# Sexual Segregation in Sierra Nevada Bighorn Sheep, Ovis canadensis sierrae: Ramifications for Conservation

Authors: Schroeder, Cody A., Bowyer, R. Terry, Bleich, Vernon C., and Stephenson, Thomas R.

Source: Arctic, Antarctic, and Alpine Research, 42(4) : 476-489

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-42.4.476

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 10 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

*Arctic, Antarctic, and Alpine Research, Vol. 42, No. 4, 2010, pp. 476–489*

# Sexual Segregation in Sierra Nevada Bighorn Sheep, *Ovis canadensis sierrae:* Ramifications for Conservation

*Cody A. Schroeder**
*R. Terry Bowyer*§*
*Vernon C. Bleich†‡ and*
*Thomas R. Stephenson*†*

*Department of Biological Sciences, 921 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, Idaho 83209-8007, U.S.A.
†Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, 407 West Line Street, Bishop, California 93514, U.S.A.
‡Present address: Department of Biological Sciences, 921 South 8th Avenue, Stop 8007, Idaho State University, Pocatello, Idaho 83209-8007, U.S.A.
§Corresponding author: bowyterr@isu.edu

## Abstract

We studied sexual segregation in an endangered alpine ungulate, Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) in the Sierra Nevada, California, U.S.A., during winter 2005–2006. We tested hypotheses for sexual segregation to better understand that phenomenon and to obtain information critical for the conservation of these rare mammals. Females foraged in larger groups that were closer to escape terrain than did males. Areas used by males had higher biomass of vegetation and were less open than areas used by females. Males foraged more efficiently in larger groups, whereas females foraged more efficiently when close to escape terrain. Females exhibited a higher bite rate than did males. Males traveled farther per day and in more open terrain than did females. Sexes of bighorn sheep also differed in their dietary niches. Those niches differed most where sexes of bighorn sheep overlapped more in spatial distribution, and differed less where spatial separation was more pronounced. These outcomes are most parsimoniously explained by the gastrocentric and predation hypotheses. In addition, sexes of bighorn sheep behaved as if they were separate species by exhibiting avoidance on one niche axis (space) when there was overlap on another axis (diet). Management and conservation plans must consider the disparate requirements of males and females to help assure the viability of these endangered mountain ungulates.

DOI: 10.1657/1938-4246-42.4.476

## Introduction

Populations of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) at one time occurred in $\geq$16 locations throughout that rugged mountain range. By the late 1940s, the number of extant populations had been reduced to 5 (Jones, 1950), and additional extirpations occurred in the following decades; by 1976, only two populations remained (Wehausen, 1980). A program to reestablish those alpine ungulates in areas from which they had been extirpated began in 1979 (Bleich et al., 1991), and three additional populations, totaling $\sim$120 individuals, had been established by 1986 (U.S. Fish and Wildlife Service, 2008). During the late 1980s, the total number of Sierra Nevada bighorn sheep declined substantially, reaching a low of $\sim$100 individuals by 1995; they were listed as endangered in 2000 (U.S. Fish and Wildlife Service, 2008).

Several factors may have contributed to population declines, including drought and predation (Wehausen, 1996), pneumonia epizootics (Onderka et al., 1988; Coggins and Matthews, 1992), and small group sizes, which may have resulted in decreased foraging efficiency (Berger, 1978; Molvar and Bowyer, 1994; Ruckstuhl and Festa-Bianchet, 2001; Bowyer and Kie, 2004). Nonetheless, little is known about how predation risk or habitat use and availability influence behaviors of these mountain ungulates, which are among the rarest large mammals in the world (U.S. Fish and Wildlife Service, 2008). Failure to account for life-history characteristics in the conservation of bighorn sheep could result in inappropriately designed reintroduction efforts and, thereby, hamper recovery of this endangered taxon (Festa-Bianchet and Apollonio, 2003; Whiting et al., 2008).

Foraging behavior and risk of predation play substantial roles in shaping life-history strategies for many ungulates (Bowyer, 1984, 2004; Bowyer et al., 1998, 1999; Bleich et al., 1997; Rachlow and Bowyer, 1998; Gaillard et al., 2000; Barten et al., 2001). Diet and predation risk have been studied for populations of bighorn sheep inhabiting the Sierra Nevada, California, U.S.A. (Wehausen, 1980, 1992, 1996; Chow, 1984), but those studies did not distinguish between habitats and forages used by adult males and adult females or the responses of the sexes to predators. Mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) are relatively abundant in the Sierra Nevada (Pierce et al., 2000a, 2000b). Studies of foraging behavior by bighorn sheep have addressed ecological differences between sexes for desert-dwelling populations (Bleich et al., 1997; Mooring et al., 2003), but those bighorn sheep likely differ in their diets and habitat requirements from endangered bighorn sheep inhabiting alpine zones of the Sierra Nevada.

Several investigators (Main et al., 1996; Ruckstuhl and Neuhaus, 2002) previously summarized hypotheses regarding sexual segregation in ruminants, and Bowyer (2004) identified problems with some of those hypotheses and emphasized the importance of understanding evolutionary underpinnings in obtaining critical tests. The gastrocentric hypothesis predicts that adult males will forage in habitats where food is more abundant but may be of lower nutritional quality than habitats used by adult females during periods of segregation (Barboza and Bowyer, 2000, 2001). Indeed, males require larger amounts of food per day than do females (Demment and Van Soest, 1985; Illius and Gordon, 1987; Gross et al., 1996; Ruckstuhl and Neuhaus, 2002), which may indirectly influence spatial distributions, movements, and

1523-0430/10 $7.00

proximity to escape terrain (Ruckstuhl and Neuhaus, 2001; Berger, 1978, 1991). Females also undergo changes to their digestive tract to assimilate high-quality forage required to meet physiological needs during late gestation and lactation (Barboza and Bowyer, 2000, 2001; Zimmerman et al., 2006). Even where no differences occur in habitat selection between sexes (Bowyer, 1986), spatial separation of sexes within habitats may be present (Bowyer, 1984). This outcome is likely driven by differing dietary requirements of sexes (Barboza and Bowyer, 2000, 2001).

