SEXUAL SEGREGATION AND FORAGING ECOLOGY OF SIERRA NEVADA BIGHORN SHEEP DURING WINTER

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A thesis

submitted in partial fulfillment

of the requirements for the degree of

Master of Science in the Department of Biological Sciences

Idaho State University

June 2007

ACKNOWLEDGMENTS

This project was funded by California Department of Fish and Game, the California Chapter of the Foundation for North American Wild Sheep, and the Department of Biological Sciences at Idaho State University. I would like to thank Drs. T. R. Stephenson and V. C. Bleich of the California Department of Fish and Game for providing financial assistance, field equipment, and access to maps and data used in this analysis.

I am thankful to Dr. R. T. Bowyer, my major advisor, for his patience and dedication to this research and my degree. His expertise in all aspects of science has provided me with an excellent learning experience as well as an incredible source of information and knowledge. I also thank Drs. T. R. Stephenson, V. C. Bleich, and D. J. Delehanty, my committee members, for their tireless effort in reviewing many drafts of proposals, reports, data analyses, and this thesis. They also provided me with an invaluable source of knowledge of mountain sheep ecology and behavior. I thank Drs. K. Stewart, P. Murphy and J. Kie for assistance with data analysis and moral support.

I thank D. German, H. Johnson, D. Jensen, Dr. J. Wehausen, L. Bowermaster, J. Villepique, and Dr. B. Pierce of the California Department of Fish and Game for helping me with logistical support, field assistance, and advice in developing the ideas for this project. I am further indebted to fellow graduate students in Dr. Bowyer's lab K. Monteith, J. Whiting, and P. Atwood for providing manuscript reviews, practicing professional presentation, and advice on analyzing data.

I also thank my parents, Scott and Cathy Schroeder, for believing in me and fostering a sincere love for science and nature. Finally, I could not have completed this thesis without the help of Dr. Carrie Lane, who volunteered countless hours in the field in extremely unfavorable conditions. She provided moral support, and was very patient in understanding the nature of conducting a field-oriented research project in the remote landscapes of the Sierra Nevada.

ABSTRACT

A critical aspect of the ecology of mountain sheep (*Ovis canadensis*) is the differences in behavior and foraging ecology between sexes. I compared several ecological variables between adult male and adult female mountain sheep in 4 subpopulations in the Sierra Nevada, Inyo and Mono counties, California, USA, to test hypotheses related to sexual segregation and foraging ecology during winter. Females foraged in larger groups that were closer to escape terrain than did males. Foraging areas used by males had a higher biomass of vegetation and were less open than areas used by females. Males foraged more efficiently when in larger groups, whereas females foraged more efficiently when closer to escape terrain. Male and female sheep differed in their dietary niches and in bite rates. Male mountain sheep traveled farther per day and in less rugged terrain than did females. These differences in behavior and space use are likely a result of allometric differences and associated life-history strategies between the sexes.

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INTRODUCTION

Populations of Sierra Nevada mountain sheep (*Ovis canadensis sierrae*) have declined substantially since the late 1980s. The population in the Sierra Nevada declined to a low of < 100 individuals in 1995, which resulted in their being listed as an endangered population segment in 2000 (USFWS 2003). Several factors may have contributed to population declines including drought and predation from mountain lions (*Puma concolor*) (Wehausen 1996), pneumonia epizootics from contact with domestic sheep (Onderka et al.1988, Coggins and Matthews 1992), and small group sizes which resulted in decreased foraging efficiency (Berger 1978, Molvar and Bowyer 1994, Ruckstuhl and Festa-Bianchet 2001, Bowyer and Kie 2004). Nonetheless, little is known of how predation risk or habitat use and availability influences the behavior of this small population of mountain ungulates, which are among the rarest large mammals in the world (USFWS 2003). Failure to account for life-history characteristics in the conservation of mountain sheep could result in inappropriately designed re-introduction efforts and could hamper recovery for endangered populations (Festa-Bianchet and Apollonio 2003).

Foraging behavior and risk of predation play substantial roles in shaping life-history strategies for many ungulates (Bowyer 1984, 2004; Bowyer et al. 1999; Bleich et al. 1997, Rachlow and Bowyer 1998, Gaillard et al. 2000, Barten et al. 2001). Researchers studying mountain sheep have investigated food habits and predation risk for populations inhabiting the Sierra Nevada, California, USA (Wehausen 1980, 1992, 1996;

Chow 1984; Moore 1991). Those studies provided broad-scale considerations of habitat use in winter; however, they focused mostly on female ranges and did not specifically separate habitat used by adult males from those used by adult females. Although some studies of foraging behavior by mountain sheep have addressed ecological differences between sexes (Bleich et al. 1997, Mooring et al. 2003), those studies were for desert-dwelling mountain sheep, which may differ in their diets and habitat requirements from sheep inhabiting high elevations of the Sierra Nevada.

Bowyer (2004) summarized current hypotheses regarding sexual segregation in ruminants and emphasized the importance of understanding evolutionary underpinnings when testing these hypotheses. The gastrocentric hypothesis (Barboza and Bowyer 2000, 2001) predicts that males will forage in habitats where food is more abundant but may be of lower nutritional quality than habitats used by females during periods of segregation. Differences in forage selection also can be attributed to differences in life-history strategies associated with males having a larger rumen volume than females; females also undergo physiological changes to their digestive tract to assimilate the high-quality nutrients required to meet the needs of late gestation and lactation (Barboza and Bowyer 2000, 2001). Further, males require larger amounts of food per day (Demment and Van Soest 1985, Illius and Gordon 1987, Gross 1996, Main 1998, Ruckstuhl and Neuhaus 2002), which may influence their daily spatial requirements including the total distance they must travel to acquire forage (Ruckstuhl and Neuhaus 2001) and the distance they must travel from escape terrain (Berger 1978, 1991).

Predation also contributes to differences in habitat selection between sexes and can play an important role in sexual segregation (Berger 1991, Bleich et al. 1997, Kie and Bowyer 1999); females need to provide security to offspring while maintaining nutritional reserves necessary to support the costs of gestation and lactation (Bowyer 1984, Main and Coblentz 1996, Bleich et al. 1997). Female ungulates with young often make tradeoffs between forage quality and predation risk when determining where to forage in predator-rich environments (Berger 1991, Bleich et al. 1997, Rachlow and Bowyer 1998, Bowyer et al. 1999, Kie and Bowyer 1999, Barten et al. 2001). Female sheep may try to minimize effects of predation risk by foraging close to escape terrain (Berger 1978, 1991) and by maximizing the rate of food acquisition through increased bite rates (Ruckstuhl et al. 2003). Simply stated, in species of sexually dimorphic ruminants that typically sexually segregate, females invest in direct fitness benefits through offspring survival as well as indirect fitness (future reproductive success), whereas males invest more resources in body growth and secondary sexual traits for male-male aggression to gain access to estrous females (Ralls 1977, Loison et al. 1999, Weckerly 1998, Perez-Barberia et al. 2002, Spaeth et al. 2004).

Mountain sheep are sexually dimorphic and males and females separate spatially for most of the year (Bleich et al. 1997). Because these life-history characteristics are typical for many ruminants, mountain sheep are ideal subjects for testing hypotheses related to differential use of habitat by sexes. Mountain sheep are well-known for their differential habitat use by sexes outside the mating season (Krausman and Bowyer 2003), although the ultimate causes of those differences are less clear (Bleich et al. 1997). Moreover, mountain sheep are morphologically and behaviorally well-adapted to minimize predation through vigilance and increased ability to escape predators in precipitous terrain (Berger 1978, 1991; Festa-Bianchet 1988, Bleich et al. 1997).

The primary objectives of this research were to provide a quantitative description of foraging behavior of male and female mountain sheep, and determine the specific habitat characteristics that are important to each sex. I hypothesized that male mountain sheep would feed in areas with abundant forage and with more shrub and grass biomass, whereas females would feed closer to cliffs and rock outcroppings with lower overall abundance of forage but of higher quality. I also predicted that males would use areas with an increased risk of predation (i.e., farther from escape terrain and less open habitats) where high forage abundance was available, whereas females would use areas with less risk of predation and lower food abundance than males. I hypothesized that females would have higher bite rates than would males because they need to minimize predation risk by reducing foraging time. I also hypothesized that both male and female mountain sheep would forage more efficiently when they were in large groups and close to escape terrain. I further predicted that diets of female sheep would contain more forbs and grasses and have higher fecal nitrogen (an index to forage quality) than forages consumed by males, whereas diets of males would contain more shrubs and have lower fecal nitrogen than diets of females. I hypothesized that males would travel greater distances per day to acquire the necessary resources for rumen fill, than would females. Finally, I further hypothesized that female mountain sheep would use more rugged terrain, to limit risk of predation, than would males.

STUDY AREA

The Sierra Nevada (37°24’N, 118°41’W) is a rugged, young (< 5,000,000 YBP) mountain range of far western North America, approximately 650 km long and from 75 to 125 km in width (Hill 1975). Topography is largely a result of late Pliocene uplifting, which created prominent peaks, and Pleistocene glaciers that created U-shaped canyons, moraines, and steep cirque headwalls (Phillips et al. 1996). Snow is a significant source of winter precipitation in the Sierra Nevada (National Oceanic Atmospheric and

Administration 2006) that affects seasonal vegetation and timing of green-up for mountain ungulates (Bowyer et al. 1999, Festa-Bianchet 1988, Rachlow and Bowyer 1991, 1994), but rain during spring and summer is important for growth of forage plants for mountain sheep (Wehausen 1992, Oehler et al. 2003). Most storms form in the Pacific Ocean from November to March and move eastward over the Sierra Nevada, causing a rain shadow on eastern slopes that is responsible for the desert and steppe ecosystems of the eastern Sierra Nevada (National Oceanic Atmospheric and Administration 2006). Winter storms formed in the Pacific Ocean create a variety of weather phenomena in the Sierra Nevada, including strong winds, flooding rains, heavy snows, thunderstorms, hail, winds and occasional tornados (National Oceanic Atmospheric and Administration 2006). Annual precipitation varies markedly with a range during autumn through early spring (1 October to 15 April) of 2.97-19.65 cm from 1993 to 2005 (Inyo County Water Department 2006). Snowfall also varies markedly with an annual range of 0.25-21.4 cm during winter (average minimum to average maximum from 1 December to 31 May, 1948-2006; National Oceanic Atmospheric and Administration 2006). Temperature is variable, ranging from 5.7°-27.1° C (average minimum to average maximum during winter, National Oceanic Atmospheric and Administration 2006).

Mountain sheep currently are distributed along the eastern slope of the Sierra Nevada (Wehausen 1996). The Mt. Warren and the Mt. Gibbs herds occupy the Mono Basin in the north (Fig. 1). The southern region is occupied by 4 subpopulations, 3 of which I designated as separate study areas: Wheeler Ridge, Mt. Langley, and Mt. Baxter-Sawmill Canyon (Wehausen 1996; USFWS 2003; Fig. 1). A small, isolated population also occupies the Mt. Williamson region; however, I did not sample this area due to difficult access and the low probability of observing sheep in that range. Mean (± SE) elevations used by mountain sheep during winter ranged from 1,680 to 3,665 m (2,356 ± 55 m) for radio-collared males and 1734 to 3911 m (2,514 ± 53 m) for radio-collared adult females.

Vegetation in the eastern Sierra Nevada on lower-elevation winter ranges (Wheeler Ridge, Mt. Langley, and Mt. Baxter-Sawmill Canyon) is typical of the Great Basin and is characterized by sagebrush steppe and pinyon-juniper forest (Chow 1984). The over-story is dominated by single leaf pinyon (*Pinus monophylla),* big sagebrush *(Artemisia tridentata),* bitterbrush (*Purshia tridentata),* rabbitbrush *(Chrysothamnus nauseosus),* mountain whitethorn *(Ceanothus cordulatus)*, and horsebrush (*Tetradymia canescens)*, whereas the understory is characterized by needle-grass (*Achnatherum speciosa),* buckwheat (*Eriogonum* sp*.)*, beardtongue (*Penstemon)*, and sedges (*Carex* sp.) (Chow 1984). Many areas of historical winter range for mountain sheep also have been invaded by non-native species such as cheat grass (*Bromus tectorum*) (USDA Forest Service, unpublished data). At higher elevations (e.g., Mono Basin), vegetation is typified by alpine-communities such as prickly phlox (*Leptodactylon* sp.), crested wheatgrass (*Agropyron*), sedges (*Carex*) and vetches (*Astragalus* spp.). Plant nomenclature is according to Munz (1974).

METHODS

I captured mountain sheep and measured several response variables for sheep inhabiting 4 distinct geographic areas within the Sierra Nevada. These data included habitat samples, radio-telemetry locations, and observations of sheep.

Capture and Radio telemetry.—Beginning in 2003, the California Department of Fish and Game captured adult (≥1 yr old) male and female mountain sheep in the Sierra Nevada via net-gunning from a helicopter (Krausman et al. 1985). GPS collars were used to monitor winter movements and survivorship in this exceptionally rare mammal. I used GPS data from 6 adult females and 3 adult males beginning on 1 January 2003 and ending 1 May 2005. GPS radio collars were programmed to transmit positions every 6-10 min for a 24-h period, 1 day per week for 2 years. I used 10 min fixes (locations) to analyze daily distances traveled.

