen fixation and differential fixation by plants from soil and atmospheric nitrogen sources (Heaton et al. 1966, DeNiro and Epstein 1981, Ambrose and DeNiro 1986, Ambrose 1991). Ambrose (1991) documented that tissue samples from ungulates collected in open habitats had higher mean $\delta^{15}N$ than samples from the same species collected in closed forested habitat. Thus, grazers foraging in a closed forest may have different $\delta^{15}N$ solely from foraging on the same grasses in different habitat types.

Sexual or age-related differences of diet have been proposed for ungulate species, but use of stable isotopes to assess such segregation has been limited (Kielland 2001, Post et al. 2001). The reproductive-strategy and sexual dimorphism–body size hypotheses are the 2 most accepted explanations of sexual segregation in ungulates (Main et al. 1996, Bowyer et al. 1996, Kie and Bowyer 1999). Appropriate data collection is often difficult to support a particular hypothesis (Bowyer et al. 1996, Gross 1998, Main

1998). Bowyer et al. (1996) suggested that researchers should consider scale of their study before concluding which hypothesis supported sexual segregation. Population density, habitat complexity, and social behavior should be understood before concluding what determines sexual segregation (Main et al. 1996, Kie and Bowyer 1999, Stewart et al. 2003). Assessments of $\delta^{13}C$ and $\delta^{15}N$ in biological samples may provide greater detail in understanding sexual and age-related segregation in free-ranging ungulates (Kielland 2001, Post et al. 2001).

Several factors must be considered before to making conclusions on diet using $\delta^{13}C$ and $\delta^{15}N$ (Gannes et al. 1997, Gannes et al. 1998, Dalerum and Angerbjorn 2005). Although research on captive animals has lead to increased knowledge of stable isotopes in ecological studies, more studies on free-ranging wildlife are needed (Gannes et al. 1998). Ecological studies of free-ranging ungulates should elucidate the primary factors that affect $\delta^{13}C$ and $\delta^{15}N$. These factors include: isotopic turn-over rate and fractionation, ecosystem functioning (i.e., closed forest, open grassland), sex, and age (Ambrose 1991, Kelly 2000, Jenkins et al. 2001, Kielland 2001, Post et al. 2001, Peltier and Barboza 2003). I used tissue $\delta^{13}C$ and $\delta^{15}N$ to assess dietary quality and infer nutrition of free-ranging Rocky Mountain elk (*Cervus elaphus*) occupying 3 disparate habitats in a C_4-dominated landscape using tissues of different isotopic turn-over rates that represented short-term (muscle) and long-term (hoof) diets. I also used these isotopes to evaluate sexual segregation of elk in disparate habitats.

STUDY AREA

The study was conducted on private lands and in the 23,879-ha Wichita Mountains Wildlife Refuge (WMWR) in southwestern Oklahoma, USA (34°47′–

34°57′N, 98°25′–98°50′W). The WMWR was situated along 4 sets of major vertical geologic joints composed of gabbro and granite, igneous material from the Cambrian (Buck 1964, Tyrl et al. 2002). The joints were believed to be important to the vegetational distribution in the area because they controlled rock decomposition and water availability (Buck 1964). The mountains of WMWR varied from gentle slopes with a minimum elevation of 390 m to the highest elevation of 750 m in the west. The mountainous terrain was bisected by wide grassy valleys with deep soils suitable for a variety of monocotyledonous and dicotyledonous vegetation; the U.S. Soil Conservation Service delineated 11 soil types within WMWR (Crockett 1964).

Mean annual temperature at WMWR was 15.7º C (60.3º F) in 1995–2003 with high and low mean temperatures of 29.1º C (84.3º F) in July–August and 3.0º C (37.4º F) in December–January (National Oceanic and Atmospheric Administration 2003). Mean annual total precipitation was 82.3 cm (32.4 inches) in 1995–2003 with a high of 99.3 cm (39.1 inches) in 1995 and a low of 53.1 cm (20.9 inches) in 2001. Precipitation was greatest in spring followed by a secondary peak in autumn and a typical growing season of 203 days (Buck 1964).

Forests were predominately post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), and eastern red cedar (*Juniperus virginiana*); sugar maple (*Acer saccharum*), pecan (*Carya illinoensis*), and American elm (*Ulmus americana*) occurred in riparian areas (Buck 1964). Dominant tallgrasses included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switch grass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*). Shortgrasses included buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and sideoats grama (*B. curtipendula*).

Elk, bison (*Bos bison*), white-tailed deer (*Odocoileus virginianus*), and longhorn cattle (*B. taurus*) were confined to WMWR by a 2.4-m ungulate-proof fence that was constructed in the 1960s. Feral pigs (*Sus scrofa*), black-tailed prairie dogs (*Cynomys ludovicianus*), burrowing owls (*Speotyto cunicularia*), Rio Grande turkey (*Meleagris gallopavo intermedia*), bobwhite quail (*Colinus virginianus*), and numerous resident and migratory raptors also occurred within WMWR. Elusive species such as bobcat (*Lynx rufus*), coyote (*Canis latrans*), and porcupine (*Erethizon dorsatum*) also were common.

Radiotelemetry documented 2 distinct elk herds were using different habitats on private land north of WMWR (Chapter II). Elk in the Granite Area, just north of the WMWR boundary, used habitats on private lands and WMWR seasonally, but elk in the Slick Hills, about 3–5 km north of the Granite Area, used only private lands. The Granite Area bordered WMWR to the north-northwest with igneous mountain peaks and slopes >25% extending from WMWR (Buck 1964). The Granite Area contained similar habitat types and wildlife species as WMWR, except free-ranging bison only occurred in WMWR. Unlike WMWR, a mixture of permanent and seasonal homes and primary (i.e., paved) and secondary (i.e., dirt, gravel) roads were dense and scattered throughout the Granite Area.

The Slick Hills were limestone-derived, rolling hills. The Slick Hills were used for cattle grazing and dominated by tallgrass and shortgrass species such as bluestems, gramas, and buffalograss with scattered mesquite (*Prosopis glandulosa*; Tyrl et al. 2002). Most bottomlands had ephemeral streams and forested corridors with pecan, western walnut (*Juglans rupestris*), and eastern redcedar. Residential homes and primary and secondary roads occurred throughout the Slick Hills. Unlike WMWR, the Granite

Area and Slick Hills had fields of wheat (*Triticum aestivum*), alfalfa (*Medicago sativa*), and sorghum (*Sorghum bicolor*) averaging 10 ha (range: <1–180 ha) and 18 ha (range: <1–251 ha), respectively, used for cropped forages, hunting plots, and cattle grazing.

METHODS

Muscle and hoof samples were collected from elk harvested on private land and WMWR in December 2001–2004. Sex and location of harvested elk were recorded, and muscle was collected from the sternum incision made during field dressing of the harvested animal. Muscle was extracted about 5 mm inside the incision to avoid contamination of sample with dirt, skin, hair, or dried muscle. The right hind toe of the right hind leg, when available, was removed at the hairline and rinsed thoroughly in water. Muscle and hoof were stored frozen prior to being oven-dried at 70°C to a constant weight. Dried hoof samples were cleaned with an alcohol pad then filed across the entire exterior from proximal to distal end producing a composite of the entire hoof. Dried muscle samples were ground by hand using a mortar and pestle. About 2 mg of muscle and hoof were loaded into 5 x 8-mm tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis with an isotope ratio mass spectrometer (IRMS) at the Stable Isotopes Facility, University of California, Davis.

Values of $\delta^{13}C$ and $\delta^{15}N$ were calculated where δ was the ratio of heavy to light isotopes in the sample compared with the δ in the Peedee Belemnite marine fossil limestone formation from South Carolina ($^{13}C/^{12}C = 0.01124$) and atmospheric nitrogen ($^{15}N/^{14}N = 0$) standards for $\delta^{13}C$ and $\delta^{15}N$ isotopes, respectively (Tieszen et al. 1983, Peterson and Fry 1987). Difference of δ for sample and standard $\delta^{13}C$ and $\delta^{15}N$ were subtracted from one, multiplied by 1,000, and expressed in per mil notation (‰).

Standard deviations for replicated internal standards were 0.08 for $\delta^{13}C$ and 0.22‰ $\delta^{15}N$. Because the heavy isotopes of carbon and nitrogen were most limited in organic matter, enrichment resulted in more positive values than those depleted in the heavy isotope (Schroeder and Ben-Ghedalia 1986, Sponheimer et al. 2003c).

Lipid content in muscle can be depleted in ^{13}C resulting in lower $\delta^{13}C$ for muscle samples that contain lipids (Abelson and Hoering 1961, Peterson and Fry 1987, Kelly 2000). To determine the influence of lipids in my samples, lipids were removed from dried, ground muscle using a Soxhlet apparatus (Bligh and Dyer 1959) at the Meat Science Research Laboratory, Department of Animal Sciences, Oklahoma State University, Stillwater. Levels of $\delta^{13}C$ and $\delta^{15}N$ were determined for 1–2 mg of lipid-free and non-lipid extracted muscle samples and compared with a paired Student's *t-test* (Zar 1996). There was no difference in mean $\delta^{13}C$ for lipid-free (-21.62 ± 0.36‰) and nonlipid-extracted (-21.95 ± 0.36‰) muscle samples ($t = 0.65$, $P = 0.522$). Mean $\delta^{15}N$ in lipid-free (3.67 ± 0.58‰) and nonlipid-extracted (3.71 ± 0.57‰) muscle samples also did not differ ($t = -0.04$, $P = 0.967$). Therefore, I concluded lipid content in muscle samples did not affect estimates of muscle $\delta^{13}C$ and $\delta^{15}N$.