Risk of predation also may contribute to sexual segregation and can play an important role in differences in habitat selection by the sexes (Berger, 1991; Bleich et al., 1997; Kie and Bowyer, 1999; Hay et al., 2008); females seek areas that provide security for themselves and their offspring while maintaining nutritional reserves necessary to support the high costs of reproduction (Bowyer, 1984; Bleich et al., 1997). Thus, females incur fitness benefits directly through survival of offspring as well as indirectly via future reproductive success. In contrast, males invest more resources in body growth and secondary sexual traits, allowing them to compete effectively for access to estrous females (Ralls, 1977; Loison et al., 1999; Weckerly, 1998; Perez-Barberia et al., 2002; Spaeth et al., 2004).

Although a number of competing hypotheses potentially explain sexual segregation (Main, 2008), many are neither independent nor, in some instances, even testable (Bowyer, 2004). We focus herein mostly on ecological hypotheses of value in understanding the conservation of bighorn sheep. Consequently, we limited our efforts to the gastrocentric and predation hypotheses, because they make clear predictions concerning sexual segregation, and have not been eliminated as an explanation by empirical research (for review, see Bowyer, 2004). Resurrecting old rejected hypotheses is unlikely to advance our knowledge of sexual segregation (Bleich et al., 1997; Bowyer, 2004). Other investigators recently have adopted this same approach successfully for framing viable hypotheses concerning sexual segregation (Long et al., 2009).

Bighorn sheep exhibit extreme sexual dimorphism in body size (Bleich et al., 1997; Weckerly, 1998; Loison et al., 1999). Adult males and females separate spatially for much of the year (Bleich et al., 1997), and sexes of these ungulates are well known for differential habitat use outside the mating season (Bleich et al., 1997; Krausman and Bowyer, 2003; Mooring et al., 2003). Moreover, bighorn sheep are morphologically and behaviorally well adapted to minimize risk of predation through vigilance and for their ability to evade predators in precipitous terrain (Berger, 1978, 1991; Festa-Bianchet, 1988; Bleich et al., 1997; Bleich, 1999). Finally, the extreme sexual size dimorphism and accompanying allometric differences in many ruminants may lead to sexes behaving as if they were separate but coexisting species (Kie and Bowyer, 1999; Bowyer, 2004; Bowyer and Kie, 2004). This potential outcome necessitates a niche-based approach for understanding the ecology of the sexes, wherein overlap by sexes on one niche axis may result in avoidance on another (Kie and Bowyer, 1999; Bowyer, 2004; Bowyer and Kie, 2004).

Our objectives were to provide a quantitative description of foraging behavior of adult male and adult female bighorn sheep, determine the specific habitat characteristics important to each sex, and test predictions of the gastrocentric and predation-risk hypotheses that have been posited to explain sexual segregation in dimorphic ruminants. We then discuss the relevance of those results to the conservation of Sierra Nevada bighorn sheep.

Hypotheses related to the gastrocentric hypothesis include the prediction that females should obtain a higher-quality diet than would males (as indexed by fecal nitrogen). We also postulated that males would feed in areas with a greater biomass of forage that areas used by females. Moreover, we predicted that effects of predation on sexual segregation should result in females occurring in larger groups than males, because of their greater vulnerability. Likewise, females should occur closer to escape terrain, and occupy more rugged areas with greater visibility than those used by males. Variables related to risk of predation also should modify foraging efficiency (percent of active time spent foraging), with group size, distance to escape terrain, ruggedness of terrain, and visibility all playing a greater role in females. Because of their vulnerability to predation, females would be expected to travel less than males to reduce risk; males would be predicted to travel greater distances than females to meet their absolute needs for more forage—predictions that could support both gastrocentric and predation hypotheses. Similarly, bite rate would be expected to be greater for females, which forage more selectively than males. Nonetheless, females also may expend less time foraging (resulting in a higher bite rate) because of increased vigilance for predators.

As a result of morphological and behavioral disparities, sexes of bighorn sheep should differ in their dietary niches. We predicted that differences in dietary niche would be most marked where sexes of bighorn sheep overlapped more in spatial distribution, and would differ less where spatial separation was more pronounced. We further postulated that sexes of bighorn sheep should behave as if they were separate species by exhibiting avoidance on one niche axis (diet) when there was overlap on another axis (space).

## Methods

### *STUDY AREA*

The Sierra Nevada (37°24′N, 118°41′W) is a young (<5,000,000 yr BP), rugged mountain range of far western North America, approximately 650 km long and from 75 to 125 km wide (Hill, 1975). Snow is a significant source of winter precipitation in the Sierra Nevada (National Oceanic and Atmospheric Administration, 2006), which affects availability of vegetation and timing of green-up for mountain ungulates (Festa-Bianchet, 1988; Rachlow and Bowyer, 1991, 1994; Bowyer et al., 1999); rain during spring and summer also is important for growth of forage plants used by bighorn 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, which casts a rain shadow and is responsible for the desert and steppe ecosystems typical of the eastern portion of that range (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 to 27.1°C (average minimum to average maximum during winter; National Oceanic Atmospheric and Administration, 2006).