I used telemetry coordinates from GPS data combined with a Digital Elevation Model (DEM) using ArcGIS 9.1 (Environmental Systems Research Institute Inc., Redlands, CA, USA) and Spatial Analyst extension to estimate daily use of space for mountain sheep. I calculated mean distance traveled per day for each sheep using the Home Range Extension for ArcGIS^{TM} (Rodgers and Carr 1998). I calculated the elevation of each GPS location by overlaying a shapefile for each individual with a 10-m DEM and used the Surface Spot function in ArcMap to derive the elevation of each location from the underlying DEM.

I developed a terrain-ruggedness index for locations of male and female sheep based on ground observations in each of 4 study areas. I used ArcGIS to build 3 layers derived from the DEM to calculate slope, aspect, and elevation for each 10 by 10 pixel in the grid. Locations from all sheep were then overlaid on the terrain layers and a 300-m buffer was delineated around each point. I used the Grid Statistics tool to calculate the mean and SD for physical characteristics (slope, aspect, and elevation) of each 300-m circle.

Habitat variables.—I indexed diet quality and composition for adult male and adult female mountain sheep from levels of fecal nitrogen (Blanchard et al. 2003) and microhistological analyses (Hodgman et al. 1996) of feces, respectively. I collected fecal pellets during winter (1 January to 5 May) 2005 from 4 study areas (Mt. Baxter, n = 28; Mt. Langley, n = 31; Wheeler Ridge, n = 46; Mono Basin, n = 38) and pooled those data by area, sex, and month. I collected fresh fecal pellets (≤ 3 days old) from observed individuals or from live animals that were handled during capture. A pellet group (from a single animal) was considered an independent sample. Fecal pellets were analyzed for percent nitrogen, ash, and moisture content, and converted to an ash-free, dry-matter basis. Microhistological analysis included identification of plants to their genus (Sparks and Malechek 1968). Fecal pellets were analyzed under contract by the Wildlife Habitat Laboratory at Washington State University, Pullman, Washington, USA.

Characteristics of habitat for mountain sheep were measured at random locations and at locations where mountain sheep were observed. I assessed biomass of forage using double-sampling (Reese et al. 1980; Reich et al. 1993, Barten et al. 2001) within 1-m^2 plots. I developed predictive equations for vegetation biomass using the double-sampling method described by Reese et al. (1980) and Reich et al. (1993). I used wet-weight biomass of forbs, grasses, and shrubs from male (n = 11), female (n = 20), and random (n = 18) locations during winters 2004 and 2005, and pooled those data to obtain sufficient sample sizes for statistical analyses. Estimates of wet weights of biomass were used because I clipped vegetation plots in the field and developed predictive biomass equations for estimating plots that were not clipped. Because of the differential dry weights of various functional groups of plants (e.g., forbs, grasses, and shrubs) and individual differences within species, I could not estimate dry weights in plots where I used visual estimates of forage biomass.

I calculated the greatest distance mountain sheep were observed foraging from escape terrain by measuring the distance from the central point of the group to the nearest escape terrain using a GPS. I defined escape terrain similar to previous studies (Risenhoover and Bailey 1985, DeCeasare and Pletscher 2006) as any geomorphic feature > 5 m in height and diameter, which is part of a larger, contiguous geological formation. Measurements of distance to escape terrain were collected at observed locations of mountain sheep immediately following behavioral observations or within 7 days of the initial observation in a manner that did not disturb sheep (Rachlow and Bowyer 1998). I estimated visibility at male and female group locations using a 2-m high cover pole; I took measurements from a distance of 15 m in 4 cardinal directions and recorded the percent of the pole (in 25-cm increments) obscured by vegetation or geomorphic features (Bleich et al. 1997; Bowyer et al. 1999). I used the mean percent of the cover pole visible from 4 directions as the value for visibility.

Field observations.—I observed behavior of sheep with 10 × 40 binoculars or a 20 × 60 spotting scope. To help ensure independence of observations, I randomly selected a radio-collared sheep from each of the 4 main study areas (Mt. Langley, Mt. Baxter, Wheeler Ridge, and Mono Basin) and attempted to locate that sheep via radio-telemetry. Once a marked sheep was located at ≤ 300 m, I selected an individual from the group using a random numbers table. I categorized sheep into sex and age classes according to Geist (1968): (1) adult females (including yearlings); (2) young; (3) class I males (yearlings); and (4) class II-IV males (adults). The rarity of sheep precluded further subdivisions of adult males.

I recorded activities of mountain sheep on a hand-held personal computer and timed observations on a stopwatch using a combination of scan and focal-animal sampling (Altmann 1974). I used 10 m activity scans (Altmann 1974) and categorized mountain sheep activities similar to Risenhoover and Bailey (1985) as foraging (head down in feeding posture), bedding, aggressive, vigilant (head in upward position with ears erect) or alarmed (running to escape terrain). I used focal sampling (Altmann 1974) to count bites taken by male or female sheep to obtain a bite rate for individuals of each sex. I randomly selected an individual sheep from the group to do so. The individual was then viewed continuously for at least 3 min and the number of bites of each forage class (forbs, graminoids, shrubs, or unidentified plants) was recorded with a hand-held computer. Feeding efficiency (percent of active time spent foraging; Berger 1978) was calculated by dividing the time spent feeding by the total time active and multiplying by 100 ($t_{foraging}/t_{active}$ x 100).

Statistical analyses.—I used a mixed generalized linear model (PROC MIXED, SAS Institute 1999) to analyze data on percent fecal nitrogen (dependent variable) and sex as the independent variable. I used study area as random effect (Littell et al. 1996) and Julian date and elevation as covariates. Percentage data were arcsine-square root transformed prior to analysis. I used Tukey's test (HSD; Zar 1999) for multiple comparisons between groups when I obtained significant main effects ($\alpha = 0.05$).

I used multivariate analysis of variance (MANOVA) to compare differences in forage abundance between sites used by sexes. Independent variables were males (≥ 2 yrs), females and young (including males < 2 yrs old), and random sites. Dependent variables were total wet weight of live and dead biomass (g/m^2) and live and dead biomass of forbs and grasses, and live biomass of shrubs. I used wet weight of biomass because it is more closely related to rumen fill than dry weight (Belovsky 1978). Berger (1991) and Bleich et al. (1997) have reported that female mountain sheep use more open areas than do males; thus, I used a 1-tailed *t*-test (which predicted males in less-open areas) to compare habitat openness at male and female foraging locations.

I conducted principal components analysis (PCA) of diet composition of sheep using the variance-covariance matrix (McGarigal et al. 2000) to reduce dimensionality of those data. I reduced the number of species identified by microhistological analysis to 8 genera (Kie and Bowyer 1999) because they met the following criteria: 1) consumed by $>$ 20% of all mountain sheep; 2) comprised $\geq$ 30% of the diet in at least 1 mountain sheep of each sex; and 3) comprised $\geq$ 5% of diets averaged over all samples. The genera selected included wheat grass (*Agropyron*), big sagebrush (*Artemisia tridentata*), milk-vetch (*Astragalus*), sedge (*Carex*), fescue grass (*Festuca*), prickly phlox (*Leptodactylon pungens*), blue grass (*Poa*), and desert needlegrass (*Acnatherum speciosum*). I further delineated 2 separate study areas, Mono Basin and Southern Region (consisting of Mt. Langley, Mt. Baxter, Sawmill Canyon, and Wheeler Ridge study areas), because the Mono Basin herd spent winters at high elevations, and the Southern Region herds spent winters at low elevations. I used MANOVA and Tukey's HSD for multiple comparisons to test for differences in diet composition of forage species among study areas and sexes. I plotted means with 95% confidence intervals as bi-variate ellipses for the first 2 principal components to examine differences between diets of sexes. I used the Shannon Index to infer differences in diet diversity between sexes and study areas, and rescaled H' to reflect the number of forage species ($e^{H'}$; Ricklef and Miller 2001). Diet diversity was estimated from genera of plants in the diets of mountain sheep that met criteria used for PCA.

I compared mean daily distances for individual male and female mountain sheep using a Satherwaite 2-tailed *t*-test for unequal variances (Zar 1999) to test for differences in daily distances traveled between sexes. I tested for differences between sexes in elevations used during winter with ANOVA using mean monthly elevation as the dependent variable, and sex, month, and year as main effects, and the pair wise interactions between sex, month, and year. I used MANOVA to test for differences between sexes for slope, aspect, and a composite index based the standard deviation of slope multiplied by the angular deviation in aspect (Nicholson et al. 1997, Bowyer et al. 1999, Pierce et al. 2004, Oehler et al. 2005). Dependent variables were slope, aspect, and ruggedness index, and independent variables were sex, herd, and a sex by herd interaction.

RESULTS

Fecal nitrogen.— Mean fecal nitrogen ranged from 1.36 to 2.82% each month for adult males and 1.36 to 2.77% for adult females across all herds (Table 1). Fecal nitrogen was not significantly different between sexes when we controlled for elevation and Julian date and used study area as a random effect (MIXED GLM sex $F_{1,3} = 0.28$, $P = 0.635$, Fig. 2). However, fecal nitrogen varied for mountain sheep in different herds and by month after controlling for effects of elevation (ANCOVA overall $F_{8,20} = 7.56$, $P < 0.001$; herd $F_{3,20} = 14.98$, $P < 0.0001$, month $F_{3,20} = 3.86$, $P = 0.0249$; Fig. 2). Tukey's HSD revealed that fecal nitrogen in the Mt. Baxter herd was significantly higher ($P < 0.05$) than all other areas and fecal nitrogen in the Mono Basin herd was lower ($P < 0.05$) than all areas except Mt. Langley (Fig. 2).

Forage abundance and visibility.—Total biomass ranged from 6 to 138 g/m^2 at female locations, 34 to 182 g/m^2 at male locations, and 13-127 g/m^2 at random locations.

Biomass of forage classes (forbs, grasses, shrubs, and total) varied for sexes and random locations (MANOVA; overall $F_{8,68} = 2.12$, $P = 0.04$; Fig. 3) and herds (MANOVA; herd $F_{12,90} = 2.12$, $P = 0.002$), but group type (male, female, or random) and herd interactions were not significant (MANOVA; $F_{24,119} = 1.16$, $P = 0.29$). Male locations had higher biomass of shrubs ($P < 0.05$) and total vegetation ($P < 0.05$) than did sites used by females or random locations (Fig. 3). Female locations did not differ from random ones in shrub biomass or total biomass (Fig. 3). Moreover, biomass of forbs and grasses was not significantly different among male, female, or random locations (Tukey's HSD; $P > 0.05$ Fig. 3). Visibility (percentage of 2-m cover pole viewed from 15-m) ranged from 62% to 91% at female locations, and 28% to 93% at male locations. A *t*-test indicated that mean (± SE) visibility at locations used by females (76 ± 9%) was significantly higher ($P = 0.05$) than locations used by male sheep (56 ± 25%).

Foraging behavior.—Female mountain sheep foraged in larger groups (6.40 ± 0.99; mean ± SE) than did males (3.78 ± 1.01; ANOVA: $F_{1,27} = 5.04$, $P = 0.03$; Fig. 4). Females foraged closer to escape terrain (30.7 ± 5.10 m) than males (118.1 ± 18.92 m; ANOVA: $F_{2,26} = 9.24$, $P < 0.001$; Fig. 4). When I controlled for group size and distance to escape terrain, feeding efficiency (percentage of active time spent feeding) did not differ between sexes (ANCOVA $_{\text{overall}} F_{3,25} = 1.72$, $P = 0.18$; $_{\text{sex}} F_{1,25} = 0.78$, $P = 0.39$, Fig. 4), indicating the importance of those co-variates in affecting vigilance behavior. Similarly, when group size and distance to escape terrain were used as covariates, individual vigilance (e.g., percent alert) did not differ between sexes of mountain sheep (ANCOVA $_{\text{overall}} F_{3,25} = 1.76$, $P = 0.18$; $_{\text{sex}} F_{1,25} = 1.03$, $P = 0.319$, Fig. 4).

Females had higher mean (± SE) bite rates (bites/min) (forbs 30.88 ± 2.49, grasses 33.05 ± 2.00, shrubs 31.92 ± 2.69, unidentified plants 27.46 ± 2.68) on all forage classes than did males (forbs 24.26 ± 1.68, grasses 24.83 ± 1.60, shrubs 28.01 ± 2.36, unidentified plants 19.05 ± 0.79). The overall bite rate for female sheep (31.31 ± 1.26) was higher than for males (24.46 ± 0.96) for all forage classes combined (ANOVA $_{\text{sex}}$ $F_{1,95} = 7.36$, $P = 0.007$, Fig. 5). Bite rates were not significantly different between study areas (ANOVA $_{\text{study area}}$ $F_{3,95} = 0.85$, $P = 0.467$) or forage classes (ANOVA $_{\text{forage class}}$ $F_{3,95} = 1.86$, $P = 0.140$, Fig. 5) for both sexes combined. Similarly, there was no significant interaction between sex and forage class (ANOVA $_{\text{sex x forage class}}$ $F_{3,95} = 0.22$, $P = 0.883$). A Pearson Correlation test indicated that foraging efficiency was positively related to group size for males ($r = 0.62$, $P = 0.011$), but that relationship between foraging efficiency and group size was not significant ($r = 0.002$) for females ($P = 0.88$, Fig. 6). Foraging efficiency was negatively related to the distance from escape terrain for females ($r = -0.59$, $P = 0.021$), but the relationship between foraging efficiency and distance from escape terrain was not significant ($r = -0.34$) for males ($P = 0.21$, Fig. 7).