Levels of $\delta^{13}C$ in hooves met the criteria for Levene's test for homogeneity of variance ($P = 0.807$), but variance of hoof $\delta^{15}N$ and muscle $\delta^{13}C$ and $\delta^{15}N$ were heterogeneous ($P < 0.001$). Therefore, data were analyzed in a mixed-model analysis of variance with a correction for the denominator degrees of freedom (Spilke et al. 2005). Main effects and interaction by area (i.e., private land and WMWR) and sex were analyzed independently in PROC MIXED using the Statistical Analyst Systems software (SAS; SAS Institute Inc. 2003). Tests of significance of fixed effects were determined using the Kenward-Roger approximation for the denominator degrees of freedom in the MODEL statement (DDFM = KR) in SAS based on the restricted maximum likelihood approach (Kenward and Roger 1997). The Kenward-Roger approximation was chosen over the Satterthwaite approximation because it was more appropriate for small samples and unbalanced designs (Kenward and Roger 1997, Spilke et al. 2004, Spilke et al. 2005). I treated area and sex as fixed effects with year and interactions of year with area and sex as random effects in the RANDOM statement. Least squares means were calculated and differences tested for significance with Tukey's test for multiple comparisons of all possible pairs of means in the LSMEANS statement (PDIFF CL ADJUST=TUKEY). To assess potential differences in $\delta^{13}C$ and $\delta^{15}N$ between the 2 elk herds on private land, an additional mixed-model analysis of variance was conducted using site (i.e., Granite Area, Slick Hills, WMWR) and sex as fixed effects and year as the random effect.

To enhance interpretation of results from tissue $\delta^{13}C$ and $\delta^{15}N$, various C_3 and C_4 plants were collected in the study area, air dried, ground in a Wiley mill through a 40-mm screen and analyzed in the IRMS. Alfalfa leaves, fruit, and new stem growth were dried and ground in a mixture because elk bite size likely prevented selective removal of individual plant parts; acorn sheath and meat also were prepared as composite samples. About 5 cm of the distal end of other plants were harvested and dried and did not include any part of the root system; wheat grain was ground and sampled without leaves or stems. Correlation analyses between tissue $\delta^{13}C$ and $\delta^{15}N$ and plant $\delta^{13}C$ and $\delta^{15}N$ were determined using PROC CORR (Cody and Smith 1997, SAS Institute Inc. 2003). A priori significance was set at $P \leq 0.05$ for all analysis.

RESULTS

There were overall negative correlations between $\delta^{13}C$ and $\delta^{15}N$ for both hoof and muscle (Fig. 1a). There was a negative correlation between hoof $\delta^{13}C$ and $\delta^{15}N$ (Fig. 1b) and muscle $\delta^{13}C$ and $\delta^{15}N$ (Fig. 1c). There was no correlation between hoof $\delta^{13}C$ and muscle $\delta^{13}C$ (Fig. 2a), but there was a positive correlation between hoof $\delta^{15}N$ and muscle $\delta^{15}N$ (Fig. 2b) for elk on private land. There was a positive correlation between hoof $\delta^{13}C$ and muscle $\delta^{13}C$ (Fig. 2a) and hoof $\delta^{15}N$ and muscle $\delta^{15}N$ (Fig. 2b) for elk in WMWR.

No sex-area interaction occurred for hoof $\delta^{13}C$ ($P = 0.123$) and hoof $\delta^{15}N$ ($P = 0.194$; Table 1). Mean $\delta^{13}C$ in hoof samples were lower ($P = 0.033$; Fig. 3a) for elk on private land ($\bar{x} = -20.83‰ \pm 0.626$ *SE*) than in WMWR ($\bar{x} = -18.96 \pm 0.606‰$). Mean $\delta^{15}N$ in hoof samples were higher ($P = 0.001$; Fig. 3b) for elk on private land ($\bar{x} = 4.84 \pm 0.382‰$) than in WMWR ($\bar{x} = 1.71 \pm 0.361‰$). An area-sex interaction occurred for muscle $\delta^{13}C$ ($P = 0.031$; Fig. 4a) but not muscle $\delta^{15}N$ ($P = 0.735$; Table 1; Fig. 4a). Mean $\delta^{13}C$ in muscle samples of elk on private land did not differ between females and males but were lower than in WMWR females and males (Table 1); $\delta^{13}C$ in muscle samples differed between sexes in WMWR. Mean $\delta^{15}N$ in muscle samples differed between elk on private land ($\bar{x} = 4.77 \pm 0.339‰$) and in WMWR ($\bar{x} = 1.41 \pm 0.319‰$, $P < 0.0001$; Fig. 4b) but not between sexes for $\delta^{15}N$ ($P = 0.191$; Table 1).

No sex-site interaction occurred for hoof $\delta^{13}C$ ($P = 0.305$; Table 1), but hoof $\delta^{13}C$ differed among sites ($P = 0.006$; Fig. 5a). Hoof $\delta^{13}C$ for elk in the Slick Hills were more negative than in WMWR ($P = 0.006$), but elk in the Granite Area did not differ from those in the Slick Hills or WMWR. A sex-site interaction occurred for hoof $\delta^{15}N$ (P = 0.017) with greater $\delta^{15}N$ for both sexes of elk in the Granite Area and Slick Hills than in WMWR (Table 1; Fig. 5b). No sex-site interaction occurred for muscle $\delta^{13}C$ ($P = 0.188$) and muscle $\delta^{15}N$ ($P = 0.139$). Muscle $\delta^{13}C$ differed by site ($P < 0.001$; Fig. 6a) and sex ($P < 0.002$; Table 1). Muscle $\delta^{13}C$ for elk in the Granite Area ($P < 0.006$) and Slick Hills ($P < 0.001$) were more negative than in WMWR, but they did not differ from each other ($P < 0.367$). Muscle $\delta^{13}C$ ($P < 0.002$) were lower for female elk than male elk (Table 1); muscle $\delta^{15}N$ ($P < 0.0001$; Fig. 6b) differed by site for all possible comparisons (Fig. 6b), but not sex ($P = 0.186$).

Mean $\delta^{13}C$ values ranged from -30.00 to -22.69‰ in C_3 plants and -13.29 to -13.15‰ in C_4 plants, and mean $\delta^{15}N$ values ranged from -2.11 to 1.96‰ in C_3 plants and -5.18 to -2.43‰ in C_4 plants (Table 2). There was a negative correlation between percent nitrogen and $\delta^{13}C$ of plants (Fig. 7a) and a positive correlation between percent nitrogen and $\delta^{15}N$ of plants (Fig. 7b).

DISCUSSION

Both $\delta^{13}C$ and $\delta^{15}N$ in tissues collected in mid-December indicated that diets of elk within 1–2 (i.e., muscle) and >6 (i.e., hoof) months of harvest differed consistently between private land and WMWR. Tissues with different metabolic rates have been used as an indicator of temporal variation in diet because more metabolically active tissue (i.e., liver, blood, muscle) identifies more recent diet than less metabolically active integument (i.e., hoof, hair, skin; DeNiro and Epstein 1978, Tieszen et al. 1983). Correlations between $\delta^{13}C$ and $\delta^{15}N$ (Fig. 1a,b) suggested that hoof and muscle were less enriched in the heavier isotope of carbon (i.e., ^{13}C) and more enriched in the heavier isotope of nitrogen (i.e., ^{15}N) for elk on private land than in WMWR. Less enrichment of ^{13}C indicated that a greater proportion of C_3 plants were consumed by elk on private land than WMWR. Greater consumption of C_3 plants by elk on private lands was more apparent in muscle $\delta^{13}C$ (e.g., short-term diet) suggesting consumption of primarily C_3 plants occurred during late autumn–early winter compared with elk in WMWR. Consumption of winter wheat (i.e., C_3 plant) was indicated by the lower $\delta^{13}C$ in elk tissues on private land compared with WMWR, which was supported by evaluation of home range and habitat use (Chapters II and III).

Higher hoof $\delta^{13}C$ (e.g., long-term diet) on private land and WMWR compared to muscle $\delta^{13}C$ suggested that diets varied throughout the year and contributed to tissue $\delta^{13}C$ signatures. Isotopic enrichment between tissue types was different for elk on private land than in WMWR as reflected by correlations of hoof and muscle $\delta^{13}C$ (Fig. 2a) and $\delta^{15}N$ (Fig. 2b). The positive relationship between tissue $\delta^{13}C$ and $\delta^{15}N$ for elk in WMWR showed that muscle $\delta^{13}C$ and $\delta^{15}N$ increased with hoof $\delta^{13}C$ and $\delta^{15}N$. However, there was no relationship between hoof and muscle $\delta^{13}C$ in elk on private land suggesting that dietary components were contributing differently to elk tissues on private land than WMWR. Diet quality (i.e., protein versus carbohydrate) has been found to influence tissue isotope values because nutrients from endogenous (i.e., tissue catabolism) and exogenous (i.e., dietary components) sources are routed differently depending on the physiological needs of the animal (MacAvoy et al. 2005, Parker et al. 2005, Martinez del Rio and Wolf 2005).

Studies on free-ranging African ungulates suggested that water and nutritional stress and variability in $\delta^{15}N$ of plants consumed (-20–+45‰) should be considered before interpretations of $\delta^{15}N$ in ungulate studies (Ambrose and DeNiro 1986, Sealy et al. 1987, Kelly 2000). Ambrose's "urinary-nitrogen-excretion" hypothesis, as it pertains to water stress, stated that urine tends to be depleted in ^{15}N and animals that lose more urinary nitrogen should lose relatively more ^{14}N (Ambrose 1991, Sponheimer et al. 2003c). If the majority of nitrogen is not excreted as urea (e.g., excreted as ^{15}N-enriched feces), herbivores that recycle ^{15}N-depleted urea should have lower tissue $\delta^{15}N$ values relative to the diet and to non-recyclers (Ambrose 1991). This typically occurs in animals that are in a state of isotopic disequilibrium or negative nitrogen balance (i.e., during growth, pregnancy, dietary change, negative nitrogen balance, thermal stress), which likely describes free-ranging elk because of seasonal variation in nitrogen content of forages consumed (Mattson 1980, Nelson and Leege 1982, Leslie et al. 1984). Based on this hypothesis, animals that have excreta depleted in ^{15}N (i.e., non-urea recyclers) must have tissues enriched in ^{15}N (Sponheimer et al. 2003c). Water stress would be expected to have a similar influence on tissue $\delta^{15}N$ for elk on private land and WMWR and would not explain the observed difference in tissue $\delta^{15}N$ between private land and WMWR because both areas occur in a small region (about 60,000 ha) with similar climatic variability (National Oceanic and Atmospheric Administration 2003).