Bighorn sheep currently are distributed in 4 subpopulations occupying 4 distinct areas (Mono Basin, Wheeler Ridge, Mt. Baxter, and Mt. Langley; Fig. 1) along the eastern slope of the Sierra Nevada (Wehausen, 1996). The Mt. Warren and the Mt. Gibbs subpopulations occupy the Mono Basin in the north. The Southern Region is occupied by 3 subpopulations, which we

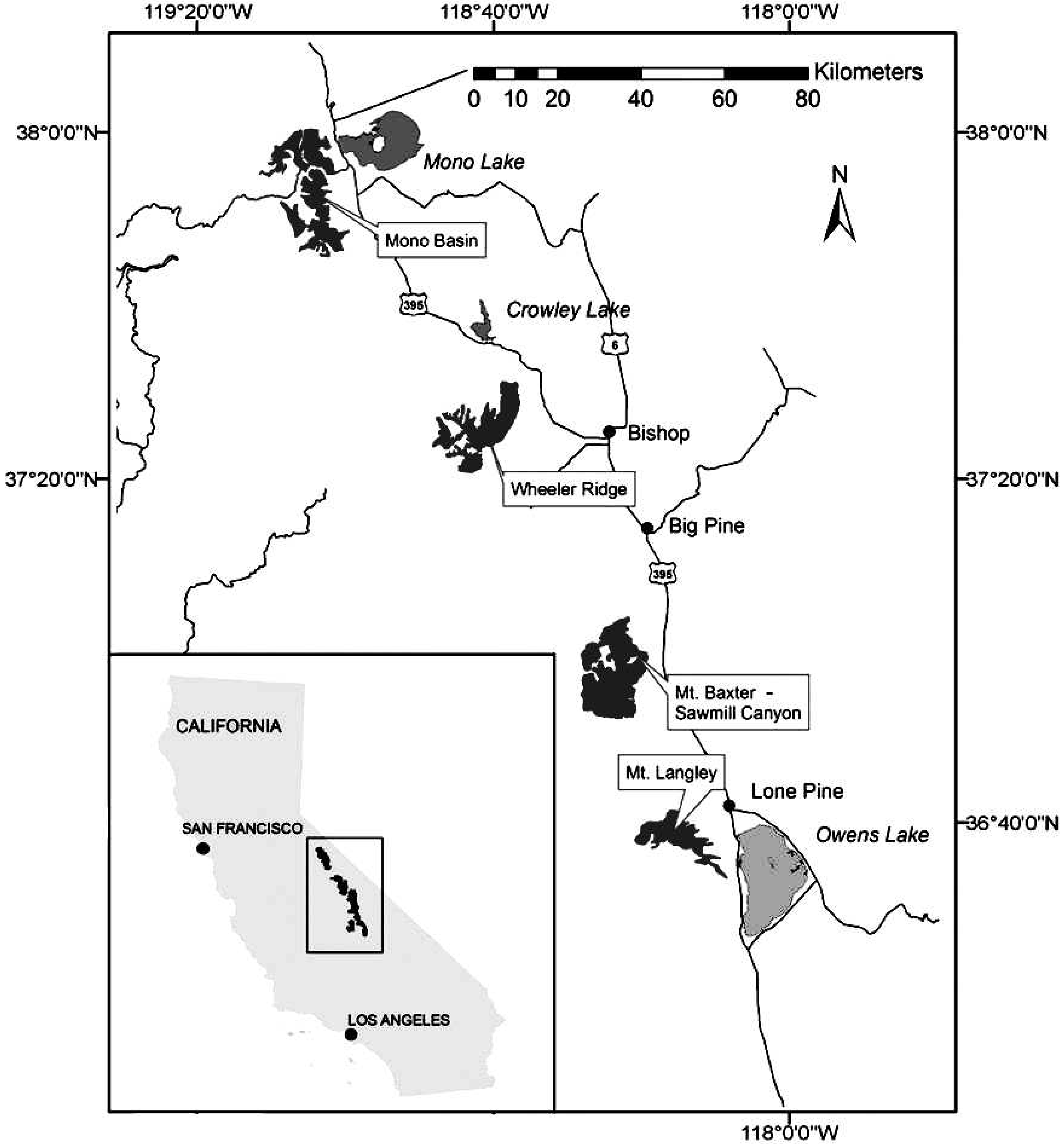

**FIGURE 1. Location of subpopulations of bighorn sheep (black polygons) in Inyo and Mono counties, California, U.S.A., 2005–2006. The Mono Basin subpopulation was in the northern Sierra Nevada, whereas Wheeler Ridge, Mt. Baxter–Sawmill Canyon, and Mt. Langley were combined into the Southern Region.**

designated for separate study: Wheeler Ridge; Mt. Langley; and Mt. Baxter–Sawmill Canyon (Wehausen, 1996; U.S. Fish and Wildlife Service, 2008).

Vegetation in the eastern Sierra Nevada on lower-elevation (1500–2000 m) 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 overstory 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* spp.), beardtongue (*Penstemon* spp.), and sedges (*Carex* spp.; Chow, 1984). At higher elevations (3300–4300 m), vegetation is typified by alpine communities such as prickly phlox (*Leptodactylon* spp.), crested wheatgrass (*Agropyron* spp.), sedges (*Carex* spp.), and vetches (*Astragalus* spp.). Plant nomenclature follows Munz (1974).

### CAPTURE AND RADIOTELEMETRY

Beginning in 2003, the California Department of Fish and Game captured male and female bighorn sheep ≥1-yr-old via net-gunning from a helicopter (Krausman et al., 1985). The department held the necessary permits, and all research was consistent with guidelines published by the American Society of Mammalogists for research on wild mammals (Gannon et al., 2007). Our research also was approved by an independent Animal Care and Use Committee at Idaho State University (protocol no. 616). We used GPS collars to monitor winter movements and survivorship of this exceptionally rare mammal. Data were gathered via GPS collars from 6 adult female and 3 adult male bighorn sheep beginning on 1 January 2003 and ending 1 May 2005. These radio collars were programmed to record positions every 6–10 min for an 8-h period, 1 day per week for 2 years. These 8-h periods varied over time. Hourly locations were used to analyze movements.