Diet composition.—Mountain sheep exhibited diverse diets as estimated from microhistological analyses of their feces; 57 species of plants were detected in male and female fecal samples. Mountain sheep in the Mono Basin consumed mostly forbs and shrubs (*Astragalus* and *Leptodactylon*) during winter (Table 2). Mountain sheep ate mostly shrubs (*Artemisia*) and graminoids (*Acnatherum*) in the southern region (Table 3, Fig. 8). Principal components analysis (PCA) indicated that mountain sheep in the Mono Basin exhibited differential patterns (Fig. 8) in diet composition when compared with mountain sheep in the Southern Region. Principal component 1 explained 43.9% of the variation in diets among mountain sheep and likely represented a continuum in altitude from lower elevation (positive loadings) to higher elevations (negative loadings). Principal component 2 explained 24.0% of the variation in diets among mountain sheep and probably represented a continuum from browsing (negative loadings) to grazing (positive loadings). Diets of male and female mountain sheep overlapped in both study regions, but mean PCA (PC1 and PC2) scores and their 95% confidence intervals indicated that patterns of separation in diets existed (Fig. 9).

MANOVA indicated there was an overall effect of gender on mean PCA scores of diet composition ($F_{2,77} = 4.09$, $P = 0.021$). Similarly, mean PCA scores of diet composition differed between mountain sheep from the Mono Basin and mountain sheep from the southern region ($F_{2,77} = 66.20$, $P < 0.0001$). The sex by region interaction was not significant ($F_{2,78} = 2.01$, $P = 0.14$). A Shannon index indicated diet diversity ($e^{\mathrm{H'}}$) was similar between sexes at the level of genus ($e^{\mathrm{H'males}} = 9.68$, $e^{\mathrm{H'females}} = 9.85$). A Shannon index indicated diet diversity was higher for male mountain sheep in the Mono Basin ($e^{\mathrm{H'}} = 34.42$) than for females ($e^{\mathrm{H'}} = 26.95$). Diet diversity was similar between sexes in the southern region (male $e^{\mathrm{H'}} = 18.80$, female $e^{\mathrm{H'}} = 21.97$).

Daily Movements.— Hourly movements (mean ± SE) for males ($n = 3$) ranged from 27 to 998 m ($\bar{X} = 208.13 \pm 20.6$ m). Hourly movements for females ($n = 6$) ranged from females ranged from 16 to 301 m ($\bar{X} = 69.27 \pm 8.28$ m). Daily movements for sexes ranged from 1.12 to 14.50 km ($\bar{X} = 4.10 \pm 3.69$ km). Daily movements of males (5.27 ± 1.85 km) also were significantly greater ($t_7 = -2.39$, $P = 0.048$) than for females (2.36 ± 0.096 km, Fig. 10).

Terrain ruggedness.—A 1-way MANOVA indicated significant overall differences in the use of rugged terrain between sexes ($F_{3,54} = 3.26$; $P = 0.02$; Fig 11). Moreover, there was a significant difference in ruggedness among areas (ANOVA $F_{3,56} = 10.04$; $P < 0.0001$). Mono Basin had the most rugged terrain overall ($P < 0.05$) and Wheeler Ridge had more rugged terrain ($P < 0.05$) than the Mt. Langley and Mt. Baxter study areas. Overall, females used more rugged terrain (2924.05 ± 1628.05, mean ± SE) than did males (2096.43 ± 1104.09, ANOVA $F_{1,56} = 9.19$, $P = 0.003$). Females used areas with significantly more variation in slope (70.77 ± 27.11) than males (66.71 ± 13.79, ANOVA $F_{1,56} = 9.66$ $P = 0.003$, Table 4). Angular deviation of aspect in female areas (124.20 ± 26.02) was not significantly different from areas used by males (117.36 ± 29.59, ANOVA $F_{1,56} = 0.15$, $P = 0.703$, Table 4).

DISCUSSION

I detected several important differences in foraging by male and female mountain sheep. Males foraged in smaller groups than did females and in areas that had a higher total biomass of forage than areas used by females, as predicted by the gastrocentric hypothesis (Barboza and Bowyer 2000, 2001). Females were observed in larger groups in areas that had less total biomass of forage than those used by males. This pattern is consistent with other studies involving mountain sheep, where males foraged in smaller groups than did females (Mooring et al. 2003), and males used areas with more available forage (Bleich et al. 1997) than those used by females. Additionally, males foraged farther from escape terrain (Fig. 4) than did females. This pattern of behavior has also been reported by Berger (1991) for mountain sheep in a desert environment.

Females had higher bite rates than did males for all forage classes (Fig. 5). The higher bite rates I detected in females most likely occurred because of smaller bite sizes taken by females than males, which may result in reduced handling time (e.g., mastication and rumination, Ruckstuhl et al. 2003). Females may have higher bite rates because of the trade-off between foraging efficiency and predation risk. Increasing bite rates combined with a more rapid rate of digestion (Barboza and Bowyer 2000, 2001) by females would allow them to spend less time with the head in a foraging position, which increases the chance of detecting a predator (Berger 1978, 1991; Ruckstuhl et al. 2003). Female mountain sheep also may need to increase bite rates in late spring when energy requirements are much higher because of costs of late gestation and lactation (Gross et al. 1996). These findings are consistent with previously published studies of sexual segregation in ungulates where females took smaller bites and foraged more selectively than did males (Miquelle et al. 1992, Spaeth et al. 2004). Additionally, males may be less selective of plant parts because they can more easily digest large quantities of low-quality forage (Barboza and Bowyer 2000, 2001); hence, males take larger bites with a concomitant increase in handling time. By taking larger bites, males must increase the amount of the time to masticate and breakdown plant tissue before entering the rumen, thus increasing handling time and reducing bite rate.

Differences in feeding behavior between sexes also were related to group size and distance to escape terrain. Foraging efficiency was positively correlated with group size for males, but not for females (Fig. 6). This outcome probably occurred because most (72%) groups of females usually had young present, and were larger overall, than groups of males. Foraging efficiency was more influenced by distance from escape terrain for females, and was negatively correlated with that variable (Fig. 7). Foraging efficiency of males was not significantly correlated with distance from escape terrain (Fig. 7); females, regardless of group size, remained much closer to escape terrain than did males. These results support patterns of mountain sheep feeding behavior in other studies, where foraging efficiency was positively related to group size (Berger 1978) and negatively related to distance from escape terrain for both sexes (Risenhoover and Bailey 1985), although those authors did not test for differences between sexes. These results are consistent with patterns observed by Bleich et al. (1997), who noted that proximity to escape terrain may be more important in defining habitat selection by female than male mountain sheep.

I rejected the hypothesis that visibility would not differ at foraging sites used by male and female sheep. Even though our sample sizes were small, males foraged in areas with significantly less visibility (56%) than areas where females foraged (74%). Visibility and distance to escape terrain influence how mountain sheep allocate time spent foraging, vigilance for predators, and other behaviors, such as alert-alarm postures. Further, interactions between forage quality, availability of escape terrain, and visibility may influence where females with young feed; foraging efficiency increased when mountain sheep were closer to escape terrain and visibility was high in a population of mountain sheep in the Rocky Mountains (Risenhoover and Bailey 1985). I observed variation in the openness of habitats used by the sexes and my results are similar to those of previous authors (Berger 1991, Bleich et al.1997), who reported that females preferred more open habitats than males. Furthermore, because there was more variation in visibility in habitats used by males, those individuals may be willing to occupy riskier foraging sites with abundant forage to obtain the amount of food necessary for maintenance of body reserves during winter. Indeed, a larger proportion of male mountain sheep have been killed by mountain lions (*Puma concolor*) than females in the Sierra Nevada (California Department of Fish and Game, unpublished data). Additionally, Bleich et al. (1997) reported that males occupied areas with more predators than did females when the sexes were segregated.

I detected several important patterns in the diets of male and female mountain sheep in the Sierra Nevada during winter. Most notably, diet composition of mountain sheep varied by sex and study area. PCA indicated that mountain sheep from the 2 study regions differed considerably in composition (Fig. 8), most likely as a result of foraging in differing plant community types associated with different elevations. Mountain sheep in the Mono Basin foraged mostly on plants of the alpine fell-fields community (Munz 1974), and included *Leptodactylon, Astragalus,* and *Carex*. Mountain sheep in the southern region, however, foraged mostly on plants in the sagebrush scrub community and included more *Artemisia, Acnatherum, Festuca,* and *Agropyron* in their diets during winter. Further, diets of male and female mountain sheep in the southern region exhibited significant separation in diets (Fig. 9); males had a broader dietary niche (PC2) than those of females and tended to eat more shrubs such as *Artemisia*, wheras females in the southern region tended to eat more graminoids such as *Acnatherum, Poa,* and *Festuca*. In the Mono Basin, males diets were more characteristic of lower-elevation community types (PC1) and contained more *Artemisia, Acnatherum, Poa, and Festuca*, whereas diets of females in the Mono Basin were associated with higher elevations and contained mostly *Leptodactylon*, *Astragalus*, and *Carex*. Consistent with my predictions, larger-bodied males exhibited a broader dietary niche in the southern region and generally consumed more shrubs than smaller-bodied females that had a narrower dietary niche and that consumed more graminoids. Nonetheless, males and females in the Mono Basin exhibited the opposite pattern driven mostly by the disparity in habitat types that each sex used for foraging. Females used higher elevation plant communities during winter, resulting in a much greater abundance of *Leptodactylon* in the diet (Table 2), whereas males foraged in plant communities of lower elevation that contained more *Artemesia* and *Acnatherum*.

The differences in diet composition I detected are consistent with a niche-based approach to understanding sexual segregation (Bowyer 2004, Bowyer and Kie 2004, Kie and Bowyer 1999), where overlap on 1 niche axis is accompanied by avoidance on another axis. I identified spatial separation of sexes in both the Mono Basin and the southern region; however, there was less spatial separation between sexes in the Mono Basin because of limited wind-swept areas (in which sheep forage) at high elevation, especially during the heavy snow winter under which we observed them. Mountain sheep in the southern region spatially segregated, with females using higher-elevation sites than males. In that region, there was considerably less overlap on the dietary niche axis because the sexes were partitioning space. These results are consistent with previous studies where dietary and spatial niches between sexes and species of ungulates were compared (Kie and Bowyer 1999, Stewart et al. 2003*b*). These results provide additional support for the concept that the sexes of dimorphic ungulates should be managed as if they were different, but co-existing species (Bowyer 2004, Bowyer et al. 2001; Kie and Bowyer 1999; Stewart et al. 2003*a*).

Although differences occurred between sexes in diet composition and forage biomass, my hypothesis that diets of male and female mountain sheep were of different quality during winter (as indexed by fecal nitrogen) was rejected. These results may be confounded by the role that sexual dimorphism and differences in allometry between sexes play in digesting forages of differing fibrosity and quality (Jenks et al. 1994, Barboza and Bowyer 2000, 2001). Previous studies have demonstrated females, because of changes in gut allometry, may be better at extracting nitrogen from forage than are males (Jenks et al. 1994). Furthermore, there is a potential for some forages, such as *Artemisia*, to contain large amounts of tannins (Dearing 1996) that inhibit the extraction of protein in the diets of many ungulates. Some species, however, may have evolved saliva characteristics that can mitigate complex tannins (Robbins et al. 1987, Hagerman and Robbins 1993, Spaeth et al. 2002). Indeed, diets of male sheep in both the Mono Basin and the southern region contained more *Artemisia* than those of females. If females are more efficient at extracting nitrogen from forage, and they select forages of higher quality than do males, then fecal nitrogen may not be the appropriate index of diet quality to test for differences between sexes. Additionally, differences occurred between study areas for some months (Table 1, Fig. 2). Moreover, diet quality for mountain sheep in the Mono Basin was significantly lower than all other study areas, likely a result of occupying high elevations with lower quality forages during winter. Although fecal nitrogen levels were lower for mountain sheep occupying the higher elevations of Mono Basin (1.3 to 2.2%), these levels are within or higher than other published values reported for mountain sheep in the Rocky Mountains (0.8 – 3.2 %, Irwin et al. 1993; 1.2 – 1.5%, Blanchard et al. 2003) during winter. Furthermore, these fecal nitrogen levels are above the necessary minimum level of 1.3% reported by Irwin et al. (1993) for a winter maintenance diet, indicating mountain sheep in the Mono Basin were not nutritionally deficient during the 2005 winter.

On average, male mountain sheep moved farther per day than did females (Fig. 10). The larger daily movements of males may be explained by the need to acquire a greater overall amount of food per day (Gross 1996, Barboza and Bowyer 2000, 2001) than needed by females. Male mountain sheep, owing to their larger rumen, can use lower-quality forage with higher fiber content (Bowyer 2004). Further, allometric differences in gut length between males and females predict male ruminants require longer periods of non-activity for rumination (Demment and Van Soest 1985, Jenks et al. 1994, Ruckstuhl 1998, Bowyer and Barboza 2000, 2001). Female mountain sheep are approximately 60% the size of males (Bleich et al. 1997, Weckerly 1998, LeBlanc et al.

2001), and spend more time foraging and less time ruminating throughout the day (Ruckstuhl 1998). The combination of these gastronomical requirements and sparsely vegetated winter ranges in the Sierra Nevada, could explain why male mountain sheep exhibit greater movements per day than did females.