Nutritional stress results in trophic-level fractionation and enrichment from recycling of nitrogen in urea, bacterial consumption of nitrogen, and diffusion through the rumen wall that may lead to differences in tissue $\delta^{15}N$ (Sealy et al. 1987, Ambrose 1991). Sealy et al. (1987) suggested that ungulates on a low-protein diet would be expected to recycle ^{15}N-depleted urea and, thus, have higher tissue $\delta^{15}N$ due to extensive fractionation and enrichment of $\delta^{15}N$ by microorganisms than ungulates on a high-protein diet. However, this “nutritional stress” hypothesis was not supported for several captive, foregut-fermenting herbivores fed known diets of varying protein quality (Sponheimer et al. 2003b, but see Parker et al. 2005). Sponheimer et al. (2003b) documented that hair $\delta^{15}N$ from herbivores on high-protein diets were higher than hair $\delta^{15}N$ from herbivores on low-protein diets. However, study animals in positive nitrogen balance and bermudagrass (*Cynodon dactylon*) diets above crude protein (CP) for maintenance (Asleson et al. 1996) may have prevented nitrogen recycling.

Population density directly affects forage availability and would influence nutritional stress for elk on private land and WMWR. In 2001, elk densities of 0.31, 0.62, and 3.0 elk/km^2 in the Granite Area, Slick Hills, and WMWR, respectively (Chapter II, S. Waldstein, WMWR Manager), were well below densities considered low in other studies (Hobbs et al. 1996, Stewart et al. 2005). If population density resulted in private-land elk being nutritionally stressed, Sealy’s “nutritional stress” hypothesis could explain the higher tissue $\delta^{15}N$ for private-land elk compared with those in WMWR. However, the low population densities on private land and high CP of winter wheat (25% CP or 4% N, Fig. 7a) and alfalfa (30% CP) in elk diets suggested that protein requirements could be met during seasons of low natural forage availability thus limiting urea recycling. Elk in WMWR at higher densities without winter wheat and alfalfa would be expected to have higher tissue $\delta^{15}N$ than elk from private land if nitrogen recycling occurred, but that was not the case.

Nitrogen isotopes in animal tissues are influenced by plant species consumed, and $\delta^{15}N$ of plants differ because those that fix atmospheric nitrogen ($\delta^{15}N = 0‰$) have lower $\delta^{15}N$ than non-N_2-fixing plants (Virginia and Delwiche 1982, Ambrose and DeNiro 1986, Hobbie et al. 2000). With the typical 3‰ enrichment of tissue over diet, consumption of a variety of plants such as winter wheat (mean $\delta^{15}N$ = 1.96‰), alfalfa (mean $\delta^{15}N$ = -0.22‰), and C_3 grass (mean $\delta^{15}N$ = 0.45‰) by elk on private-land makes interpretations difficult because of the variability in plant $\delta^{15}N$ consumed. Therefore, more detailed analysis on the different landscapes that elk occupied on private land (i.e., Granite Area and Slick Hills) was conducted (Figs. 5, 6). Elk in both the Granite Area and Slick Hills had higher hoof $\delta^{15}N$ than WMWR. Elk in the Granite Area occupied similar forested habitat within a mosaic of grasslands as elk in WMWR. Ambrose (1991) found that species foraging in open grasslands had higher $\delta^{15}N$ than the same species foraging in a closed forest. Assuming both populations used open grasslands and closed forests seasonally in similar fashion, I expected no difference in tissue $\delta^{15}N$ between elk in the Granite Area and WMWR, but that was not the case. Elk in the Granite Area had higher $\delta^{15}N$ for both long- and short-term dietary indices suggesting additional dietary components, unrelated to $\delta^{15}N$ of forages consumed in a closed, forested landscape, influenced their tissue $\delta^{15}N$. Elk in the Slick Hills should have had higher $\delta^{15}N$ than elk in the Granite Area and WMWR (i.e., open grassland vs. closed forest) if foraging in an open grassland was solely responsible for determining $\delta^{15}N$ in elk tissues (Ambrose 1991). Higher tissue $\delta^{15}N$ for elk in both areas of private land compared with WMWR was either from higher nitrogen content of agricultural crops or variability in $\delta^{15}N$ of similar plant species consumed in contrasting habitats, but fractionation comparisons would be required to decipher between the two (Table 2).

Data for muscle and hoof $\delta^{15}N$ for elk on private-land supports Sponheimer's "state of disequilibrium" hypothesis (i.e., animals in negative nitrogen balance) suggesting that herbivores consuming high-protein diets should have higher diet-tissue fractionations than the same animals (i.e., elk in WMWR) consuming low-protein diets and that continued consumption of high protein diets would cause continued accumulation of ^{15}N over time (Ponsard and Averbuch 1999, Sponheimer et al. 2003b, Sponheimer et al. 2003c). More importantly, regardless of the amount of fractionation that may occur in specific parts of the ruminant digestive system, mass balance suggests that if nitrogen is not entering the system (i.e., through dietary nitrogen intake), it can not leave or be incorporated into a consumer's tissues (Ambrose 1991, Ponsard and Averbuch 1999, Martinez del Rio and Wolf 2005). Ponsard and Averbuch (1999) suggested that a relatively constant intake of high or low dietary $\delta^{15}N$ would result in increased or decreased levels, respectively, of whole animal $\delta^{15}N$ composition over time. Continued consumption of ^{15}N-depleted forages by elk in WMWR may be resulting in decreasing tissue $\delta^{15}N$, whereas elk consuming diets high in $\delta^{15}N$ on private lands continually incorporate the heavy isotope (^{15}N) into tissue.

To further elaborate on the "state of disequilibrium" hypothesis, an understanding of the relationship of tissue $\delta^{13}C$ and $\delta^{15}N$ as it relates to nutrition would be beneficial. Free-ranging ungulates consume forages that vary seasonally in CP and dry-matter digestibility resulting in intra- and inter-seasonal variation in nitrogen balance (Nelson and Leege 1982, Post et al. 2001). For example, male bison that shifted to a diet of C_3 grass had increased percent fecal nitrogen (Post et al. 2001), suggesting nitrogen balance may have been achieved only after the shift to C_3 grass. Most C_3 plants have a lower cell-wall content, higher dry-matter digestibility, and higher nutritional value than C_4 plants (Wilson and Hacker 1987, Wilson and Hattersley 1989). For plants in my study area, $\delta^{13}C$ increased as percent nitrogen decreased (Fig. 7), supporting past research that C_3 plants provided more dietary nitrogen than C_4 plants. There was a strong negative relationship between $\delta^{13}C$ and $\delta^{15}N$ in hoof ($r = -0.615$) and muscle ($r = -0.675$) suggesting an inverse relationship between $\delta^{13}C$ and $\delta^{15}N$ regardless of tissue analyzed. It has been hypothesized that tissue $\delta^{15}N$ primarily depends on $\delta^{15}N$ in forage consumed (Ambrose 1991), and my data show that for a mixed feeder, such as elk, tissue $\delta^{15}N$ increased with a greater proportion of C_3 plants in the diet (i.e., a decrease in $\delta^{13}C$).

Use of $\delta^{13}C$ and $\delta^{15}N$ as indices of ungulate nutritional ecology should consider influences of sex and age on tissue $\delta^{13}C$ and $\delta^{15}N$. Effects of age on tissue $\delta^{13}C$ and $\delta^{15}N$ were minimal in previous research (Minagawa and Wada 1984, Ponsard and Averbuch 1999, Jenkins et al. 2001) and in my study because tissue samples were collected primarily from adult elk (>95% were ≥2 years old). In contrast, tissue $\delta^{13}C$ and $\delta^{15}N$ of elk showed sexual differences depending on the habitat occupied and supported both the “reproductive-strategy” and “sexual dimorphism-body size” hypotheses (Barboza and Bowyer 2000, Post et al. 2001, Bowyer et al. 2002). Several authors have encouraged consideration of factors such as population density, spatial scale, and forage distribution before assessing sexual segregation in ungulates (Gross 1998, Bowyer et al. 2002, Stewart et al. 2003). By assessing sexual segregation in elk on private land and WMWR, where elk occupied several different landscapes with alternate forages available (Chapter III), different effects on sexual segregation were evaluated.

There were no sexual differences for hoof $\delta^{13}C$ or $\delta^{15}N$ suggesting long-term diets were similar between sexes by area. In contrast, muscle $\delta^{13}C$ indicated sexual differences only in WMWR. Gross (1998) stated that the “sexual dimorphism–body size” hypothesis would only predict sexual segregation during limited forage availability. The primary difference between the 2 landscapes was the large quantity of C_3 forage (i.e., winter wheat) available to elk primarily during forage-limited autumn and winter on private land but not WMWR. Main (1998) stated that one of the few instances that high-quality forages would be more abundant than poor-quality forages would be in some agricultural settings. My short-term $\delta^{13}C$ data support the "sexual dimorphism–body size" hypothesis as reflected in sexual segregation by diet in elk from the forage-limited WMWR but not by diet of elk on forage-abundant private lands.

Interestingly, our short-term data also support the "reproductive-strategy" hypothesis (Main et al. 1996): when vast amounts of high-quality forage (i.e., winter wheat) are available, segregation should not occur. Muscle $\delta^{13}C$ of female elk did not differ from muscle $\delta^{13}C$ of male elk on private land where elk used agricultural crops during forage-limited winter months (Chapter II). However, in a landscape with limited availability of high-quality forage (i.e., WMWR), male elk should segregate (Gross 1998, Main 1998) presumably to increase intake rate of lower-quality forage than females. This rationale is similar to the "gastrocentric" hypothesis (Barboza and Bowyer 2000) that predicts males consume abundant forages high in fiber because greater retention would result in greater use of fiber for energy compared to less fibrous forages. In the C_4-dominated landscape of the Southern Great Plains (Teeri and Stowe 1976), lower-quality forage available in sufficient quantity to fill the gut capacity of male elk would likely be C_4 grasses; large enough quantities of native C_3 forages (i.e., cool-season grasses, browse) would be unlikely with the presence of female elk, bison, longhorn cattle, and white-tailed deer in WMWR. Consumption lower-quality forage appears to be supported by male elk in WMWR having the highest muscle $\delta^{13}C$ (-20.55‰), reflective of a greater C_4 diet, compared with females and males from private-land and females from WMWR. Support for the "reproductive-strategy" hypothesis becomes more apparent when we consider that there were no sexual differences in muscle $\delta^{15}N$ on private lands with a high-quality agricultural landscape or in WMWR in the low-quality grasslands.