We combined telemetry coordinates from GPS data and Digital Elevation Models (DEM) with ArcGIS 9.1 (Environmental Systems Research Institute Inc., Redlands, California, U.S.A.); Spatial Analyst Extension was employed to estimate daily movements of bighorn sheep. We determined mean distance traveled per day for each bighorn sheep with the Home Range Extension for ArcGIS$^{TM}$ (Rodgers and Carr, 1998). The elevation of each GPS location was calculated by overlaying a shapefile for each individual with a 10-m DEM, and the Surface Spot function in ArcMap then was used to derive the elevation of each location from the underlying DEM.

A terrain-ruggedness index (Nicholson et al., 1997) was developed for locations of male and female bighorn sheep. We used the program ArcGIS to construct 3 layers derived from the DEM to calculate slope, aspect, and elevation for each 10 × 10 pixel in the grid. Locations from all bighorn sheep then were overlaid on the terrain layers and a 300-m radius buffer was delineated around each point to obtain an adequate representation of terrain and habitat features available to bighorn sheep. The Grid Statistics tool was used to calculate the mean and SD for physical characteristics (slope, aspect, and elevation) of each circle.

### COLLECTION OF FECES AND HABITAT VARIABLES

We collected fecal pellets during winter (1 January to 5 May) 2006 from the 4 subpopulations (Mt. Baxter, $n = 28$; Mt. Langley, $n = 31$; Wheeler Ridge, $n = 46$; Mono Basin, $n = 38$), and data were pooled by area, sex, and month. We collected fresh (≤3 days old) fecal pellets, confirmed organoleptically, from observed individuals or from live animals that had been captured. Each pellet group (from a single animal) was considered an independent sample.

Diet quality was indexed for adult male and adult female bighorn sheep from levels of nitrogen in feces (Blanchard et al., 2003; Leslie et al., 2008). We analyzed fecal pellets for percent nitrogen on an ash-free, dry-matter basis. Diets were estimated microhistologically (Sparks and Malechek, 1968; Hodgman et al., 1996), and plants were identified to genus. Fecal pellets were analyzed under contract by the Wildlife Habitat Laboratory at Washington State University, Pullman, Washington, U.S.A.

We measured characteristics of habitat for bighorn sheep at random locations and at locations where bighorn sheep were observed. We determined biomass (wet weight) of forage with double sampling (Reese et al., 1980; Reich et al., 1993; Barten et al., 2001) within 1-m$^2$ plots. We sampled wet-weight biomass of forbs, grasses, and shrubs from male ($n = 11$), female ($n = 20$), and random ($n = 18$) locations during winters 2005 and 2006, and pooled years to obtain sample sizes sufficient for statistical analyses.

We calculated the greatest distance bighorn sheep were observed foraging from escape terrain by measuring the distance from the central point of the group to the nearest escape terrain with either a tape measure or from GPS coordinates. Escape terrain was defined as any geomorphic feature >5 m in height and diameter, which was part of a larger, contiguous geological formation (Risenhoover and Bailey, 1985; DeCesare and Pletscher, 2006). Measurements of distance to escape terrain were determined immediately following behavioral observations of bighorn sheep, or within 7 days of the initial observation where it seemed likely our immediate presence would disturb bighorn sheep (Rachlow and Bowyer, 1998). We estimated visibility at locations of male and female groups with a 2-m cover pole to make our data comparable with other research on bighorn sheep. Measurements were collected from a distance of 15 m in 4 cardinal directions, and percent of the pole (in 25-cm increments) obscured by vegetation or geomorphic features was recorded (Griffith and Youtie, 1988; Bleich et al., 1997; Bowyer et al., 1999). The mean percentage of the cover pole visible from 4 directions was used as the value for visibility.

### FIELD OBSERVATIONS

We observed the behavior of bighorn sheep with 10 × 40 binoculars or a 20 × 60 spotting scope. A radio-collared bighorn sheep was selected randomly from each of the 4 general study areas (Mt. Langley, Mt. Baxter, Wheeler Ridge, and Mono Basin) and an attempt was made to locate that bighorn sheep via radio telemetry. Once that marked bighorn sheep was observed (≤300 m) and group size recorded, we selected an individual from the group containing that animal with a random numbers table and behavioral observations began. Bighorn sheep were categorized into sex and age classes according to Geist (1968): (1) adult females, (2) young, (3) class I males (yearlings), and (4) class II–IV males (adults).

We recorded activities of bighorn sheep on a hand-held personal computer, with an internal clock, using a combination of scan- and focal-animal sampling (Altmann, 1974). We used scans at 10-min intervals (Altmann, 1974) to categorize bighorn sheep activities, in a manner similar to that of Risenhoover and Bailey (1985): foraging (head down in feeding posture); bedding; aggressive; vigilant (i.e., alert; head in upward position with ears erect and directed forward); or alarmed (running to escape terrain). We used focal sampling (Altmann, 1974) of randomly selected individuals to collect data on bites taken by males or females stratified by forage class. The individual was then viewed continuously for at least 3 min and the number of bites of each forage class (forb, graminoid, shrub, or unknown plant) was recorded. We subsequently calculated foraging efficiency (percent of active time spent foraging; Berger, 1978) for each individual.

### STATISTICAL ANALYSES

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

We used multivariate analysis of variance (MANOVA) to compare differences in forage abundance between sites used by sexes of bighorn sheep (Zar, 1999). Independent variables were locations of males (≥2 yrs), adult females and young (including males <2 yrs old), and random sites. Dependent variables for the MANOVA were total wet weight of both live and dead biomass ($g\ m^{-2}$), live and dead biomass of forbs and grasses, and live biomass of shrubs. Wet weight of biomass was used because that variable is more closely related to rumen fill than is dry weight (Belovsky, 1978). We employed Tukey's HSD for multiple comparisons between groups with significant main effects (male, female, and random locations). Berger (1991) and Bleich et al. (1997) reported that female bighorn sheep use more open areas than did males; thus, a 1-tailed *t*-test (which predicted males in less-open areas) was used to compare habitat openness at foraging locations of males and females.