Female mountain sheep provide all parental care to young and use steep, rocky terrain to detect and evade predators (Festa-Bianchet 1988, Berger 1991, Bleich et al. 1997, Rachlow and Bowyer 1998). Consequently, females remain closer to escape terrain than do males. Movements by males likely increase the rate at which they encounter new foraging areas (Mysterud et al. 2001), thereby enabling them to acquire resources important for weight gain and horn growth, both of which are essential for future reproductive success (LeBlanc et al. 2001). Males require abundant, but lower-quality forage than females; therefore, males may move longer distances to obtain enough biomass for rumen fill (Main and Coblentz 1996, Gross et al. 1996). Differences in daily movements between sexes of mountain sheep could result from intersexual differences in activity budgets (Ruckstuhl 1998), because males have a larger gut capacity (absolute rumen size) and require longer periods of rumination between foraging bouts (Barboza and Bowyer 2000, 2001) than do females. Nevertheless, my data are inconsistent with those of Ruckstuhl (1998), who reported that females moved greater distances per day than males.

Females occupied more rugged terrain than did males (Fig 11). Those results are consistent with those of Bleich et al. (1997), who reported that females used more rugged terrain than did males, and that males occupied more gentle slopes (and even flat terrain) when foraging. I also observed that overall terrain ruggedness was significantly different across geographic locations, but the pattern of females using more rugged terrain was consistent, with the exception of the Mt. Langley population. Females likely used areas of more rugged terrain to reduce the risk of predation and for protection of their more-vulnerable offspring (Festa-Bianchet 1988, Berger 1991, Bleich et al. 1997). Several studies have reported that male ungulates often use less-rugged terrain while incurring a cost in predation risk to obtain high-quality or abundant food sources (Wehausen 1980, Berger 1991, Molvar and Bowyer 1994, Bleich et al. 1997). Main and Coblentz (1990) attributed this phenomenon to the differing life-history strategies between sexes: females maximize the chance for successful gestation and protection of offspring, and males attempt to maximize the increase in post-rut body condition.

These results also support hypotheses related to predation (Bleich et al. 1997, Bowyer 2004) as a mechanism for sexual segregation in mountain sheep. The predation-risk hypothesis explains behavioral differences whereby ruminants either minimize the predation risk to forage ratio, or make trade-offs between forage and security (Bowyer et al. 1998, Kie and Bowyer 1999). Female mountain sheep, especially those with young, may have smaller daily spatial movements as a result of the conflict between nutritional requirements for future reproduction (i.e., gestation and lactation) and security for recruiting existing young into the breeding population (Wehausen 1980). Indeed, 72% of female groups in this study contained ≥ 1 young (California Department of Fish and Game, unpublished data). Bleich et al. (1997) reported male mountain sheep were more likely to occupy risky habitats (defined as >300 m from escape terrain and with decreased visibility) than females either with or without young. My results are consistent with other published data where female mountain sheep without young, as well as non-pregnant individuals, exhibit behaviors similar to other reproductive conspecifics because of group foraging benefits (Festa-Bianchet 1988).

I identified several important differences in the feeding behavior and habitat use of male and female mountain sheep in the Sierra Nevada. Those differences provide conservationists and land managers with detailed knowledge of sex-specific habitat requirements for these endangered herbivores. Furthermore, behavioral differences exist in mountain ungulates that could be used in population-level management decisions and monitoring. For instance, male mountain sheep in my study used ranges with more shrub and overall biomass of vegetation than ranges used by females in winter. Additionally, I observed variation in visibility of habitat used by male and female mountain sheep, with females using more open habitats while males used areas with less visibility.

MANAGEMENT IMPLICATIONS

Group size and escape terrain should be considered when making some management decisions because of their effects on foraging behavior (Risenhoover and Bailey 1985). This study indicated that group size may be more important for males to enhance foraging efficiency, whereas proximity to escape terrain may be a more important requirement for females to increase foraging efficiency. These differences could be used when determining a minimum number of animals for translocation and whether the potential translocation sites provide adequate habitat (e.g. escape terrain for females, abundant forage for males). Translocations that move only a few large males may be a poor conservation practice because mountain sheep are highly polygynous (Krausman and Bowyer 2003).

Habitat loss, protection, and management are key issues for the conservation of many wildlife species and, especially, for mountain sheep (Rubin and Bleich 2005); however, land managers traditionally have considered habitat needs identical for males and females. My research indicates that specific habitat requirements may be important for each sex. For instance, protection of meadow systems containing an abundance of forbs and grasses that are located immediately adjacent to escape terrain could be beneficial for females to enhance foraging efficiency. Similarly, habitat treatments that are designed with sex-specific considerations, such as removal of over-story vegetation (i.e., pinyon juniper and other conifers) adjacent to escape terrain may be a useful for increasing habitat on female winter ranges. Additionally, habitat treatments beneficial to one sex may be detrimental to the other (Bowyer et al. 2001; Rubin and Bleich 2005; Stewart et al. 2003*a*). In the Sierra Nevada, the use of fire as range-management tool could potentially benefit females by increasing regeneration of forbs and grasses while simultaneously increasing visibility, but to the short-term detriment of males. Controlled burns in areas occupied by male sheep may reduce the overall biomass of vegetation and reduce shrub cover. Nonetheless, management that favors females may be prudent given the polygynous mating system and the need to favor population growth for recovery of mountain sheep in the Sierra Nevada.

When niche requirements vary greatly between male and female ungulates, managers might best consider them as if they were different species (Kie and Bowyer 1999, Bowyer et al. 2001, Stewart et al. 2003*a*, Bowyer 2004). Thus, recovery of mountain sheep in the Sierra Nevada could be enhanced by management strategies that incorporate those differential niche requirements. For example, proposals for translocation should acknowledge that females prefer areas with a diversity of terrain features that provide security from predation. Further, spatial use of habitats may vary greatly between sexes of mountain sheep. Males in this study exhibited much larger movement rates on a daily basis. These longer distances traveled should be considered when making land-management decisions such as determining risks associated with grazing allotments for domestic sheep, which can serve as a source of diseases for mountain sheep (DeCeasare and Pletcher 2006). Moreover, sexes use space differently during segregation and this has implications for wildlife managers seeking to improve performance of population estimation methods (Bleich et al. 1997, Bowyer 2004, Rubin and Bleich 2005). During winter, mountain sheep are sexually segregated, which may affect estimates of male to female ratios if one sex or the other is undercounted during surveys (Bleich et al. 1997). I demonstrated that females generally occupy more rugged terrain, which could affect visibility bias associated with population estimates. Estimating the number of males in a population survey also could be problematic if sheep are more likely to move greater distances on a daily basis, and thereby create the potential for double counting or under-estimation if surveys are not properly designed. Mountain sheep in the Sierra Nevada are endangered, and may require extreme measures to ensure their survival. Management and conservation plans must consider the disparate requirements of the sexes of this unique mountain ungulate.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-276.

BARBOZA, P. S., AND R. T. BOWYER. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. Journal of Mammalogy 81:473–489.

BARBOZA, P. S., AND R. T. BOWYER. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. Alces 37:275–292.

BARTEN, N. L., R. T. BOWYER, AND K. J. JENKINS. 2001. Habitat use by female caribou: tradeoffs associated with parturition. Journal of Wildlife Management 65:77-92.

BELOVSKY, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology 14:105-134.

BERGER, J. 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. Behavioral Ecology and Sociobiology 4:91-99.

BERGER, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Animal Behaviour 41:61-77.

BLANCHARD P., M. FESTA-BIANCHET, J. M. GAILLARD, AND J. T. JORGENSON. 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. Journal of Wildlife Management 67:477-484.

BLEICH V. C., R. T. BOWYER, AND J. D. WEHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1–50.

BOWYER, R. T. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy 65:410–417.

BOWYER, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy 85:1039-1052.

BOWYER, R.T., AND J.G. KIE. 2004. Effects of foraging activity on sexual segregation in mule deer. Journal of Mammalogy 85:498-504.

BOWYER, R. T., B. M. PIERCE, L. K. DUFFY, AND D. A. HAGGSTROM. 2001. Sexual segregation in moose: effects of habitat manipulation. Alces 37:109-122.

BOWYER, R. T., J. G. KIE, AND V. VANBALLENBERGHE. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415-425.

BOWYER, R. T., V. VAN BALLENBERGHE, J. G. KIE, AND J. A. K. MAIER. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. Journal of Mammalogy 80:1070-1083.

CHOW, L. S. 1984. Population dynamics and movement patterns of bighorn sheep reintroduced in the Sierra Nevada, California. M.S. Thesis. University of California, Berkeley.

COGGINS, V. L. AND P. E. MATTHEWS. 1992. Lamb survival and herd status of the Lostine bighorn herd following a *Pasteurella* die-off. Proceedings of the Biennial Symposium of North American Wild Sheep and Goat Council 8:147-154.

DECESARE, N. J., AND D. H. PLETSCHER. 2006. Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. Journal of Mammalogy 87:531-538.

DEARING, M. D. 1996. Disparate determinates of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. Oecologia 108:467-478.

DEMMENT, M. W., AND P. J. VAN SOEST. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. American Naturalist 125:641-672.

FESTA-BIANCHET, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580-586.

FESTA-BIANCHET, M., AND M. APOLLONIO. 2003. Animal behavior and wildlife conservation. Island Press, Washington, Covelo, and London.

GAILLARD, J. M., M. FESTA-BIANCHET, N. G. YOCCOZ, A. LOISON, AND C. TOIGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

GEIST, V. 1968. On the interrelation of external appearance, social behavior, and social structure of mountain sheep. Zeitschrift für Tierpsychologie 25:199-215.

GROSS, J. E, P. U. ALKON, AND M. W. DEMMENT. 1996. Nutritional ecology of dimorphic herbivores: digestion and passage rates in Nubian ibex. Oecologia 107:170-178.

HAGERMAN, A. E., AND C. T. ROBBINS. 1993. Specificity of tannin-binding salivary proteins relative to diet selection by mammals. Canadian Journal of Zoology 71:628-633.

HILL, M. 1975. Geology of the Sierra Nevada. University of California Press, Berkeley.

HODGMAN, T. P., B. B. DAVITT, AND J. R. NELSON. 1996. Monitoring mule deer diet quality and intake with fecal indices. Journal of Range Management 49:215-222.

ILLIUS, A. W. AND I. J. GORDON. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology 56:989-999

INYO COUNTY WATER DEPARTMENT. 2006. Owens Valley Monitor 2005-2006 annual report. http://www.inyowater.org/Annual_Reports.

JENKS, J. A, D. M. LESLIE, R. L. LOCHMILLER, AND M. A. MELCHIORS. 1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. Journal of Mammalogy 75:1045-1053.

KIE, J. G., AND R. T. BOWYER. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80:1004–1020.

KRAUSMAN, P. R., AND R. T. BOWYER. 2003. Mountain sheep (*Ovis canadensis and O. dalli*). Pages 105-118 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. The Johns Hopkins University Press, Baltimore, Maryland.

KRAUSMAN, P. R., J. J. HERVERT, AND L. L. ORDWAY. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.

LITTLE, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.

LOISON, A., M. FESTA-BIANCHET, J. M. GAILLAIRD, J. T. JORGENSON, AND J. M. JULIAN. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539-2554.

LEBLANC, M., M. FESTA-BIANCHET, AND J. T. JORGENSON. 2001. Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. Canadian Journal of Zoology 79:1661-1670.

MAIN, M. B., AND B. E. COBLENTZ. 1990. Sexual segregation among ungulates: a critique. Wildlife Society Bulletin. 18:204-210.

MAIN, M. B., AND B. E. COBLENTZ. 1996. Sexual segregation in Rocky Mountain mule deer. Journal of Wildlife Management 60:479-507.

MAIN, M. B. 1998. Sexual segregation in ungulates: a reply. Journal of Mammalogy 79:1410-1415.

MCGARIGAL, K., S. CUSHMAN, AND S. STAFFORD. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York.

MIQUELLE, D. G., J. M. PEEK, AND V. VAN BALLENBERGHE . 1992. Sexual segregation in Alaskan moose. Wildlife Monographs 122:1-57.

MOLVAR, E. M., AND R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. Journal of Mammalogy 75:621-630.

MOORE, P E. 1991. Forage site characteristics of reintroduced mountain sheep in the Sierra Nevada, California. M.S. Thesis. University of California, Berkeley.

MOORING, M. S., T. A. FITZPATRICK, J. E. BENJAMIN, I. C. FRASER, T. T. NISHIHIRA, D. D. REISIG, AND E. M. ROMINGER. 2003. Sexual segregation in desert bighorn sheep (*Ovis canadensis mexicana*). Behaviour 140:183-207.

MUNZ, P. A. 1974. A flora of southern California. University of California Press, Berkeley, California.

MYSTERUD, A., F. J. PEREZ-BARBERIA, AND I. J. GORDON. 2001. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. Oecologia 127:30-39.

NATIONAL OCEANIC ATMOSPHERIC AND ADMINISTRATION. 2006. Western Regional Climate Center Report. Reno, NV, USA. http://www.wrh.noaa.gov/vef/regionalclimate.php

NICHOLSON, M. C., R. T. BOWYER, AND J. G. KIE. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

OEHLER, M. W., R. T. BOWYER, AND V. C. BLEICH. 2003. Home ranges of female mountain sheep, *Ovis canadensis nelsoni*: effects of precipitation in a desert ecosystem. Mammalia 67:385-401.