Limited data exists on the use of tissue $\delta^{15}N$ to understand nutrition of free-ranging ungulates in North America (Bada et al. 1990, Barnett 1994, Kielland 2001, Ben-David et al. 2001). My study area provided 3 disparate habitats to investigate the influence of different dietary sources on tissue $\delta^{13}C$ and $\delta^{15}N$ of free-ranging elk. We documented considerable differences in tissue $\delta^{13}C$ and $\delta^{15}N$ resulting from seasonal availability and use of C_3 agricultural crops by elk on private land. Although my results show a positive correlation between tissue $\delta^{15}N$ and dietary nitrogen, confounding effects of plant type and their $\delta^{15}N$ signatures need to be examined (Sponheimer et al. 2003b, Sponheimer et al. 2003c). Research on captive animals is beneficial to the advancement of isotopic ecology, however, research on free-ranging species can provide valuable information on the influence of population demographics, climatic variability, and foraging habitat on tissue isotopes that may not be possible in captive animals. Many factors influence stable isotopes, and researchers should investigate several tissue types, >1 stable isotope, and variables that may influence results (i.e., climatic variability, foraging habitat, sex) prior to interpretations of stable isotopes in free-ranging species.

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Table 1. Mean (±SE) hoof and muscle $\delta^{13}C$ and $\delta^{15}N$ for female and male elk on private land (Private), Wichita Mountains Wildlife Refuge (WMWR) and 2 areas of private land (Granite Area and Slick Hills), 2001–2004.

	Hoof $\delta^{13}C$	Hoof $\delta^{15}N$	Muscle $\delta^{13}C$	Muscle $\delta^{15}N$
Private				
Female	-20.82 (0.66)	4.18 (0.47)	-23.18 (0.34)	4.44 (0.43)
Male	-20.85 (0.68)	5.50 (0.49)	-22.86 (0.35)	5.11 (0.45)
WMWR				
Female	-19.38 (0.63)	1.63 (0.45)	-21.64 (0.32)	1.21 (0.41)
Male	-18.54 (0.64)	1.80 (0.45)	-20.55 (0.32)	1.61 (0.41)
Granite Area				
Female	-20.53 (0.62)	3.90 (0.42)	-22.98 (0.34)	4.05 (0.37)
Male	-19.82 (0.69)	3.58 (0.46)	-22.56 (0.38)	3.63 (0.42)
Slick Hills				
Female	-21.71 (0.76)	5.21 (0.52)	-23.67 (0.45)	5.56 (0.49)
Male	-21.99 (0.71)	7.13 (0.48)	-23.26 (0.42)	6.54 (0.45)

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Table 2. Mean (±SE) $\delta^{13}C$ and $\delta^{15}N$ for plants consumed by elk in southwestern Oklahoma.

Plant	Month	Pathway[a]	n[b]	Classification[c]	$\delta^{13}C$	$\delta^{15}N$
Acorn	September	C_3	10	Woody	-23.32 (0.14)	-2.11 (0.17)
Alfalfa	July	C_3	5	Legume	-27.08 (0.10)	-0.22 (0.10)
Big bluestem	January	C_4	5	Graminoid	-13.15 (0.05)	-2.43 (0.32)
Broomweed	January	C_3	5	Forb	-26.17 (0.03)	-1.76 (0.10)
C_3 grass	December	C_3	5	Graminoid	-29.99 (0.28)	0.45 (0.15)
Grama spp.	January	C_4	5	Graminoid	-13.19 (0.03)	-5.18 (0.33)
Wheat grain	June	C_3	5	Graminoid	-24.27 (0.05)	0.42 (0.33)
Winter wheat	January	C_3	10	Graminoid	-24.90 (0.11)	1.96 (0.05)

[a] C_3 or C_4 photosynthetic pathway

[b] n = number of replicates analyzed to derive mean $\delta^{13}C$ and $\delta^{15}N$

[c] Classification in 4 common growth form categories (Tyrl et al. 2002)

Figure 1. Correlations of a) all hoof and muscle $\delta^{13}C$ and $\delta^{15}N$, and b) hoof, and c) muscle $\delta^{13}C$ and $\delta^{15}N$ collected from elk on private land (Private) and Wichita Mountains Wildlife Refuge (WMWR) in southwestern Oklahoma, 2001–2004.

Figure 2. Correlations of hoof and muscle for a) $\delta^{13}C$ and b) $\delta^{15}N$ collected from elk on private land (Private) and Wichita Mountains Wildlife Refuge (WMWR) in southwestern Oklahoma, 2001–2004.

Figure 3. Means (±SE) of a) $\delta^{13}C$ and b) $\delta^{15}N$ in hoof samples collected from elk on private land (Private) and Wichita Mountains Wildlife Refuge (WMWR), 2001–2004. Numbers at standard error bars represent sample size. The arrow along the y-axis in (a) reflects the expected trend in $\delta^{13}C$ with a change in the proportion of C_3 and C_4 plants in the diet.

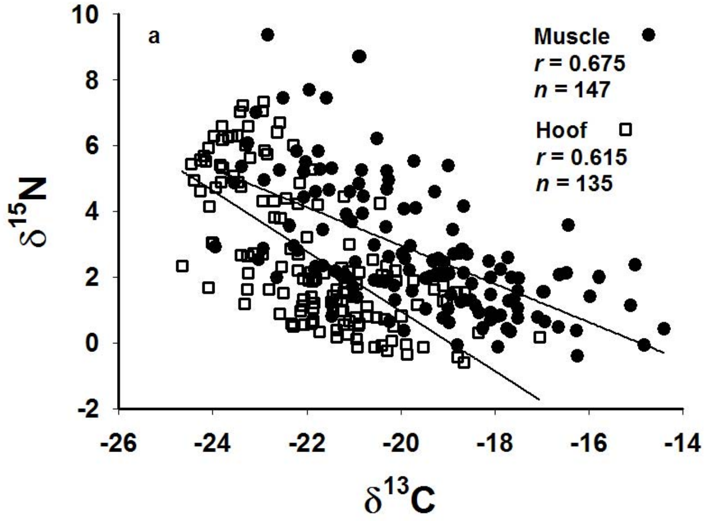
Figure 4. Means (±SE) of a) $\delta^{13}C$ and b) $\delta^{15}N$ in muscle samples collected from elk on private land (Private) and Wichita Mountains Wildlife Refuge (WMWR), 2001–2004. Numbers at standard error bars represent sample size. The arrow along the y-axis in (a) reflects the expected trend in $\delta^{13}C$ with a change in the proportion of C_3 and C_4 plants in the diet.

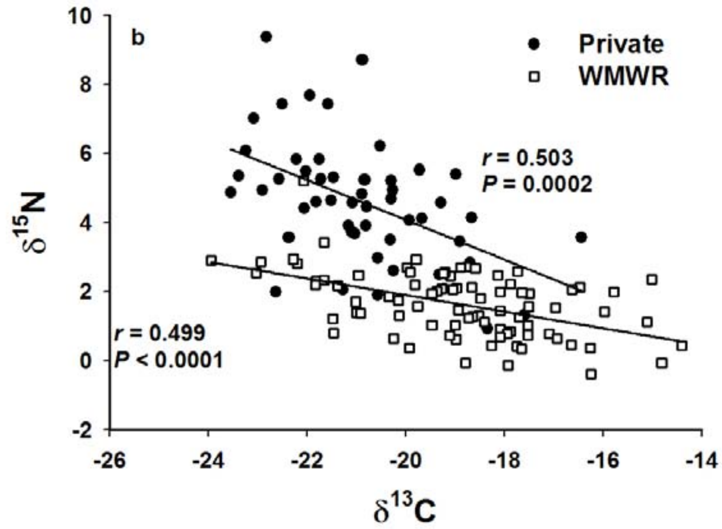
Figure 5. Means (± SE) of a) $\delta^{13}C$ and b) $\delta^{15}N$ in hoof samples collected from elk on private land (Granite Area and Slick Hills) and Wichita Mountains Wildlife Refuge (WMWR), 2001–2004. Numbers at standard error bars represent sample

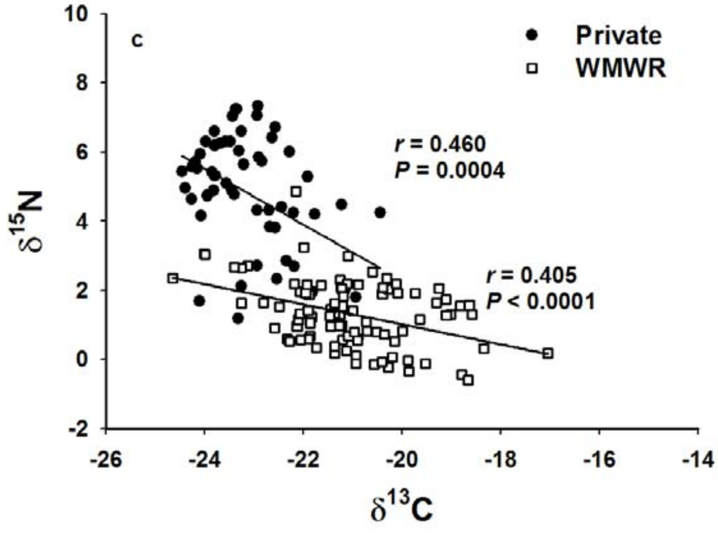
size. The arrow along the y-axis in (a) reflects the expected trend in $\delta^{13}C$ with a change in the proportion of C_3 and C_4 plants in the diet.