We used principal components analysis (PCA) of diet composition for bighorn sheep, based on the variance-covariance matrix (McGarigal et al., 2000), to reduce dimensionality of those data. The number of species identified by microhistological analysis was reduced to 8 genera (*sensu* Kie and Bowyer, 1999) because they: (1) were consumed by >20% of all bighorn sheep; (2) comprised ≥30% of the diet in at least 1 bighorn sheep of each sex; and (3) composed ≥5% of diets averaged over all samples. The 8 genera selected were *Agropyron* (wheat grass), *Artemisia* (sagebrush), *Astragalus* (milk-vetch), *Carex* (sedge), *Festuca* (fescue grass), *Leptodactylon* (prickly phlox), *Poa* (blue grass), and *Achnatherum* (desert needlegrass).

We assigned subpopulations of bighorn sheep to 2 separate regions based primarily on elevation: (1) Mono Basin; and (2) Southern Region (consisting of Mt. Langley, Mt. Baxter–Sawmill Canyon, and Wheeler Ridge subpopulations). Bighorn sheep inhabiting the Mono Basin spent winters at high elevations, whereas bighorn sheep from the Southern Region occurred at low elevations during winter. We used MANOVA and Tukey's HSD for multiple comparisons to test for differences in diet composition of forage species among study areas and sexes. Percentage data were arcsine–square root transformed (Zar, 1999). We plotted means with 95% confidence intervals as bivariate ellipses for the first 2 principal components to examine differences between diets of sexes (i.e., the dietary niche). We used the Shannon-Weiner Index to infer differences in diet diversity between sexes and study areas, and H′ was transformed to $e^{H'}$ to reflect the number of forage species (Ricklefs and Miller, 2001). We estimated diet diversity from genera of plants in the diets of bighorn sheep that met criteria used for PCA.

We examined mean daily distances traveled for individual male and female bighorn sheep with the Satherwaite 2-tailed *t*-test for unequal variances (Zar, 1999). Differences in elevations used by adult males and females during winter were tested with ANOVA with mean monthly elevation as the dependent variable, and sex, month, and year as main effects, as well as pairwise interactions between sex, month, and year. We used MANOVA to test for differences between sexes in use of slope, aspect, and a composite index based on 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 for this analysis were slope, aspect, and terrain ruggedness, and independent variables were sex, subpopulation, and a sex × subpopulation interaction.

## Results

### FECAL NITROGEN

Mean values of fecal nitrogen ranged from 1.4 to 2.8% for adult males, and from 1.2 to 2.8% for adult females across all subpopulations during winter (Table 1). Fecal nitrogen was not significantly different between sexes when controlled for elevation and Julian date, with sites used by bighorn sheep and subpopulation as random effects (MIXED GLM, $F_{1,3} = 0.28$, $P = 0.635$; Fig. 2). Nevertheless, fecal nitrogen varied for bighorn sheep in different subpopulations 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 subpopulation was significantly higher ($P < 0.05$) than for all other subpopulations, and fecal nitrogen in the Mono Basin subpopulation was lower ($P < 0.05$) than all subpopulations except Mt. Langley (Fig. 2).

### FORAGE ABUNDANCE

Total biomass of vegetation ranged from 6 to 138 $g\ m^{-2}$ at female locations, from 34 to 182 $g\ m^{-2}$ at male locations, and from 13 to 127 $g\ m^{-2}$ at random locations during winter. Biomass of forage classes (forbs, grasses, shrubs, and total) varied for locations of sexes and random locations (MANOVA; overall $F_{8,68} = 2.12$, $P = 0.04$; Fig. 3), and for subpopulations (MANOVA; $F_{12,90} = 2.12$, $P = 0.002$). Locations of males had higher biomass of shrubs ($P < 0.05$) and total vegetation ($P < 0.05$) than sites used by females or random locations (Fig. 3). Locations of females did not differ from random locations 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).

### BITE RATE

Females had higher bite rates (bites $min^{-1}$) for all forage classes during winter than did males (Fig. 4). The overall bite rate (mean ± SE) for female bighorn sheep (31.31 ± 1.26) was higher than for males (24.46 ± 0.96) for all forage classes combined (ANOVA; $F_{1,95} = 7.36$, $P = 0.007$; Fig. 4). Bite rates for bighorn sheep were not significantly different between study areas (ANOVA; $F_{3,95} = 0.85$, $P = 0.467$) or forage classes (ANOVA; $F_{3,95} = 1.86$, $P = 0.140$; Fig. 5) for both sexes combined. Similarly, there was no significant interaction between sex and forage class (ANOVA; $F_{3,95} = 0.22$, $P = 0.88$).

### DIETARY COMPOSITION AND NICHE

Bighorn sheep exhibited diverse diets as estimated from microhistological analyses of feces; 57 genera of plants were detected in fecal samples from males and females. Bighorn sheep in the Mono Basin consumed mostly forbs (*Astragalus* and *Leptodactylon*) during winter (Table 2). Bighorn sheep ate mostly shrubs (*Artemisia*) and graminoids (*Achnatherum*) in the Southern Region (Table 3, Fig. 5). Principal components analysis (PCA) indicated that bighorn sheep in the Mono Basin exhibited differential patterns in diet composition compared with bighorn sheep in the Southern Region (Fig. 5). Principal component 1 explained 43.9% of the variation in diets among bighorn sheep and likely represented a continuum in altitude from lower elevations (positive loadings) to higher elevations (negative loadings).