OEHLER, M. W., V. C. BLEICH, R. T. BOWYER, AND M. C. NICHOLSON. 2005. Mountain sheep and mining: implications for conservation and management. California Fish and Game 91:149-178.

ONDERKA, D. K., S. A. RAWLUK, AND W. D. WISHART. 1988. Susceptibility of Rocky Mountain bighorn sheep and domestic sheep to pneumonia induced by bighorn and domestic livestock strains of *Pasteurella haemolytica*. Canadian Journal of Veterinary Research. 52:439-444.

PEREZ-BARBERIA, F. J., I. J. GORDON, AND M. PAGEL. 2002. The origins of sexual dimorphism in body size of ungulates. Evolution 56:1276-1285.

PIERCE, B. M., R. T. BOWYER, AND V. C. BLEICH. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533-541.

PHILLIPS, F. M, M.G. ZREDA, L. V. BENSON, M. A. PLUMMER, D. ELMORE, AND P. SHARMA. 1996. Chronology of fluctuations in late Pleistocene Sierra Nevada glaciers and lakes. Science 274: 749-751.

RACHLOW, J. L., AND R. T. BOWYER. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. Journal of Mammology 72:487-492.

RACHLOW, J. L., AND R. T. BOWYER. 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? Journal of Mammology 75:328-337.

RACHLOW, J. L., AND R. T. BOWYER. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal tradeoffs. Journal of Zoology (London) 245:457-465.

RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. American Naturalist 122:917–938.

REESE, G. A., R. L. BAYNE, AND N. E. WEST. 1980. Evaluation of double-sampling estimators of subalpine herbage production. Journal of Range Management 33:300-306.

REICH, R. M., C. D. BONHAM, AND K. K. REMINGTON. 1993. Technical Notes: double-sampling revisited. Journal of Range Management 46:88-90.

RICKLEF, R. E., AND G. L. MILLER. 2001. Ecology. 4th ed. W. H. Freeman, New York, USA.

RISENHOOVER, K. L., AND J. A. BAILEY. 1985. Foraging ecology of mountain sheep: implications for habitat management. Journal of Wildlife Management 49:797-804.

ROBBINS, C. T., T. A. HANEY, A. E. HAGERMAN, D. L. BAKER, C. C. SCHWARTZ, AND W. W. MAUTZ. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98-107.

RODGERS, A. R., AND A. P. CARR. 1998. HRE: The home range extension for ArcView. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

RUBIN, E. S., AND V. C. BLEICH. 2005. Sexual segregation: a necessary consideration in wildlife conservation. Pages 379-391 i*n* K. E. Ruckstuhl and P. Neuhaus, editors. Sexual segregation in vertebrates: ecology of the two sexes. Cambridge University Press, Cambridge, United Kingdom.

RUCKSTUHL, K. E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. Animal Behaviour 56:99-106.

RUCKTUHL, K. E., AND M. FESTA-BIANCHET. 2001. Group choice by subadult bighorn rams: tradeoffs between foraging efficiency and predator avoidance. Ethology 107:161-172.

RUCKTUHL, K. E., AND P. NEUHAUS. 2001. Behavioral synchrony in ibex groups: effects of age, sex, and habitat. Behaviour 137:361-377.

RUCKTUHL, K. E., AND P. NEUHAUS. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. Biological Review 77:77-96.

RUCKTUHL, K. E., M. FESTA-BIANCHET, AND J. T. JORGENSON. 2003. Bite rates in Rocky Mountain bighorn sheep (*Ovis canadensis*): effects of season, age, sex, and reproductive status. Behavioral Ecology and Sociobiology 54:167-173.

SAS INSTITUTE. 1999. SAS user's manual. Version 8.02. SAS Institute, Cary, North Carolina, USA.

SPAETH, D. F., R. T. BOWYER, T. R. STEPHENSON, AND P. S. BARBOZA. 2004. Sexual segregation in moose *Alces alces*: an experimental manipulation of foraging behavior. Wildlife Biology 10:59-72.

SPAETH, D. F., R. T. BOWYER, T. R. STEPHENSON, AND P. S. BARBOZA, AND V. VAN BALLENBERGE. 2002. Nutritional quality of willows for moose: effects of twig age and diameter. Alces 38:143-154.

SPARKS, D. F., AND J. C. MALECHEK. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21:264-265.

STEWART, K. M., T. E. FULBRIGHT, D. L. DRAWE, AND R. T. BOWYER. 2003*a*. Sexual segregation in white-tailed deer: responses to habitat manipulations. Wildlife Society Bulletin 31:1210-1217.

STEWART, K. M., R. T. BOWYER, J. G. KIE, B. L. DICK, AND M. BEN-DAVID. 2003*b*. Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? Écoscience 10:297-302.

U.S. FISH AND WILDLIFE SERVICE. 2003. Draft recovery plan for the Sierra Nevada bighorn sheep. U.S. Fish and Wildlife Service, Portland, Oregon.

WECKERLY, F. W. 1998. Sexual size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 79:33–52.

WEHAUSEN, J. D. 1980. Sierra Nevada bighorn sheep: history and population ecology. Ph.D. dissertation, University of Michigan, Ann Arbor.

WEHAUSEN, J. D. 1992. The role of precipitation and temperature in the winter range diet quality of mountain sheep of the Mount Baxter herd, Sierra Nevada. Biennial Symposium on North American Wild Sheep and Goat Council. 8:279-292.

WEHAUSEN, J. D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24:471-479.

WEHAUSEN, J. D., V. C. BLEICH, AND R. R. RAMEY II. 2005. Correct nomenclature for Sierra Nevada bighorn sheep. California Fish and Game 91:216-218.

ZAR, J. 1999. Biostatistical Analysis. Fourth ed. Prentice Hall Inc., Upper Saddle River, New Jersey.

Table 1. Fecal nitrogen (ash-free basis) of adult male and female mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, USA, during winter 2006.

	Fecal N (%)					Fecal N (%)				
	Male			Elevation (m)		Female			Elevation (m)	
Herd	*n*	$\overline{X}$	*SE*	$\overline{X}$	*SE*	*n*	$\overline{X}$	*SE*	$\overline{X}$	*SE*
Langley										
Feb.	4	1.58	0.17	2262	_	5	1.92	0.18	2262	_
March	3	1.91	0.24	2097	_	7	1.51	0.08	2005	9.89
April	6	2.28	0.11	1829	5.26	6	1.87	0.11	1970	_
Baxter										
Jan.						3	2.31	0.32	1709	40.3
Feb.	1	2.63	_	1715	_	7	2.23	0.22	1680	71.5
March	2	2.48	_	1531	_	5	2.77	0.13	1530	_
April	5	2.82	0.09	1729	34.6	5	2.49	0.51	1787	36.2
Wheeler										
Jan.	7	1.74	0.07	1891	14.2	3	2.01	0.21	1737	_
Feb.	4	1.44	0.20	2045	58.4	6	1.54	0.15	2280	58.3
March	4	2.25	0.23	1836	_	10	2.07	0.22	2197	10.2
April	6	2.71	0.19	1928	27.6	6	2.25	0.20	2255	40.5
Mono										
Jan.	5	1.36	0.08	3494	_	6	1.22	0.05	3463	_
Feb.	2	1.46	_	3564	_	4	2.35	0.54	3092	226.1
March	7	1.50	0.12	3520	22.1	3	1.44	0.13	3477	21.2
April	5	1.75	0.13	3605	64.1	10	1.43	0.12	3587	64.1

Table 2. Descriptive statistics for diet analyses of male and female mountain sheep in the northern Sierra Nevada, Mono County, California, USA, during winter 2006**.**

	Mono Basin			
	Male (*n* = 16)		Female (*n* = 9)	
Genus	$\overline{X}$	*SE*	$\overline{X}$	*SE*
Agropyron	7.7	1.3	5.2	1.4
Artemisia	8.6	1.6	5.8	2.1
Astragalus	7.0	2.5	9.8	4.0
Carex	6.9	2.4	7.3	1.7
Festuca	6.4	1.3	4.6	1.4
Leptodactylon	13.4	3.3	23.0	6.2
Poa	7.0	1.5	5.9	1.2
Acnatherum	9.3	2.0	6.1	1.7
Other	33.7	-	32.3	-

*****Note: List only includes plant genera that comprised more than 5% percent of total diet.

Table 3. Descriptive statistics for diet analyses of male and female mountain sheep in the southern Sierra Nevada, Inyo County, California, USA, during winter 2006**.**

	Southern Region			
	Male (*n* = 27)		Female (*n* = 31)	
Genus	$\overline{X}$	*SE*	$\overline{X}$	*SE*
Agropyron	8.2	1.4	9.2	0.9
Artemisia	31.1	3.3	21.7	1.7
Festuca	7.3	1.4	9.5	1.2
Poa	5.9	1.0	8.7	1.1
Acnatherum	18.1	2.3	18.8	2.0
Other	29.4	-	32.1	-

*****Note: List only includes plant genera that comprised more than 5% percent of total diet.

Table 4. Mean (± SD) use of rugged terrain by population subgroups of mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, during winter 2005-2006. Ruggedness values, as indexed by variation in standard deviation of slope (SD) and angular deviation (AD) in aspect are presented with sample sizes.

		Terrain Ruggedness			
Population Subgroup	*n*	SD Slope	AD Aspect	Ruggedness	P^a
Mt. Langley					
Male	4	10.9 ± 4.1	136.2 ± 37.5	2,390.2 ± 752.4	
Female	10	13.2 ± 3.59	150.4 ± 16.4	2,196.7 ± 635.2	*
Mt. Baxter					
Male	5	10.7 ± 3.8	102.8 ± 8.5	1,124.5 ± 447.3	
Female	7	16.5 ± 4.2	97.4 ± 12.1	1,641.1 ± 568.1	**
Wheeler Ridge					
Male	16	18.5 ± 6.8	106.8 ± 19.2	2,026.1 ± 979.5	
Female	15	30.4 ± 15.2	115.1 ± 15.6	3,478.9 ± 1,686.8	**
Mono Basin					
Male	4	22.6 ± 14.6	158.8 ± 33.1	3,298.8 ± 1,450.5	
Female	3	38.4 ± 14.1	150.6 ± 23.5	5,567.5 ± 1,076.7	*

[a] P values are from within sex ANOVAs of the composite ruggedness index; * $P > 0.05$, ** $P \leq 0.05$. The overall MANOVA indicated significant differences between males and females among study areas (MANOVA, $F_{3,54} = 3.26$; $P = 0.028$).

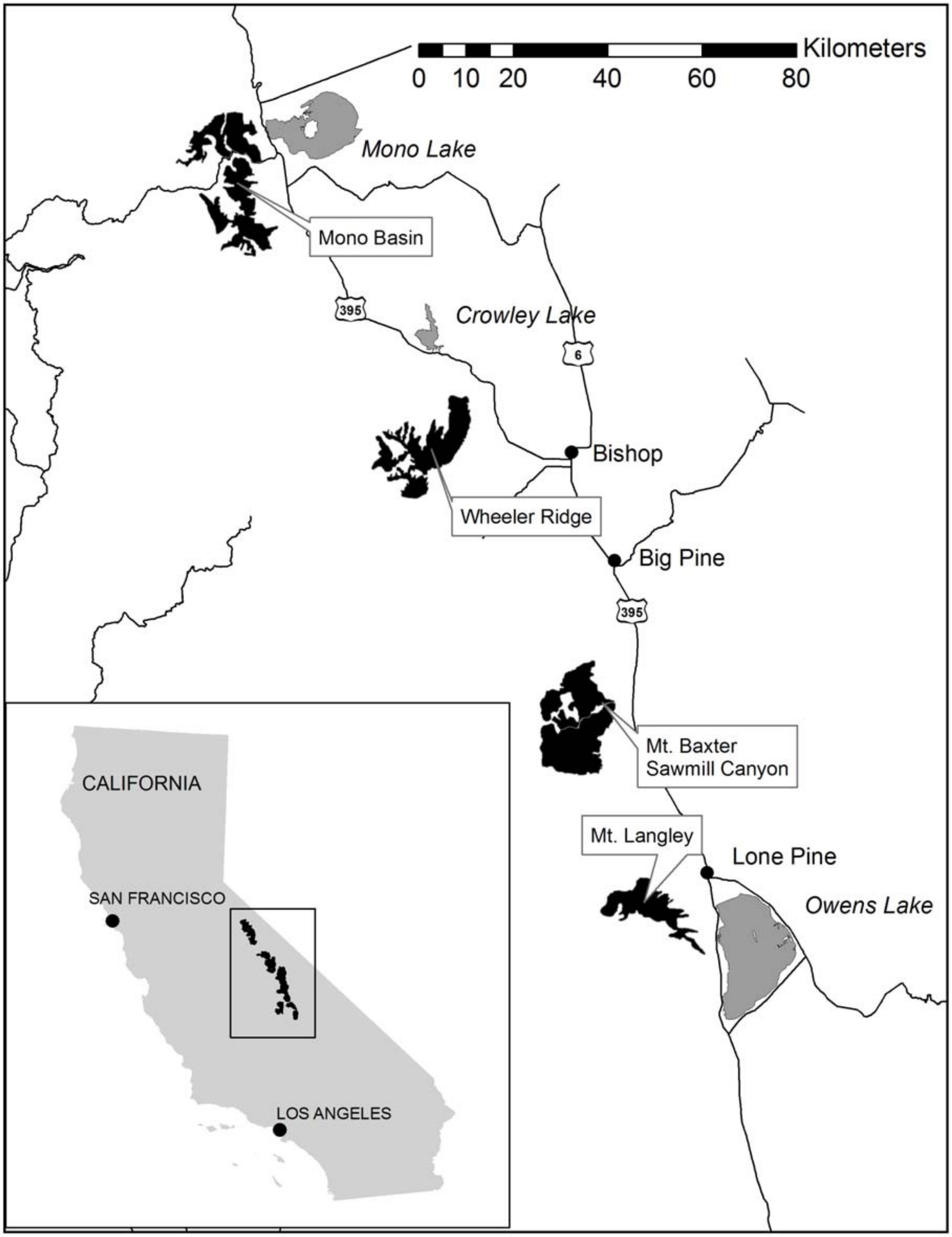

Figure 1. Location of mountain sheep study areas (black polygons), Inyo and Mono counties, California, USA, 2005-2007.