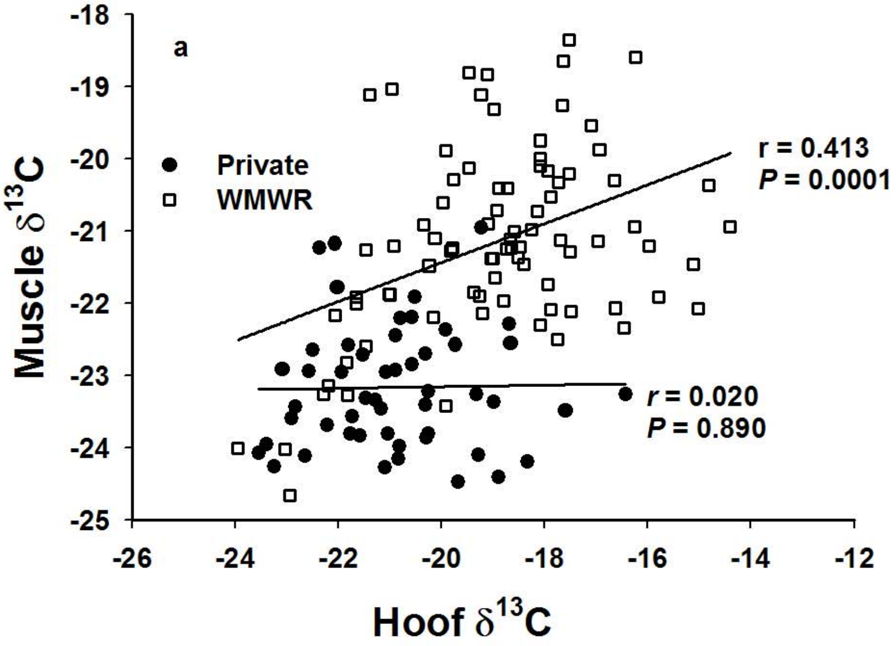
Figure 6. Means (± SE) of a) $\delta^{13}C$ and b) $\delta^{15}N$ in muscle samples collected from elk on private land (Granite Area and Slick Hills) and Wichita Mountains Wildlife Refuge (WMWR), 2001–2004. Numbers at standard error bars represent sample size. The arrow along the y-axis in (a) reflects the expected trend in $\delta^{13}C$ with a change in the proportion of C_3 and C_4 plants in the diet.

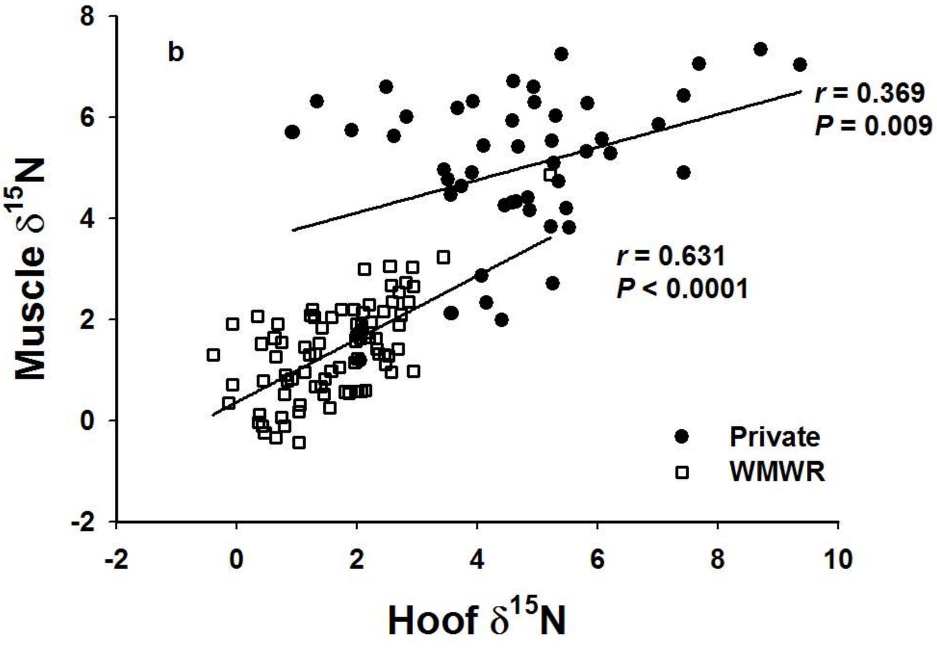
Figure 7. Correlations for a) $\delta^{13}C$ and percent nitrogen (%N) and b) $\delta^{15}N$ and percent nitrogen (%N) of plants collected in southwestern Oklahoma, 2001–2004.

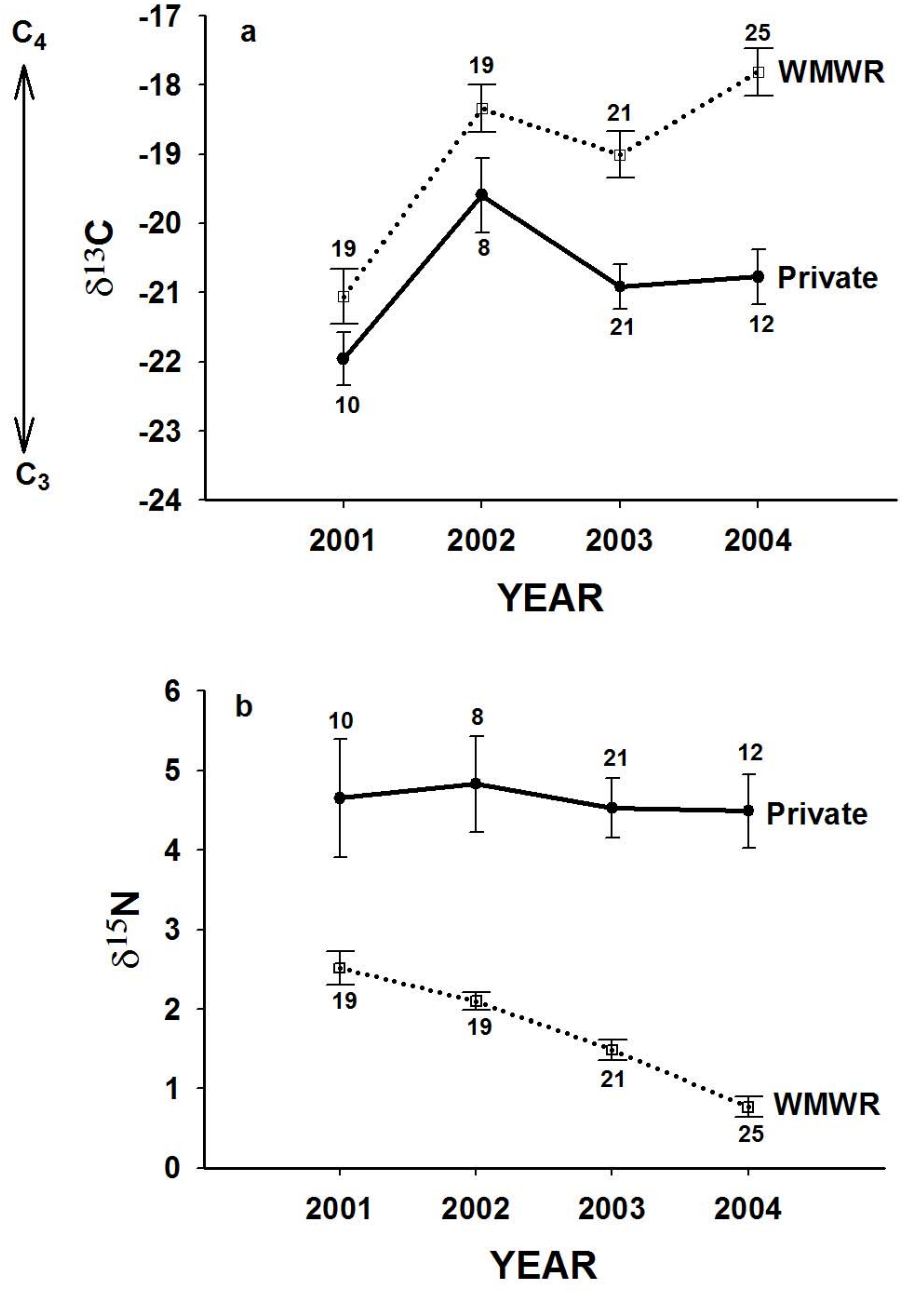

a
Muscle ●
r = 0.675
n = 147
Hoof □
r = 0.615
n = 135
δ^{15}N
δ^{13}C
10
8
6
4
2
0
-2
-26
-24
-22
-20
-18
-16
-14