## TABLE 1

**Fecal nitrogen (ash-free basis) of adult male and female bighorn sheep in the Sierra Nevada, Inyo and Mono Counties, California, U.S.A., and the elevation at which feces were collected during winter 2006.**

| | Fecal N (%) | | | Elevation (m) | | Fecal N (%) | | | Elevation (m) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Male | | | | | Female | | | | |
| Subpopulation | *n* | $\bar{X}$ | *SE* | $\bar{X}$ | *SE* | *n* | $\bar{X}$ | *SE* | $\bar{X}$ | *SE* |
| **Langley** | | | | | | | | | | |
| Feb. | 4 | 1.6 | 0.17 | 2262 | — | 5 | 1.9 | 0.18 | 2262 | — |
| March | 3 | 2.0 | 0.24 | 2097 | — | 7 | 1.5 | 0.08 | 2005 | 9.9 |
| April | 6 | 2.3 | 0.11 | 1829 | 5.3 | 6 | 1.9 | 0.11 | 1970 | — |
| **Baxter** | | | | | | | | | | |
| Jan. | | | | | | 3 | 2.3 | 0.32 | 1709 | 40.3 |
| Feb. | 1 | 2.6 | — | 1715 | — | 7 | 2.2 | 0.22 | 1680 | 71.5 |
| March | 2 | 2.5 | — | 1531 | — | 5 | 2.8 | 0.13 | 1530 | — |
| April | 5 | 2.8 | 0.09 | 1729 | 34.6 | 5 | 2.5 | 0.51 | 1787 | 36.2 |
| **Wheeler** | | | | | | | | | | |
| Jan. | 7 | 1.7 | 0.07 | 1891 | 14.2 | 3 | 2.0 | 0.21 | 1737 | — |
| Feb. | 4 | 1.4 | 0.20 | 2045 | 58.4 | 6 | 1.5 | 0.15 | 2280 | 58.3 |
| March | 4 | 2.3 | 0.23 | 1836 | — | 10 | 2.1 | 0.22 | 2197 | 10.2 |
| April | 6 | 2.7 | 0.19 | 1928 | 27.6 | 6 | 2.3 | 0.20 | 2255 | 40.5 |
| **Mono** | | | | | | | | | | |
| Jan. | 5 | 1.4 | 0.08 | 3494 | — | 6 | 1.2 | 0.05 | 3463 | — |
| Feb. | 2 | 1.5 | — | 3564 | — | 4 | 2.4 | 0.54 | 3092 | 226.1 |
| March | 7 | 1.5 | 0.12 | 3520 | 22.1 | 3 | 1.4 | 0.13 | 3477 | 21.2 |
| April | 5 | 1.8 | 0.13 | 3605 | 64.1 | 10 | 1.4 | 0.12 | 3587 | 64.1 |

Principal component 2 explained 24.0% of the variation in diets among bighorn sheep and probably represented a continuum from browsing (negative loadings) to grazing (positive loadings). Diets of male and female bighorn sheep overlapped in both study regions, but mean PCA scores and their 95% confidence intervals indicated that patterns of separation in diets existed (Fig. 6). There was an overall effect of sex on mean PCA scores reflecting diet composition (MANOVA; $F_{2,77} = 4.09$, $P = 0.021$). Similarly, mean PCA scores of diet composition differed between bighorn sheep from the Mono Basin and those from the Southern Region

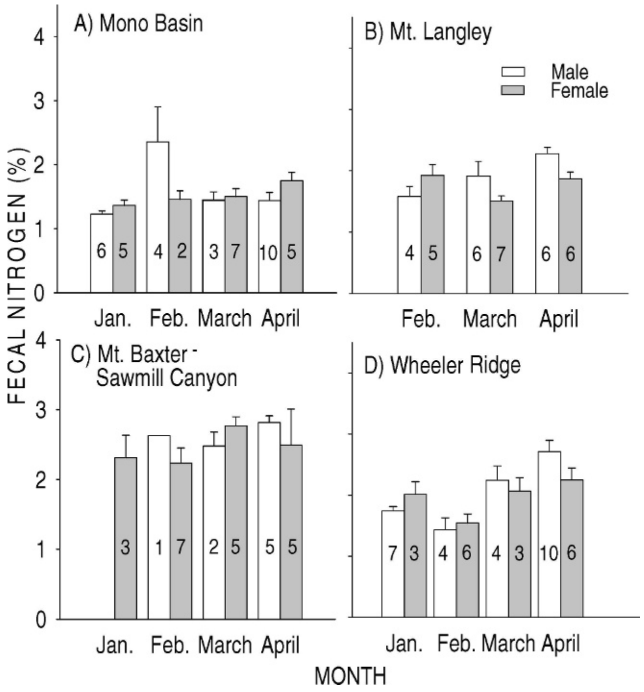

**FIGURE 2. Mean (+SE) monthly fecal nitrogen for adult male and female bighorn sheep in subpopulations inhabiting the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during 2006. Numbers inside bars indicate sample sizes.**

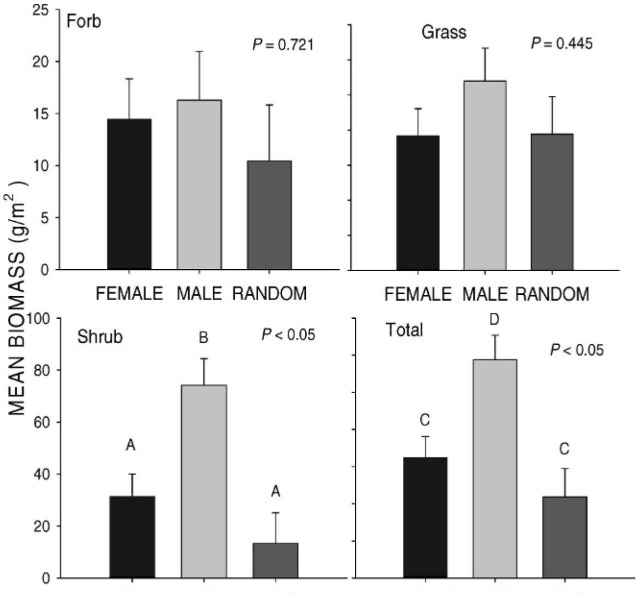

**FIGURE 3. Mean (+SE) wet weight biomass of 1-m$^2$ vegetation plots measured in male bighorn sheep ($n = 11$), female bighorn sheep ($n = 20$), and random ($n = 18$) locations for three forage classes (forbs, grasses, shrubs) and total biomass in the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2005 and 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.**