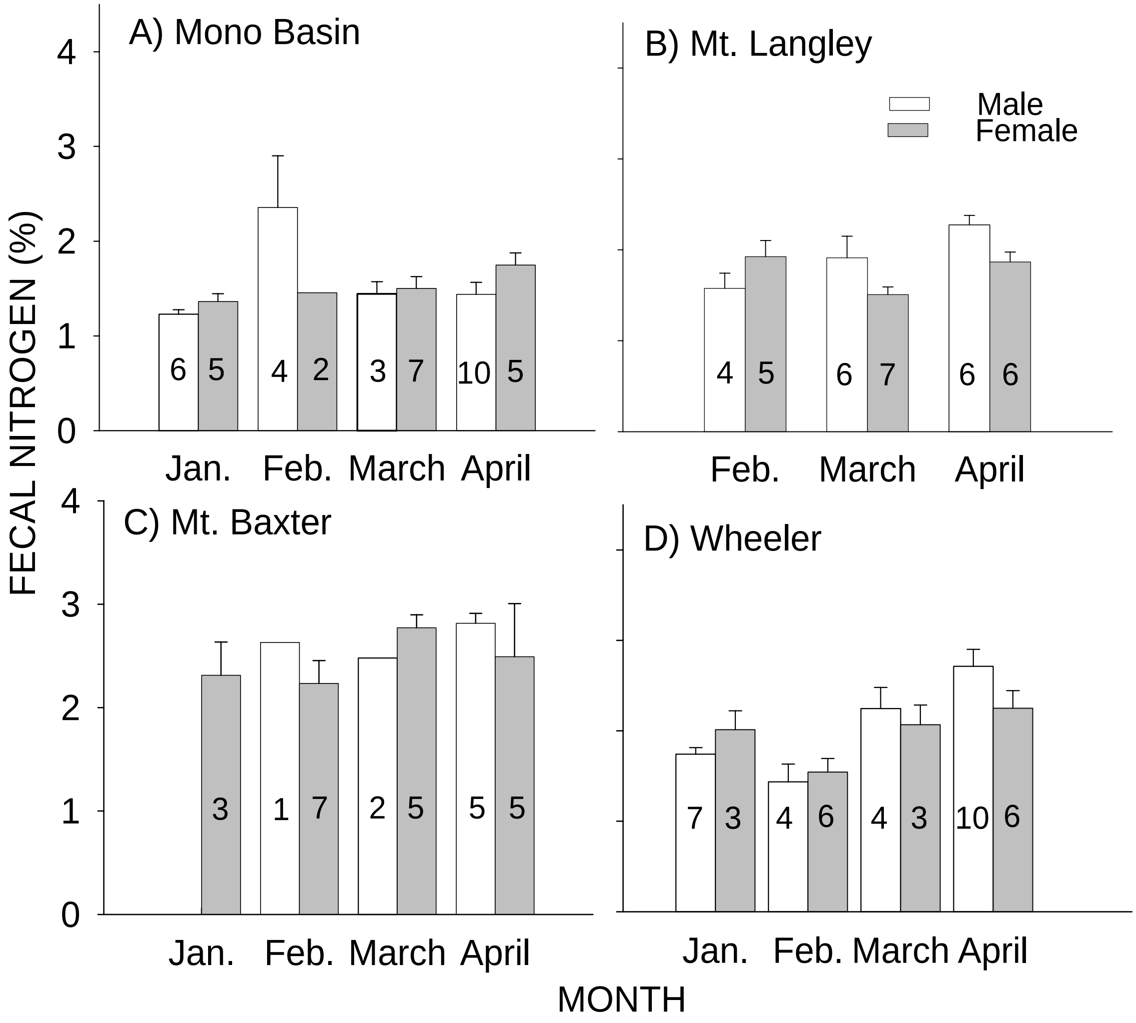

Figure 2. Mean (+ SE) monthly fecal nitrogen for adult male and female mountain sheep from the Sierra Nevada, Inyo and Mono counties, California, USA, during 2006. Numbers inside bars indicate sample sizes.

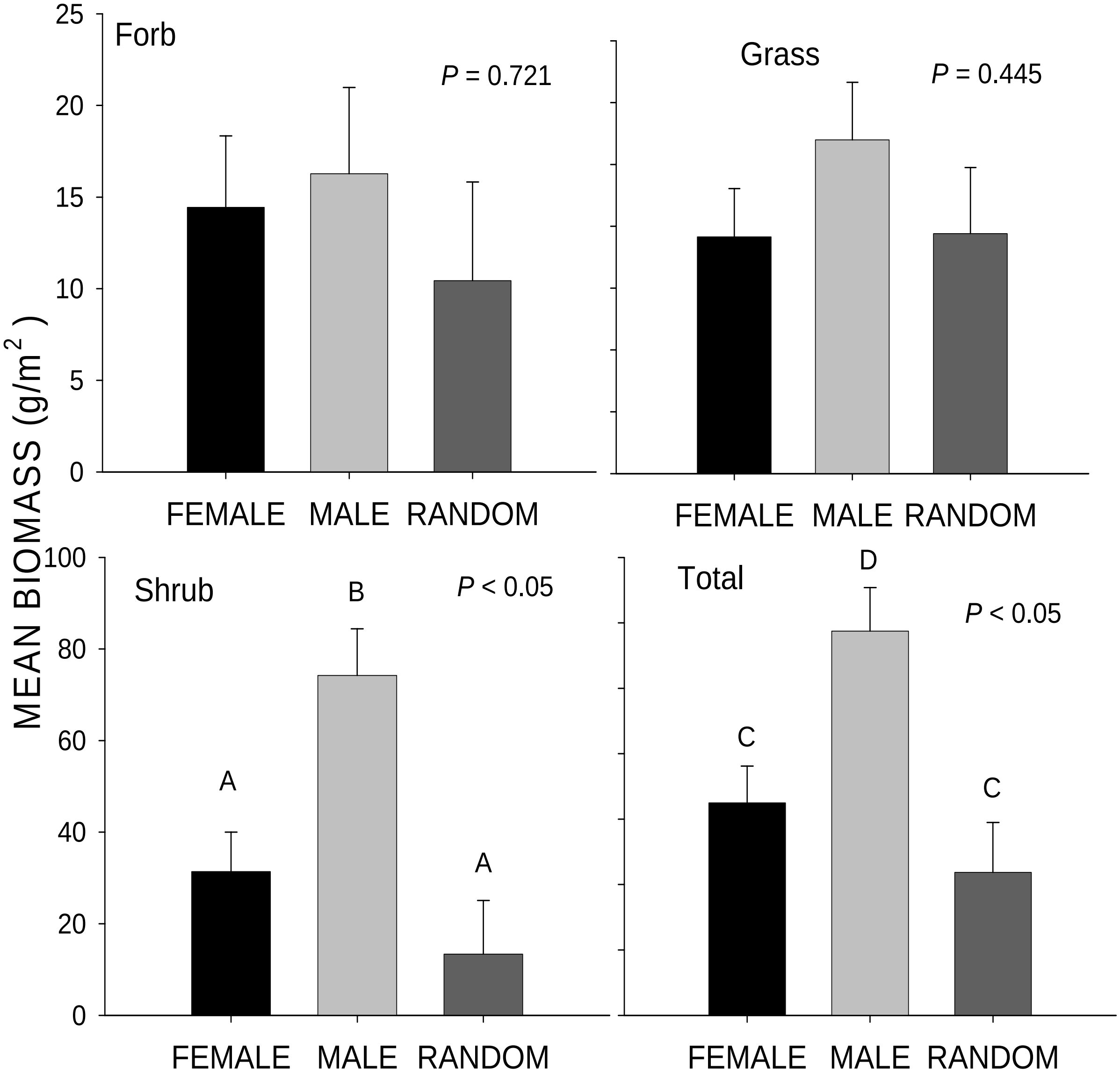

Figure 3. Mean (+ SE) wet weight biomass of 1-m vegetation plots measured in male (*n* = 11), female (*n* = 20), and random (n = 18) locations for 3 forage classes (forbs, grasses, shrubs) and total biomass in the Sierra Nevada, Inyo and Mono counties, California, USA during winters 2005-2006. Different letters indicate significant ($P < 0.05$) differences between male and female locations for shrubs and total biomass and between male and random locations ($P < 0.05$) for shrubs and total biomass.

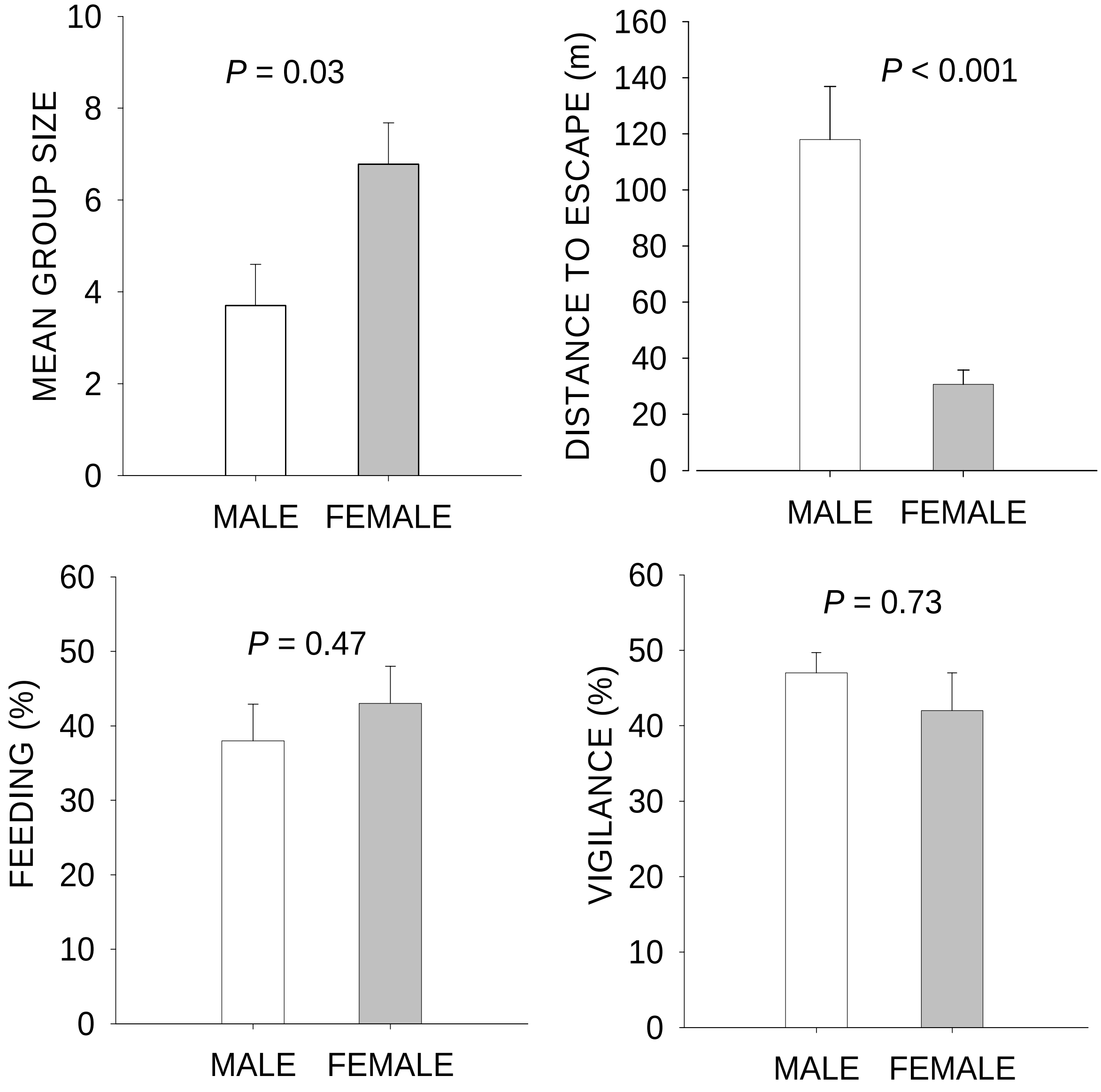

Figure 4. Mean group size (+ SE), distance to escape terrain (m), and percentage of time spent feeding and being alert (vigilance) for male (*n* = 15) and female (*n* = 14) mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, USA during winters 2005-2006. Letters above bars indicate significant differences between sexes.