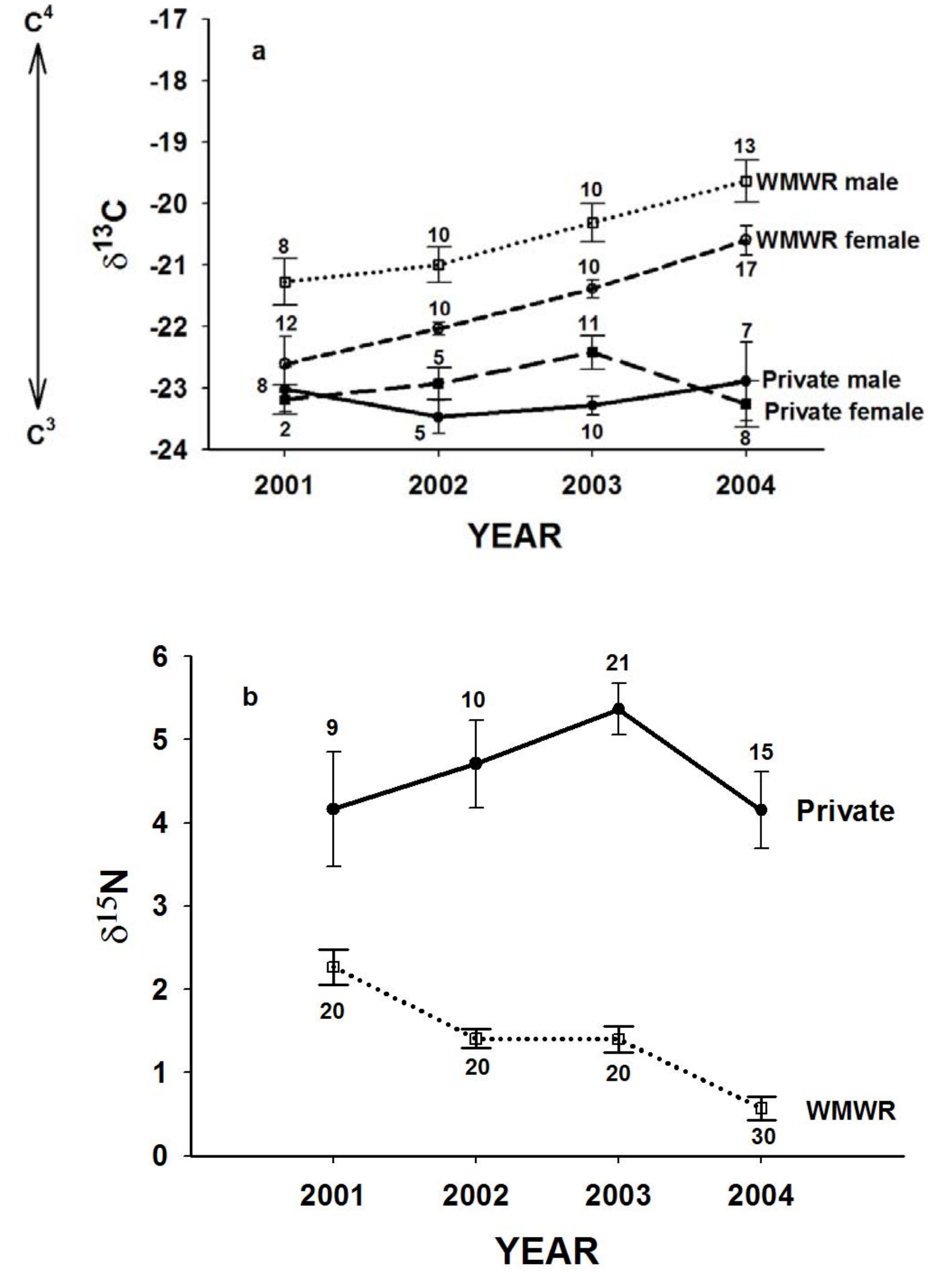

b
● Private
□ WMWR
r = 0.503
P = 0.0002
r = 0.499
P < 0.0001
δ^{15}N
δ^{13}C
10
8
6
4
2
0
-2
-26
-24
-22
-20
-18
-16
-14

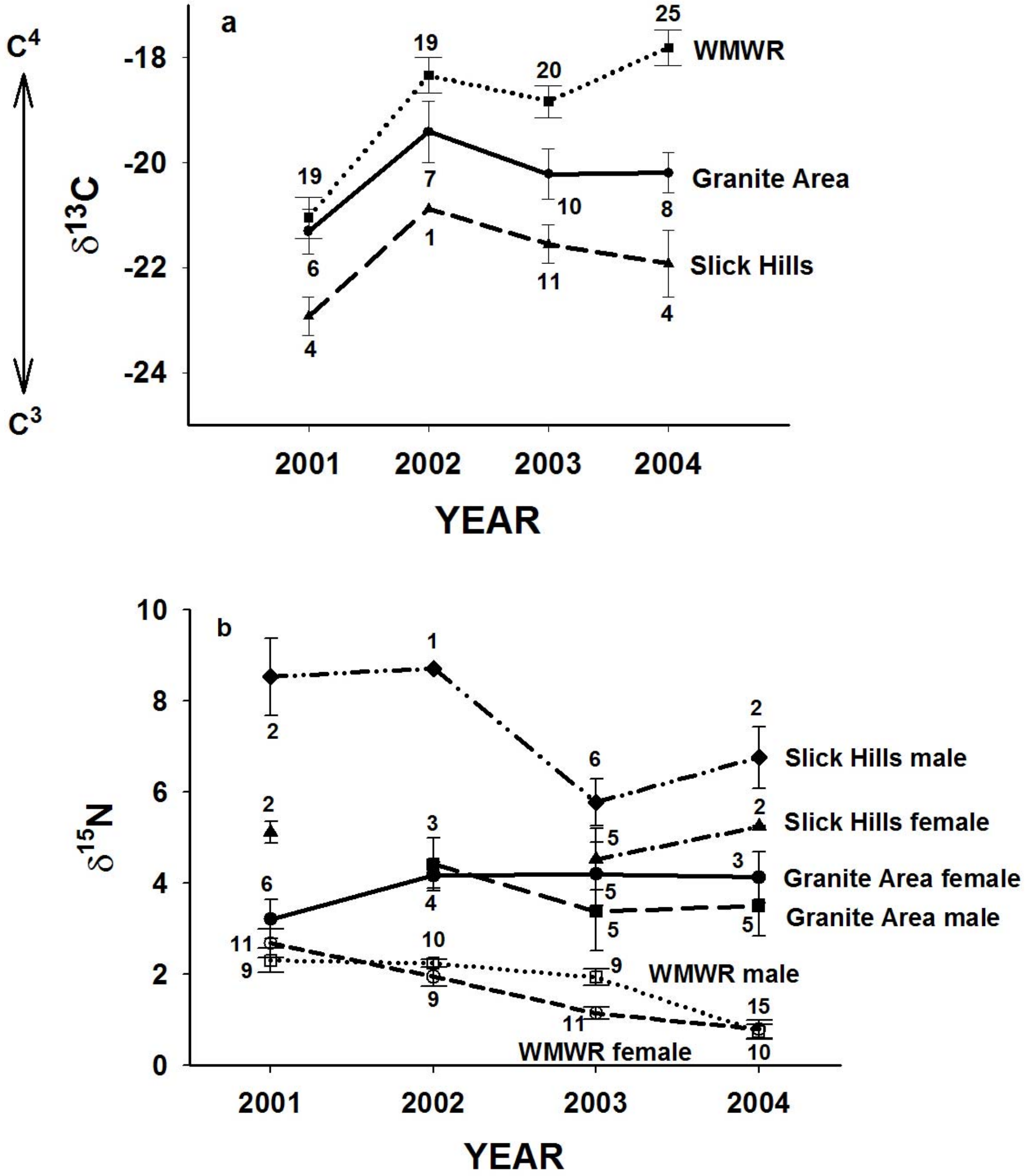

c
● Private
□ WMWR
r = 0.460
P = 0.0004
r = 0.405
P < 0.0001
δ^{15}N
δ^{13}C
10
8
6
4
2
0
-2
-26
-24
-22
-20
-18
-16
-14

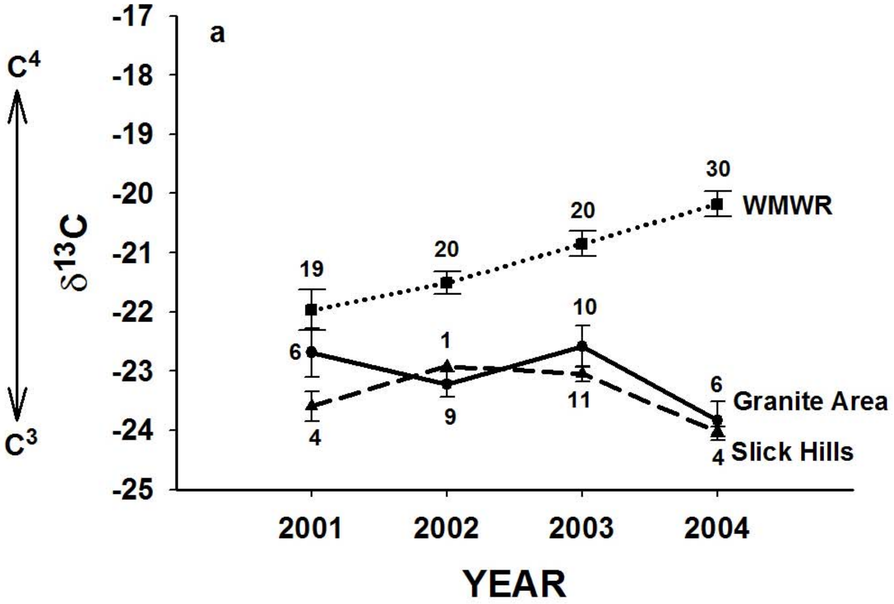

a
Private
WMWR
r = 0.413
P = 0.0001
r = 0.020
P = 0.890
Muscle δ13C
Hoof δ13C
-18
-19
-20
-21
-22
-23
-24
-25
-26
-24
-22
-20
-18
-16
-14
-12

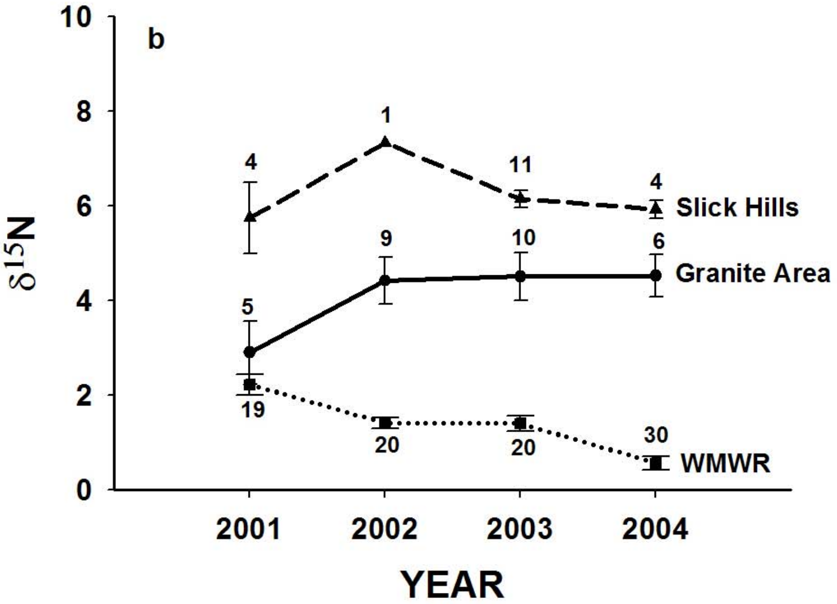

b
r = 0.369
P = 0.009
r = 0.631
P < 0.0001
Private
WMWR
Muscle δ15N
Hoof δ15N
8
6
4
2
0
-2
-2
0
2
4
6
8
10