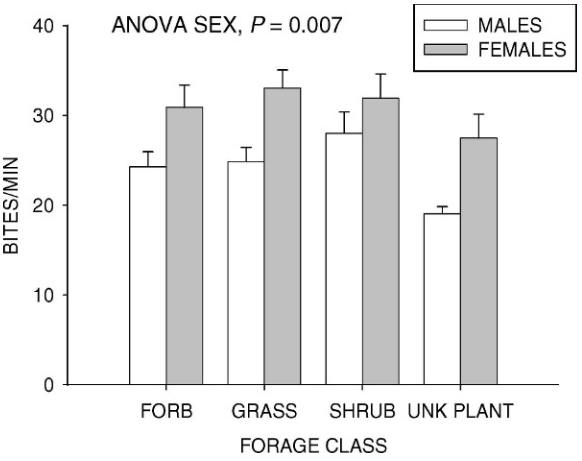

**FIGURE 4. Mean (+SE) bite rates (bites per minute) of adult male ($n = 30$) and female ($n = 29$) bighorn sheep by forage class in the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2005 and 2006.**

($F_{2,77}$ = 66.20, $P < 0.0001$). The sex by region interaction, however, was not significant ($F_{2,78}$ = 2.01, $P$ = 0.14).

The Shannon-Weiner index indicated that overall diet diversity in plant genera was similar between sexes ($e^{\mathrm{H'males}}$ = 9.68, $e^{\mathrm{H'females}}$ = 9.85). Nonetheless, this same index also revealed that diet diversity was higher for male bighorn sheep ($e^{\mathrm{H'}}$ = 34.42) than for females ($e^{\mathrm{H'}}$ = 26.95) inhabiting the Mono Basin, but was more similar between sexes in the Southern Region (male $e^{\mathrm{H'}}$ = 18.80, female $e^{\mathrm{H'}}$ = 21.97).

### *DAILY MOVEMENTS*

Hourly movements ($\overline{X}$ ± SE) for males ranged from 27 to 998 m ($\overline{X}$ = 208 ± 20.6 m). Hourly movements for females ranged from 16 to 301 m ($\overline{X}$ = 69 ± 8.3 m). Daily movements for both sexes combined ranged from 1.12 to 14.50 km ($\overline{X}$ = 4.10 ± 3.69 km). Although sample sizes were small, mean 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).

### *TERRAIN RUGGEDNESS, VISIBILITY, AND ELEVATION*

Differences in the use of rugged terrain occurred between sexes of bighorn sheep (MANOVA, $F_{3,54}$ = 3.26, $P$ = 0.02; Fig 7). Moreover, a significant difference in this ruggedness index occurred among areas occupied by subpopulations (ANOVA, $F_{3,56}$ = 10.04, $P < 0.0001$). Mono Basin had the most rugged terrain ($P < 0.05$), and Wheeler Ridge had more rugged terrain ($P < 0.05$) than Mt. Langley and Mt. Baxter. Females used more rugged terrain (2924.1 ± 1628.05; mean ± SE) than did males (2096.4 ± 1104.09; ANOVA $F_{1,56}$ = 9.19, $P$ = 0.003). Females also used areas with significantly more variation in slope (70.8 ± 27.11) than did males (66.7 ± 13.79, ANOVA $F_{1,56}$ = 9.66, $P$ = 0.003). Angular deviation of aspect in areas used by females (124.2 ± 26.02) did not differ from that used by males (117.4 ± 29.59; ANOVA, $F_{1,56}$ = 0.15, $P$ = 0.703). With the exception of the Mt. Langley subpopulation, females used more rugged terrain than did males (Fig. 7). Visibility ranged from 62% to 91% at female locations, and 28% to 93% at male locations. The $t$-test indicated that mean (±SE) visibility at locations used by females (76 ± 9%) was significantly greater ($P$ = 0.05) than locations used by male bighorn sheep (56 ± 25%).

We used locations of 29 male and 35 female groups of bighorn sheep during winter to compare differences in elevations used by sexes. Overall (ANOVA, $F_{1,56}$ = 4.72, $P$ = 0.034), females occurred at higher mean (±SE) elevations (2119 ± 60.7 m) than did males (2049 ± 73.6 m). Bighorn sheep inhabiting the Mono Basin used the highest (2826 ± 51.5 m), whereas bighorn sheep in the Mt. Baxter area used the lowest elevations (1662 ± 19.6 m). Indeed, a significant difference in elevations used by bighorn sheep occurred among subpopulations (ANOVA, $F_{3,56}$ = 47.06, $P < 0.0001$). Tukey's HSD indicated that bighorn sheep in the Mono Basin used significantly ($P < 0.05$) higher elevations than all other areas, while bighorn sheep inhabiting Mt. Baxter used lower elevations than all other subpopulations ($P < 0.05$). Bighorn sheep