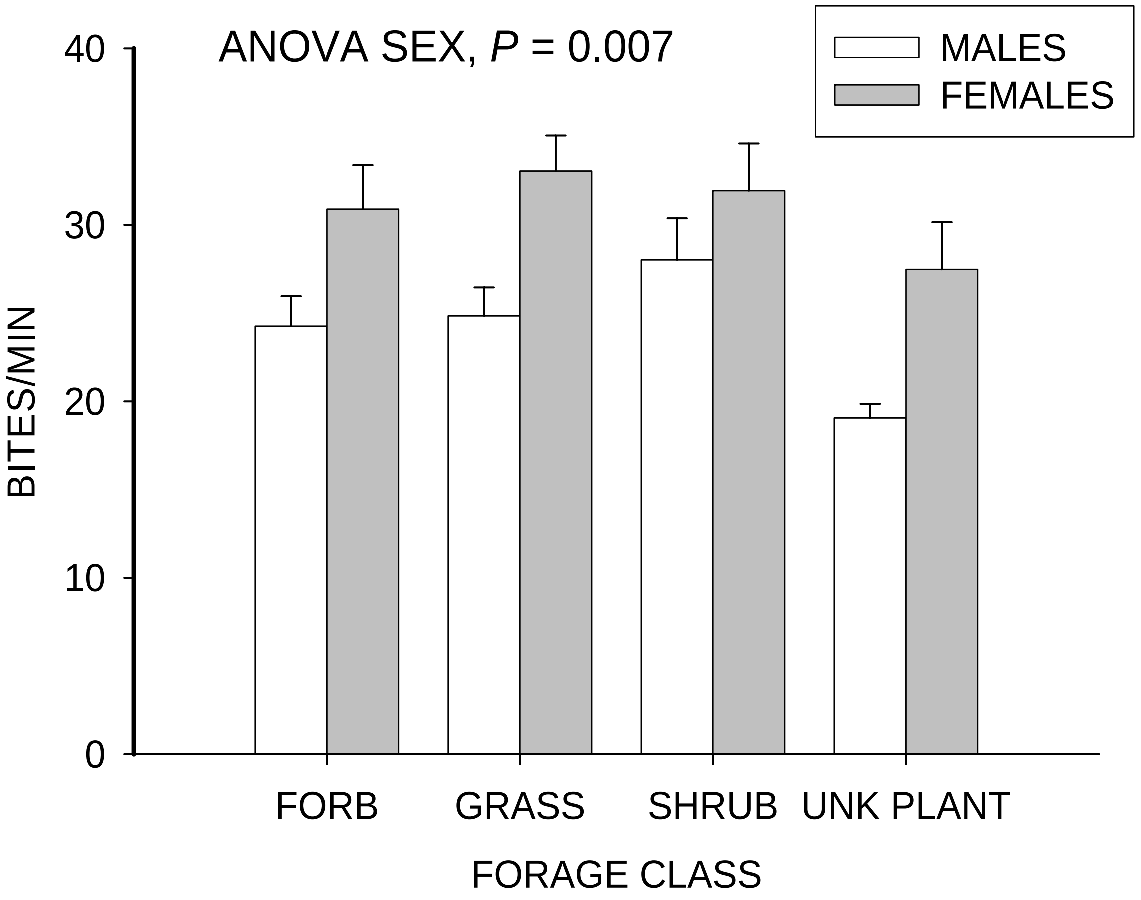

Figure 5. Mean (+ SE) bite rates (bites per minute) of adult male (*n* = 30) and female (*n* = 29) mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, USA during winters 2005-2006.

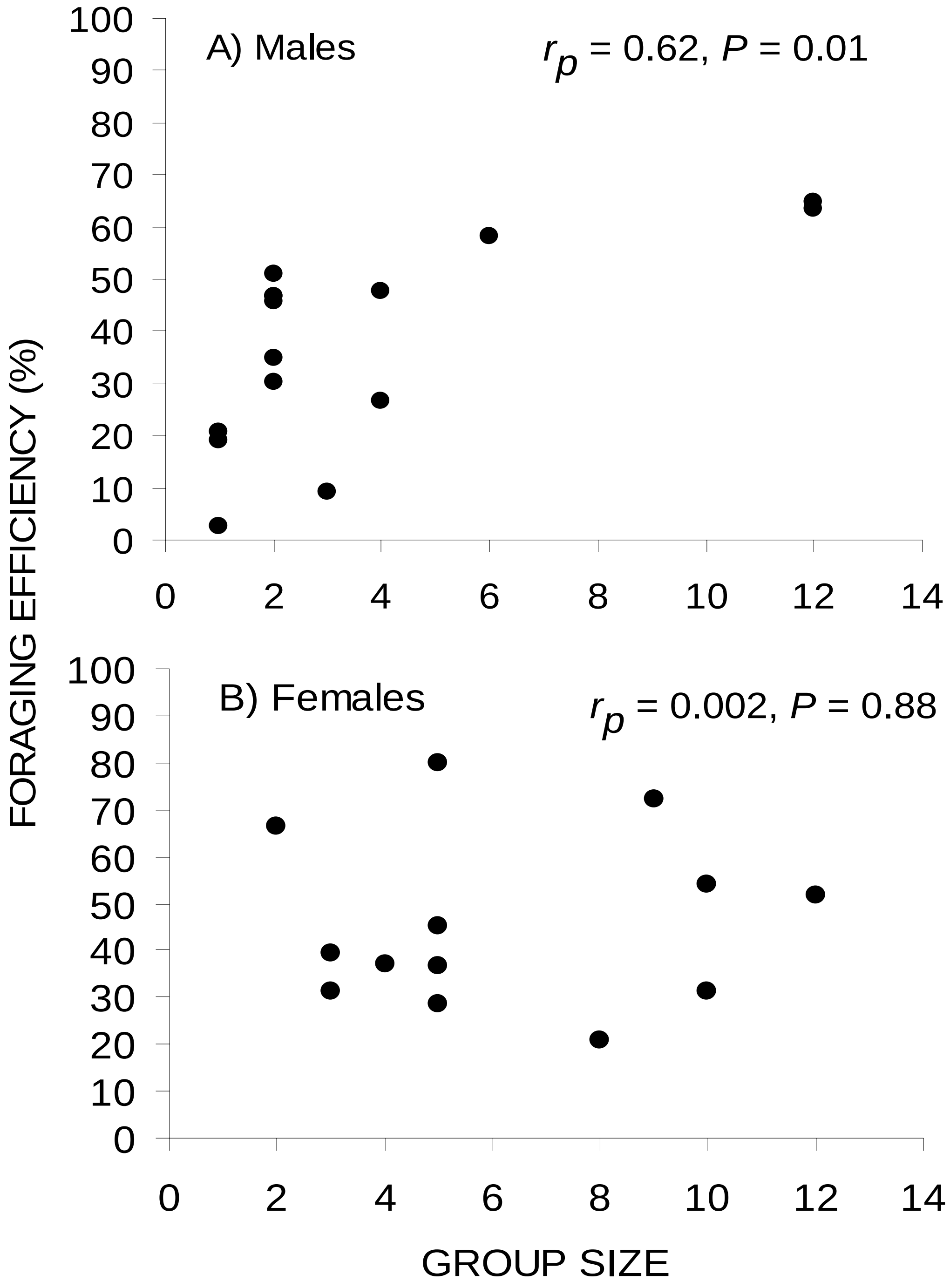

Figure 6. Relationship between foraging efficiency (percentage of active time spent feeding) and group size for (a) male (*n* = 15) and (b) female (*n* = 13) mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, USA during winter 2005-2006.

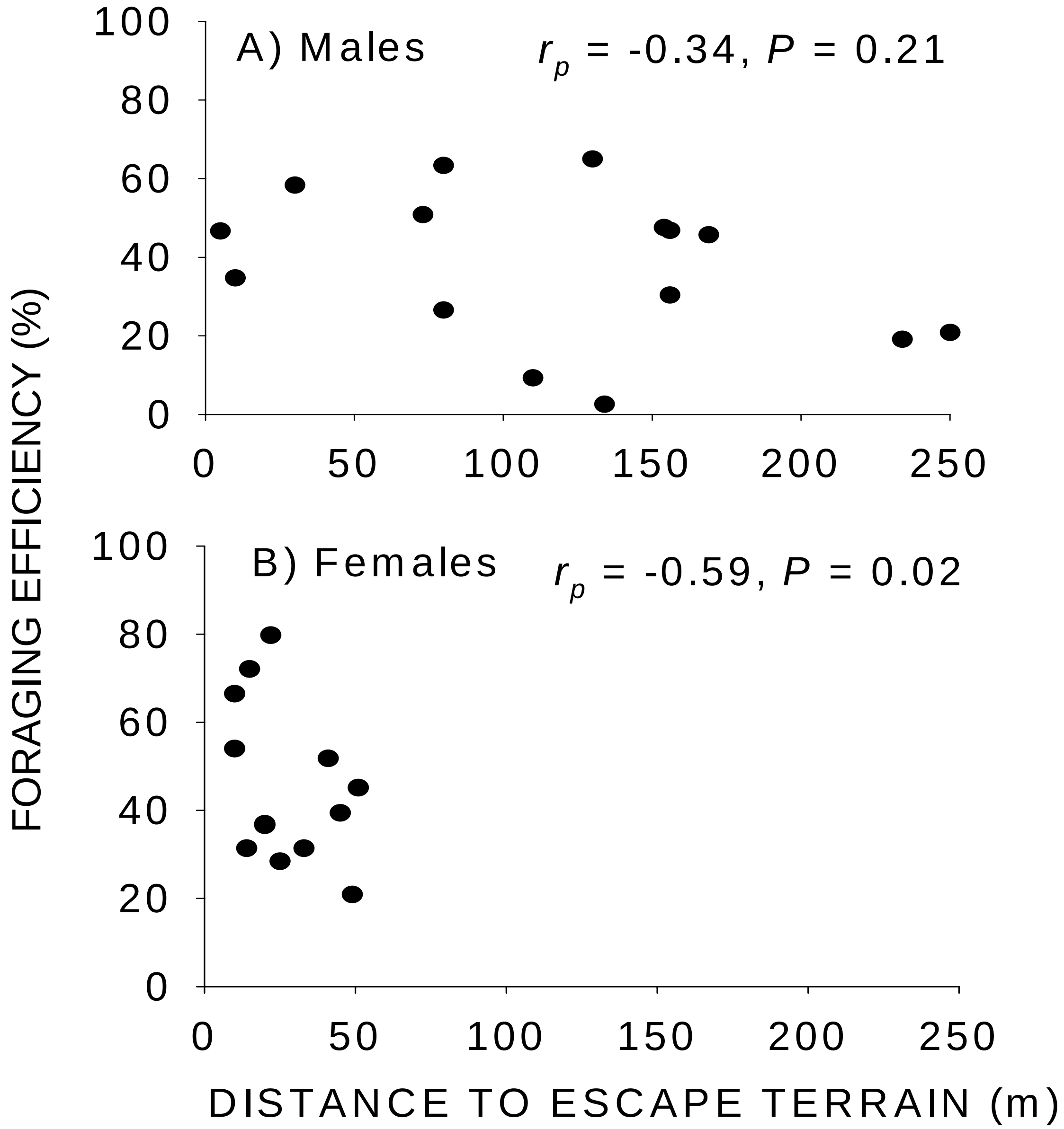

Figure 7. Relationship between foraging efficiency (percentage of active time spent feeding) and the distance to nearest escape terrain (m) for (a) male (n = 15) and (b) female (n = 13) mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, USA, during winter 2005-2006.