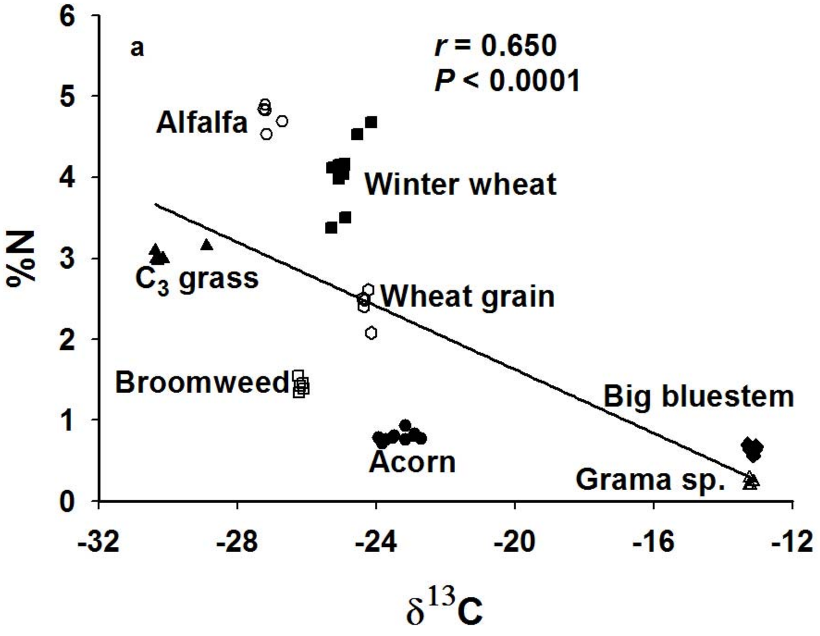
a
C₄
C₃
δ13C
-17
-18
-19
-20
-21
-22
-23
-24
19
19
21
25
10
8
21
12
WMWR
Private
2001
2002
2003
2004
YEAR
b
δ15N
6
5
4
3
2
1
0
10
8
21
12
19
19
21
25
Private
WMWR
2001
2002
2003
2004
YEAR

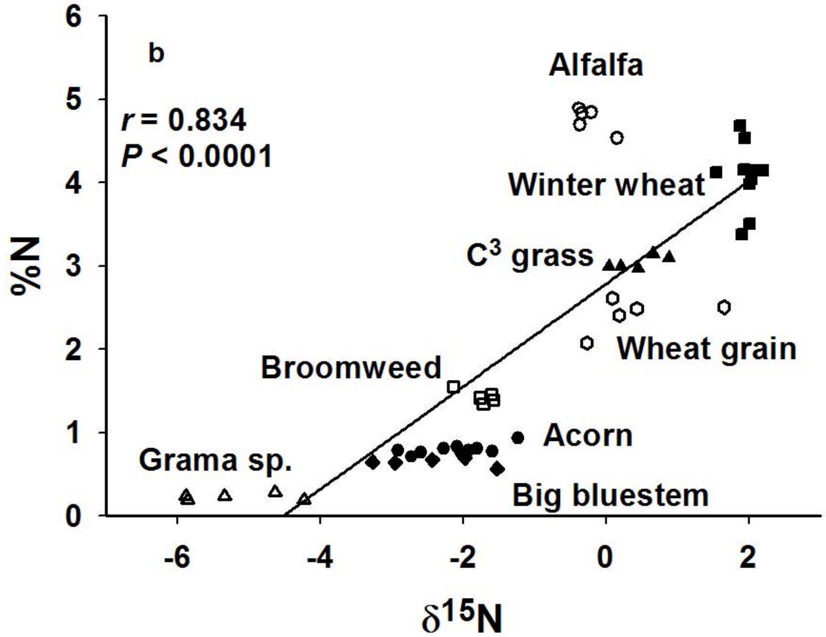

C4
C3
a
-17
-18
-19
-20
-21
-22
-23
-24
δ13C
13
10
8
10
WMWR male
WMWR female
10
17
10
12
11
7
5
8
Private male
Private female
2
5
10
8
2001
2002
2003
2004
YEAR
b
6
5
4
3
2
1
0
δ15N
21
10
9
15
Private
20
20
20
30
WMWR
2001
2002
2003
2004
YEAR


a
C4
C3
δ13C
-18
-20
-22
-24
2001
2002
2003
2004
YEAR
WMWR
Granite Area
Slick Hills
19
19
20
25
6
7
10
8
4
1
11
4
b
δ15N
10
8
6
4
2
0
Slick Hills male
Slick Hills female
Granite Area female
Granite Area male
WMWR male
WMWR female
2
1
2
6
2
2
3
5
3
6
4
5
5
5
11
10
9
9
9
11
15
10
2001
2002
2003
2004
YEAR


a
C4
C3
δ13C
-17
-18
-19
-20
-21
-22
-23
-24
-25
19
20
20
30
WMWR
6
1
10
9
11
6
Granite Area
4
4
Slick Hills
2001
2002
2003
2004
YEAR


b
δ15N
10
8
6
4
2
0
4
1
11
4
Slick Hills
5
9
10
6
Granite Area
19
20
20
30
WMWR
2001
2002
2003
2004
YEAR


a
r = 0.650
P < 0.0001
Alfalfa
Winter wheat
C3 grass
Wheat grain
Broomweed
Big bluestem
Acorn
Grama sp.
%N
0
1
2
3
4
5
6
-32
-28
-24
-20
-16
-12
δ13C


b
r = 0.834
P < 0.0001
Alfalfa
Winter wheat
C3 grass
Wheat grain
Broomweed
Acorn
Grama sp.
Big bluestem
%N
0
1
2
3
4
5
6
-6
-4
-2
0
2
δ15N

APPENDIX

Appendix A

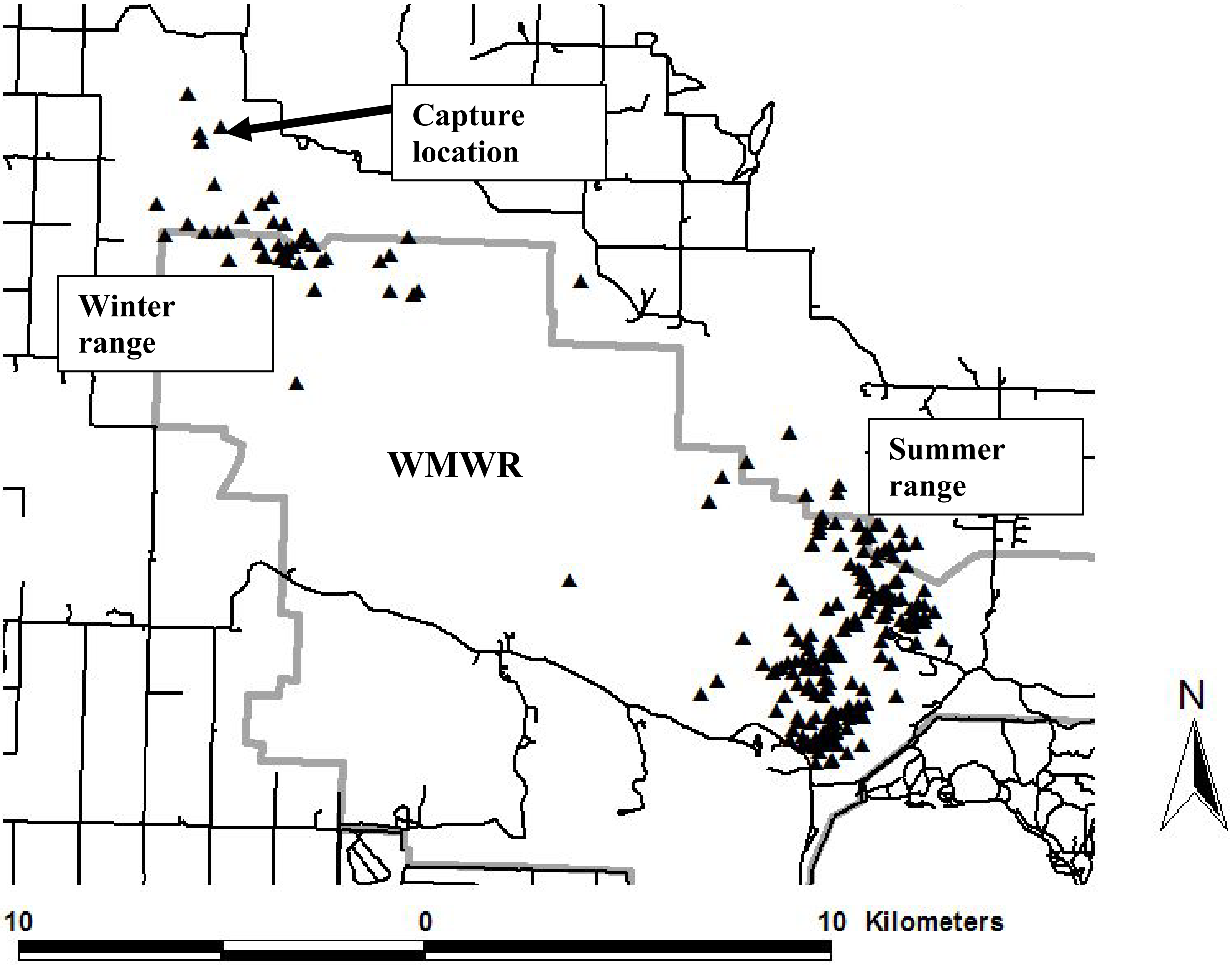
One female elk (elk 1772) had a unique movement pattern unlike the other 19 marked females. She was chemically immobilized on private lands (winter range) on 6 March 2002 about 2.6 km north of the Wichita Mountains Wildlife Refuge (WMWR) fence on a private land wheat plot (Capture location; Fig. 1). She remained on private land through 9 April 2002 prior to traveling 15 km southeast where she occupied private land and WMWR from 24 April 2002 to 22 August 2002 (summer range). Two locations (28 and 30 August 2002) documented a brief return to the winter range but then back to her summer range by 3 September 2002; she remained within WMWR through 24 October 2003. From 20 November 2003 to 19 March 2004, she was located on winter range within WMWR but was never found near the wheat plot of her capture location. She then returned to the summer range on 7 April 2004 and remained there until 6 November 2004 before returning to her winter range on 20 November 2004. She remained on her winter range, using both private land and WMWR, until 30 March 2005 when relocation activities ended for the project. On 5 June 2005, a site visit documented her back on the summer range.

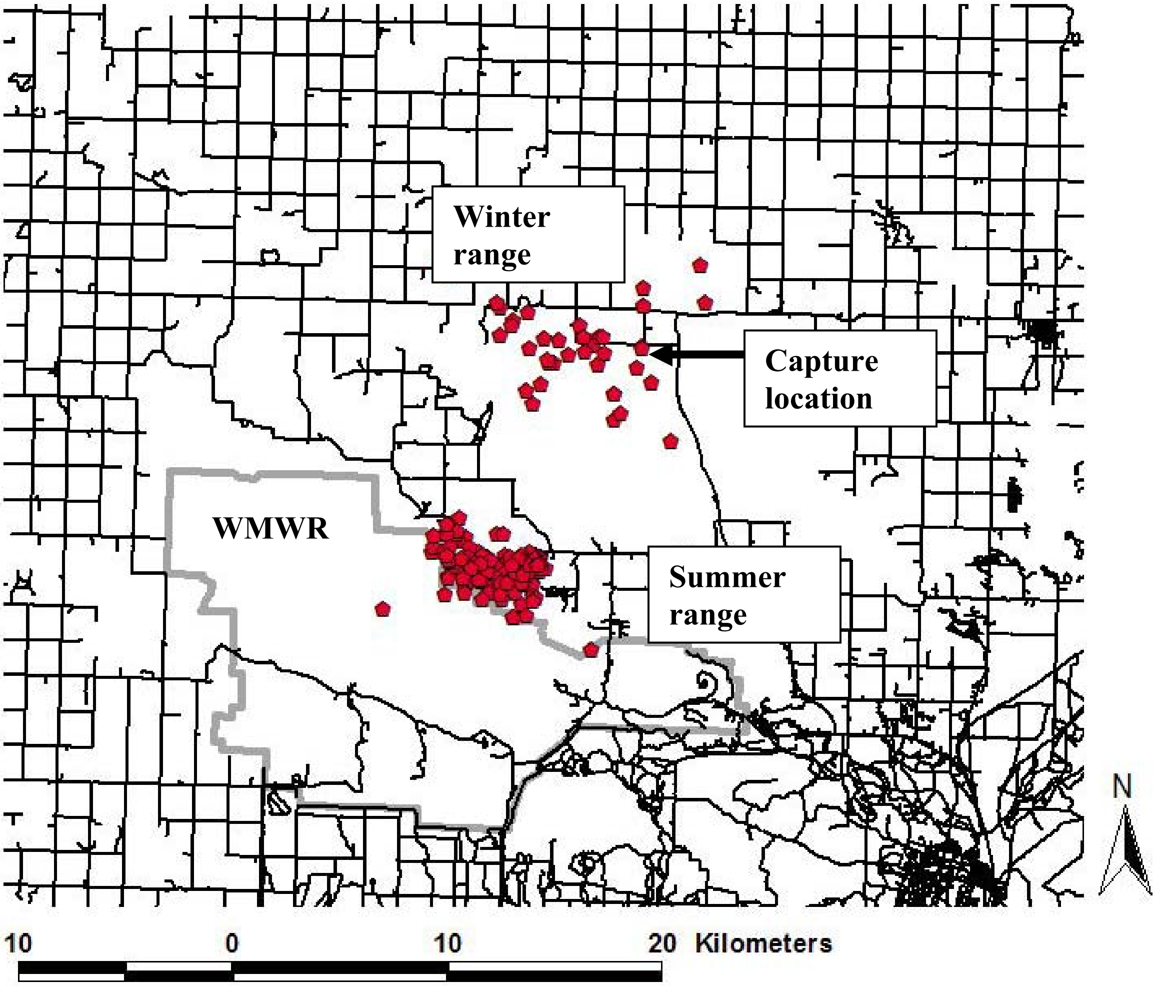
During capture, she was determined to be about 7 years of age based on tooth wear and was observed alone on several occasions from December 2003 to March 2004. Her winter and summer home range were distinct for long periods of time except, for the 2-day journey in August 2002. She did not return to winter range during winter 2002 (i.e., Dec. 2002 – Mar. 2003), and the reasons for her seasonal "migrations" were unknown. Of the 11 female elk radiocollared and monitored in the Granite Area for > 2 years, elk 1772 was the only one to show distinct summer and winter ranges.

One male elk (elk 1652) was mistakenly chemically immobilized on 18 January 2002 in the Slick Hills at 1.7 months-of-age (see figure 2; Capture location). He was captured from a group of 20 female elk with young-of-the-year and was routinely observed with a group of about 100 elk through 26 March 2002 in the Slick Hills (winter range). On 3 April 2002, he was found about 12 km south of the capture location on private land in the Granite Area (summer range). He remained on summer range through 15 December 2002 and then returned to winter range from 7 January to 5 March 2003. He was observed on several occasions with a mixed group of > 100 elk on the winter range or with several mature and immature bulls in groups of <15 while on summer range. From 18 March to 26 July 2003, he returned to the summer range in the Granite Area and was photographed with 1 adult bull with 4 and 3 points on the left and right antler, respectively, on 23 July 2003. On 15 August 2003, he returned to his winter range and was first found near several patches of alfalfa where several mature bulls were observed. He remained on the winter range until 13 December 2003 when he was illegally harvested. Because he did not meet the minimum antler points requirements set by state regulations (≥5 points on one side), the hunter reported his harvest to the County Game Warden and subsequently checked the elk in at the private-land checkstation for data collection. Although this was the only male elk radiocollared during the study, male elk with distinguishing antler characteristics have been reported to use both the Slick Hills and Granite Area within the past decade. Use of both the Granite Area and Slick Hills by male elk seems likely related to dispersal during breeding, but further study is needed to understand the specifics of movement and habitat use by male elk.

Figure 1. Capture site and radiotelemetry locations of female elk 1772 documenting use of disjunct winter and summer ranges on private lands and within Wichita Mountains Wildlife Refuge (WMWR). The solid lines represent the primary (i.e., paved) and secondary (i.e., dirt) roads in the study area.

Figure 2. Capture site and radiotelemetry locations of male elk 1652 documenting use of disjunct winter and summer ranges on private lands surrounding Wichita Mountains Wildlife Refuge (WMWR). The solid lines represent the primary (i.e., paved) and secondary (i.e., dirt) roads in the study area.


Capture location
Winter range
WMWR
Summer range
N
10
0
10 Kilometers


Winter range
Capture location
WMWR
Summer range
N
10
0
10
20 Kilometers

VITA

William David Walter

Candidate for the Degree of

Doctor of Philosophy

Thesis: ECOLOGY OF A COLONIZING POPULATION OF ROCKY MOUNTAIN ELK (*CERVUS ELAPHUS*)

Major Field: Conservation Science: Wildlife Ecology

Biographical:

Personal Data: Born in Auburn, New York, on April 19, 1973, the son of William James Walter and Sandra Jean Mack

Education: Graduated from Port Byron High School, Port Byron, New York in June 1991; received Bachelor of Science degree in biology from the State University of New York, College of Environmental Science and Forestry, Syracuse, New York in December 1995; received Master of Science in Wildlife Ecology from the University of New Hampshire in May 2000. Completed the requirements for the Doctorate of Philosophy degree with a major in Conservation Science: Wildlife Ecology at Oklahoma State University in May 2006.

Experience: Research Assistant, Oklahoma State University; Research Technician, Connecticut Department of Environmental Protection, Wildlife Division, Research Assistant, University of New Hampshire,

Professional Memberships: American Society of Mammalogists Association of Southwestern Naturalists, Ecological Society of America, Oklahoma Academy of Science, Oklahoma State University Student Chapter of the American Fisheries Society, Oklahoma State University Student Chapter of the Wildlife Society, Oklahoma State University Zoology Graduate Student Society, Rocky Mountain Elk Foundation The Wildlife Society, Wildlife Disease Association

Name: William David Walter Date of Degree: May 2006

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: ECOLOGY OF A COLONIZING POPULATION OF ROCKY MOUNTAIN ELK (*CERVUS ELAPHUS*)

Pages in Study: 151 Candidate for the Degree of Doctor of Philosophy

Major Field: Conservation Science: Wildlife Ecology

Scope and Method of Study: After reintroduction into the Wichita Mountains Wildlife Refuge (WMWR) in the early 1900s, Rocky Mountain elk (*Cervus elaphus*) established a viable population on private lands. The objectives of this study were to document home range, habitat use, and nutrition of elk on private lands surrounding WMWR. These data will provide a better understanding of the factors affecting population persistence on private lands.

Findings and Conclusions: Twenty-one radiocollared females and 1 radiocollared male were tracked, resulting in 2,657 radiolocations of marked elk from January 2002 to March 2005. Mean annual and seasonal home-range size of elk in forested habitat near WMWR (Granite Area) was smaller than home-range size of elk in a more open grassland habitat (Slick Hills). Elk in the Granite Area and Slick Hills used agricultural fields during forage-limited winter months (Dec–Mar); such fields were not available to elk in WMWR. Hoof, muscle, and fecal stable isotopes of carbon and nitrogen were evaluated from elk on private lands and WMWR. Carbon and nitrogen isotopes suggested that elk on private lands consumed more C_3 vegetation with greater nitrogen content on an annual basis compared with elk on WMWR. Agricultural crops provided alternate food resources of better quality to elk on private lands during periods of low natural forage availability (i.e., late summer, winter) compared with elk on WMWR.

ADVISER’S APPROVAL: David M. Leslie, Jr.