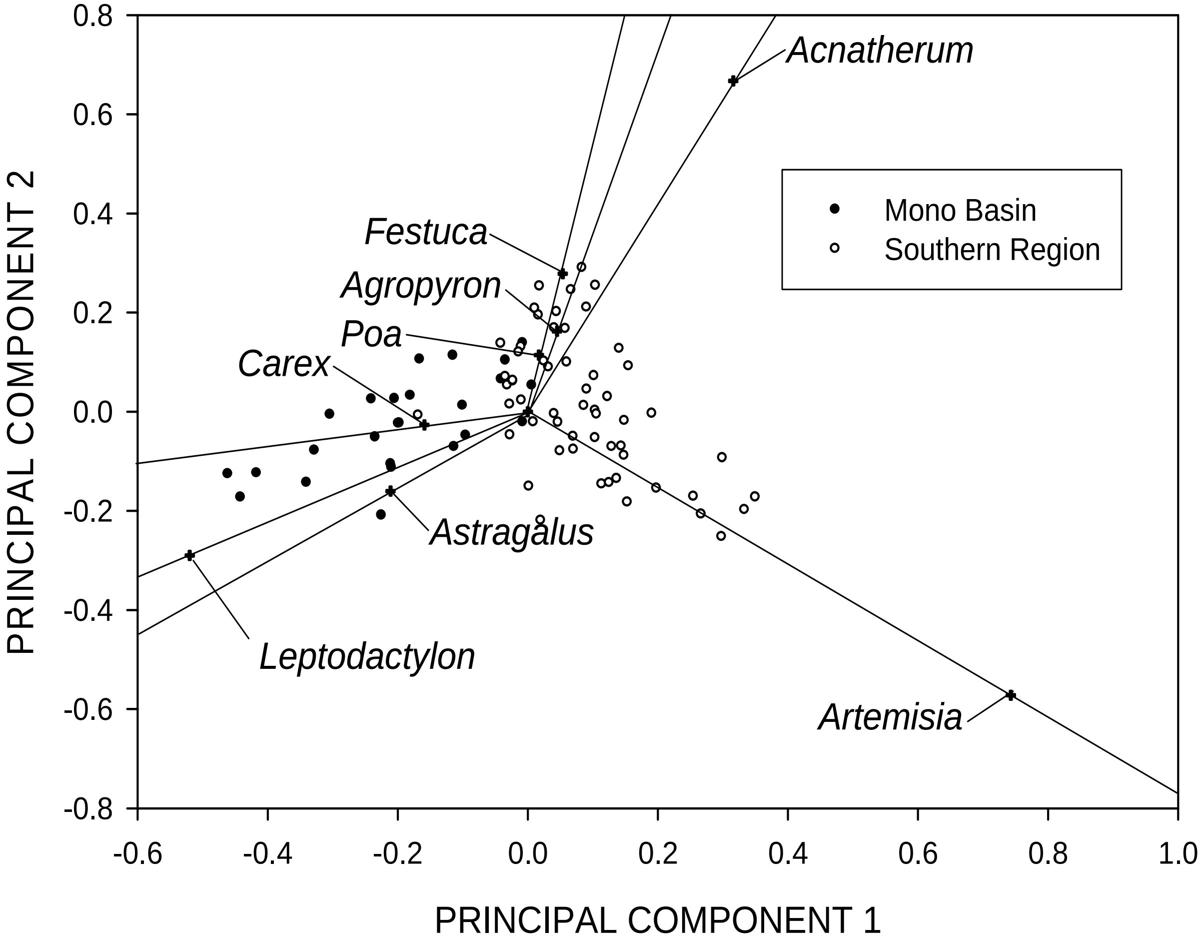

Figure 8. Bi-plot scatter of principal components analysis (PCA) scores from forage genera determined by microhistological analysis of feces from mountain sheep in 2 study areas in the Sierra Nevada, Inyo and Mono counties, California, USA, during winter 2006. Plots of principal components 1 and 2 explained 67.9% of the variation in diets (PC1 = 43.9%, PC2 = 24.0%); the lines represent PCA loadings (eigenvectors) by forage genus.

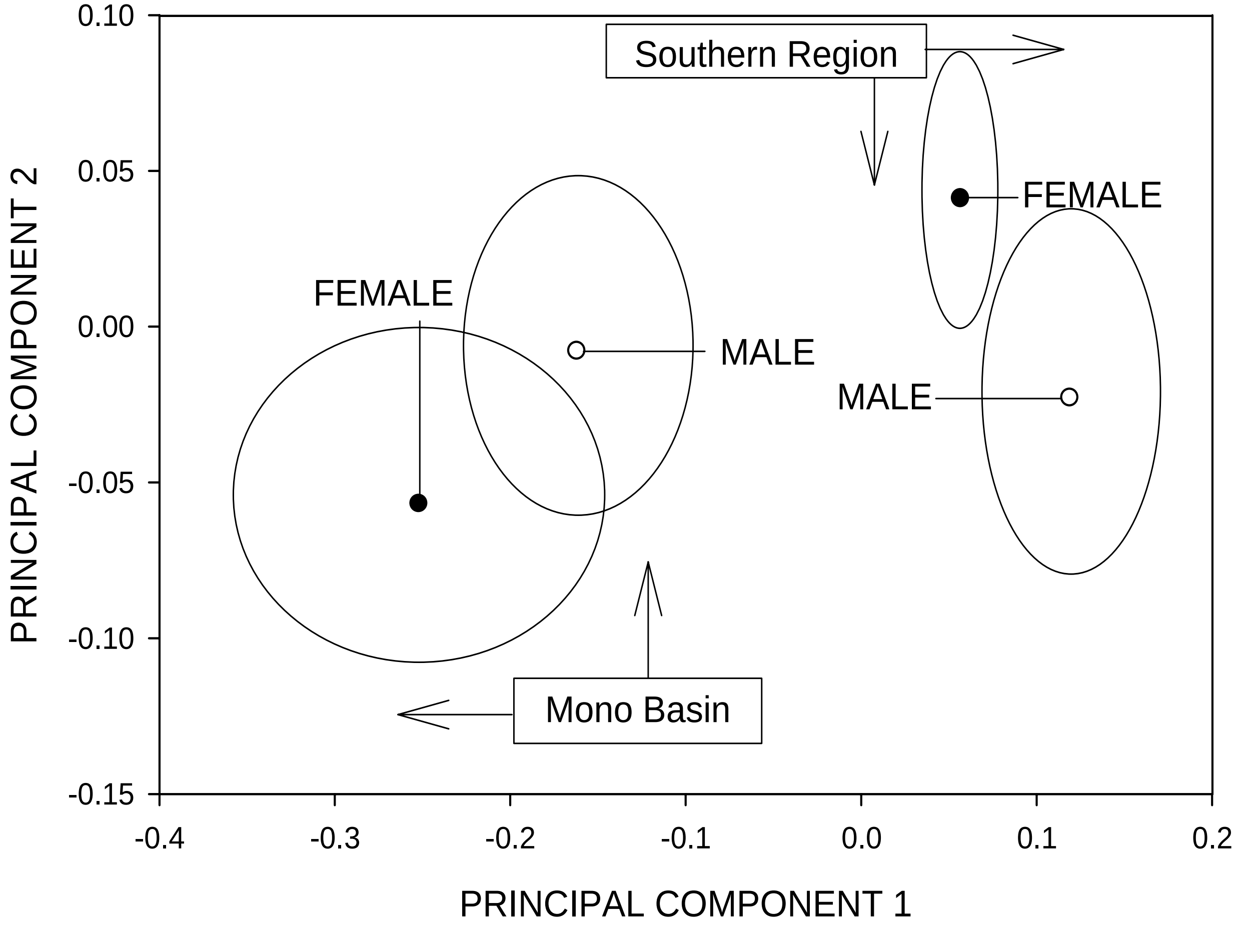

Figure 9. Principal components 1 and 2 for diets of male and female mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, USA, during winter 2006. Ellipses are mean PCA scores and 95% confidence intervals. PC1 represents a continuum from lower elevations (positive loadings) to higher elevations (negative loadings). PC2 represents a continuum from browsing (negative loadings) to grazing (positive loadings).

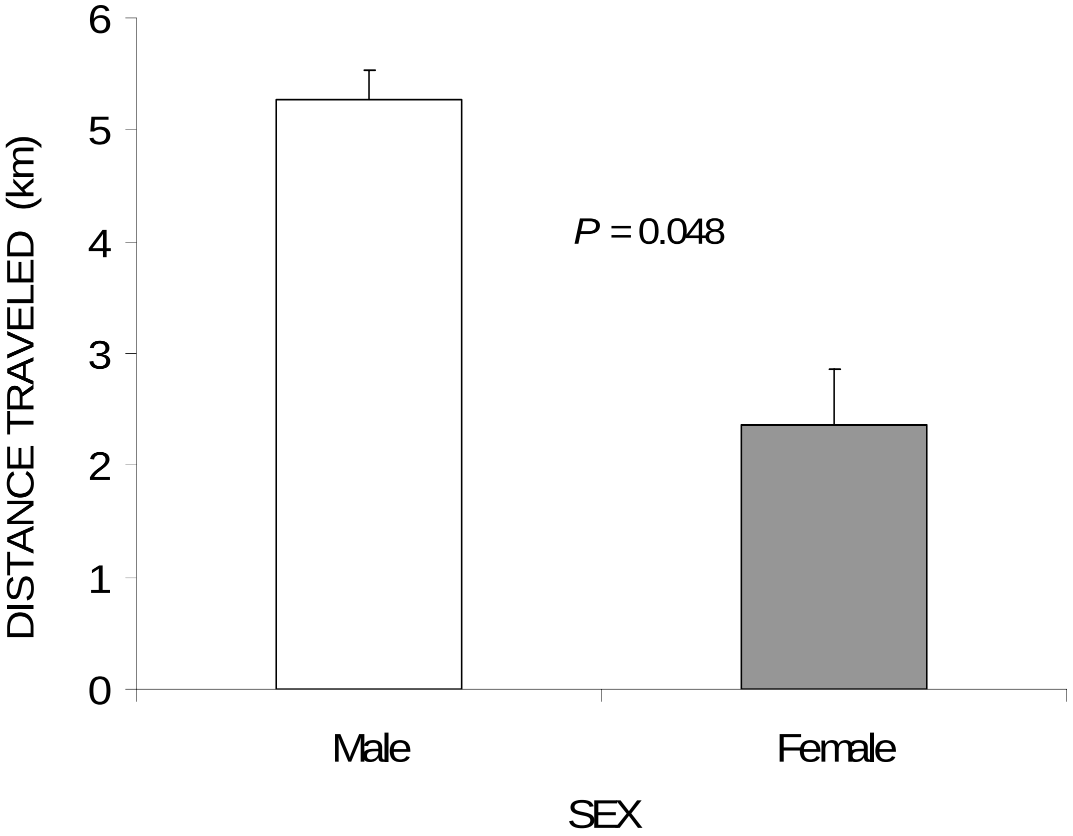

Figure 10. Mean (± SE) daily distance traveled (km) during winter for male (*n* = 3) and female (*n* = 6) mountain sheep from Wheeler Ridge, Inyo County, USA, California, during winter 2003-2005.

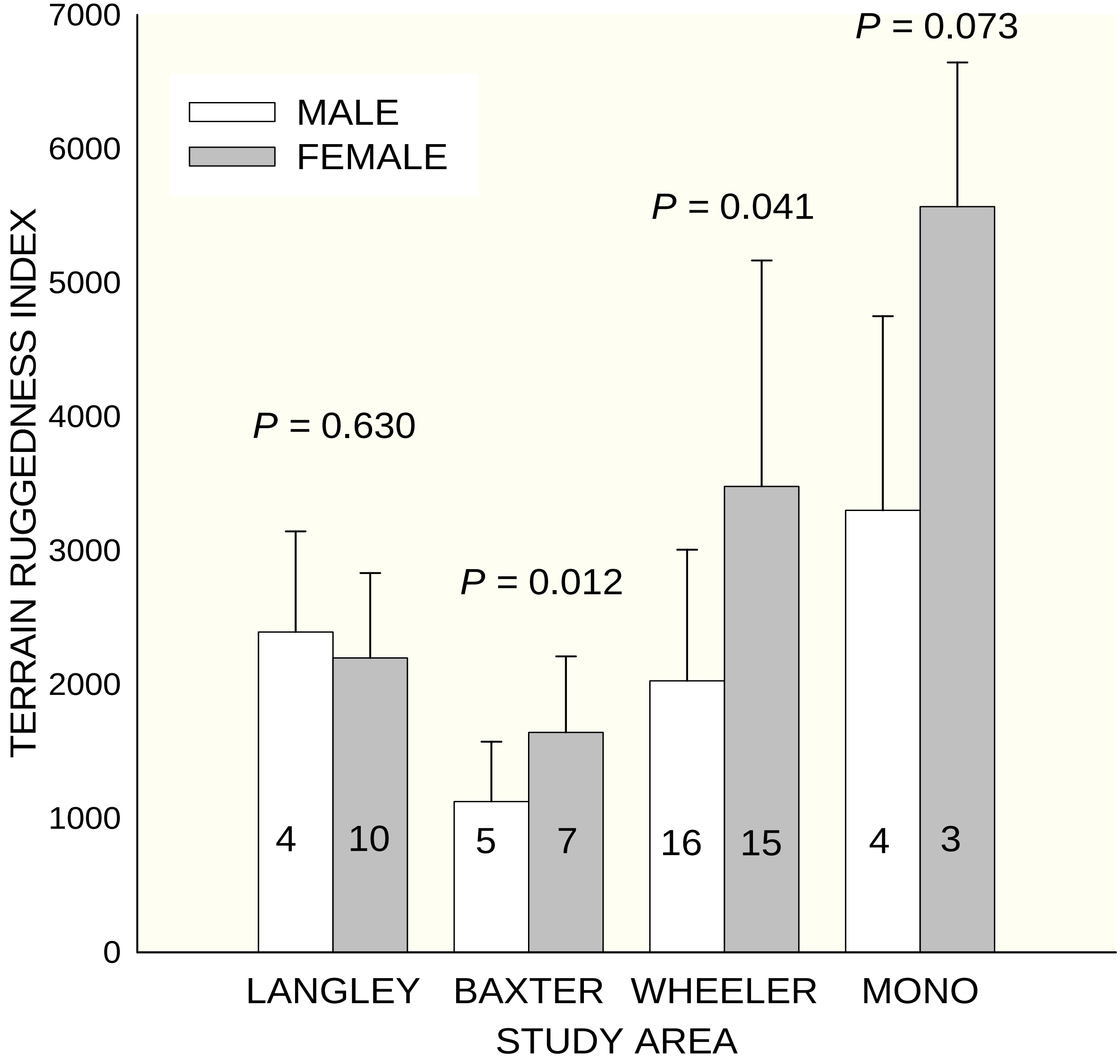

Figure 11. Mean (+ SE) use of rugged terrain during winter by population subgroups of mountain sheep in the Sierra Nevada, Inyo and Mono counties, California, USA, during winter 2005-2006. Ruggedness values, as indexed by variation in slope and aspect, are presented with samples sizes inside bars. P-values are between sex comparisons for each study area.