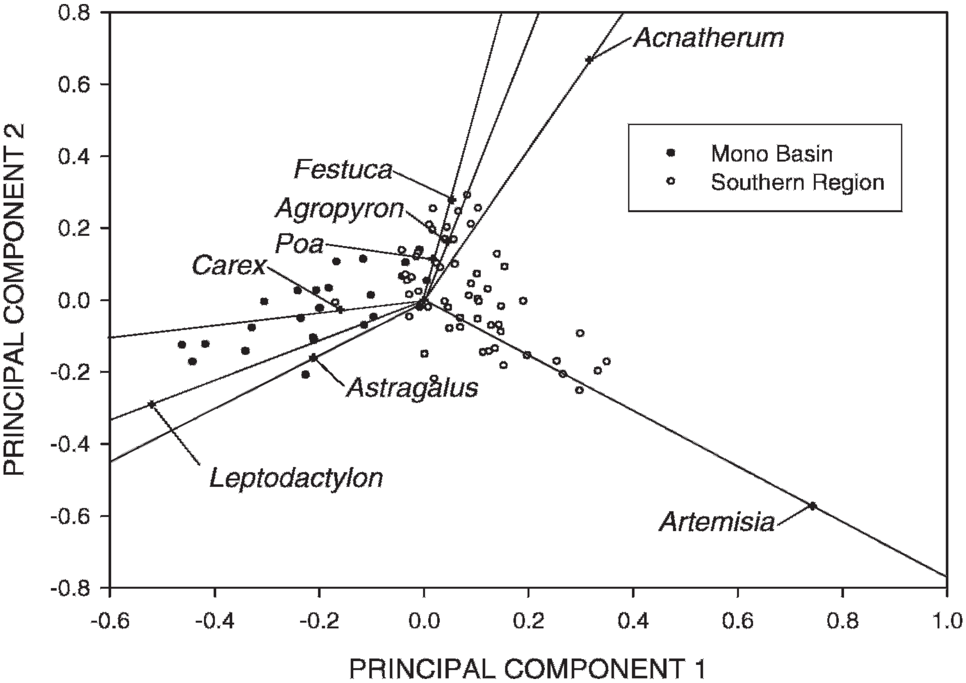

**FIGURE 5. Biplot scatter of principal components analysis (PCA) scores from forage genera determined by microhistological analysis of feces from bighorn sheep in the Mono Basin and Southern Region of the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2006. Plots of principal components 1 and 2 explained 67.9% of the variation in diets (PC1 = 43.9%, PC2 = 24.0%); the lines represent PCA loadings (eigenvectors) for genera of forages.**

### TABLE 2

**Descriptive statistics for percent of plant genera in diets (estimated from microhistological analyses of feces) of male and female bighorn sheep in the Mono subpopulation in the Sierra Nevada, Mono County, California, U.S.A., during winter 2006.**

| | Mono Basin | | | |
|---|---|---|---|---|
| | Male ($n$ = 16) | | Female ($n$ = 9) | |
| Genus* | $\bar{X}$ | *SE* | $\bar{X}$ | *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 |
| *Achnatherum* | 9.3 | 2.0 | 6.1 | 1.7 |
| Other | 33.7 | — | 32.3 | — |

* List only includes plant genera that comprised ≥5% percent of total diet.

on Wheeler Ridge (2110 ± 37.4 m) and Mt. Langley (2031 ± 51.5 m) did not differ significantly in use of elevation ($P > 0.05$).

### GROUP SIZE, DISTANCE TO ESCAPE TERRAIN, AND FORAGING EFFICIENCY

Female bighorn sheep occurred 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. 8); 72% of female groups contained young. 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. 8). Foraging efficiency was positively related to group size for males, but that relationship was not significant for females (Fig. 9). Conversely, foraging efficiency was negatively related to the distance from escape terrain for females, but that relationship was not significant for males (Fig. 10). When controlled for group size and distance to escape terrain, foraging efficiency did not differ between sexes (ANCOVA $_{\text{overall}}\,F_{3,25} = 1.72$, $P = 0.18$; $_{\text{sex}}\,F_{1,25} = 0.78$, $P = 0.39$), indicating the importance of those covariates in affecting vigilance behavior. Similarly, when group size and distance to escape terrain were included as covariates, individual vigilance (percent of time alert) did not differ between sexes (ANCOVA, $F_{3,25} = 1.76$, $P = 0.18$; $_{\text{sex}}\,F_{1,25} = 1.03$, $P = 0.319$).

### TABLE 3

**Descriptive statistics for percent of plant genera in diets (estimated from microhistological analyses of feces) of male and female bighorn sheep in the Southern Region of the Sierra Nevada, Inyo County, California, U.S.A., during winter 2006.**

| | Southern Region | | | |
|---|---|---|---|---|
| | Male ($n$ = 27) | | Female ($n$ = 31) | |
| Genus* | $\bar{X}$ | *SE* | $\bar{X}$ | *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 |
| *Achnatherum* | 18.1 | 2.3 | 18.8 | 2.0 |
| Other | 29.4 | — | 32.1 | — |

* List only includes plant genera that comprised >5% percent of total diet.

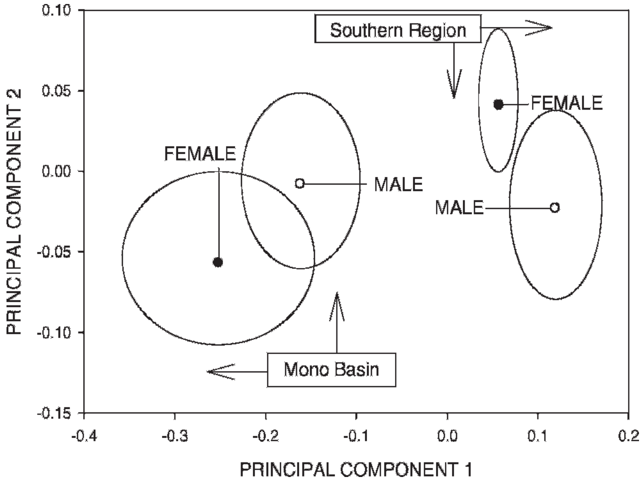

**FIGURE 6. Principal components 1 and 2 for diets of male and female bighorn sheep in the Mono Basin and Southern Region of the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2006. Ellipses are mean PCA scores and 95% confidence intervals. PC1 represents a continuum from lower elevations (positive loadings) to higher elevations (negative loadings). PC2 represents a continuum from browsing (negative loadings) to grazing (positive loadings).**

## Discussion

### PREDICTIONS FROM HYPOTHESES

The relevance of forage acquisition and risk of predation to the evolution of life-history strategies of male and female ungulates has received increasing attention (Bowyer, 2004). In

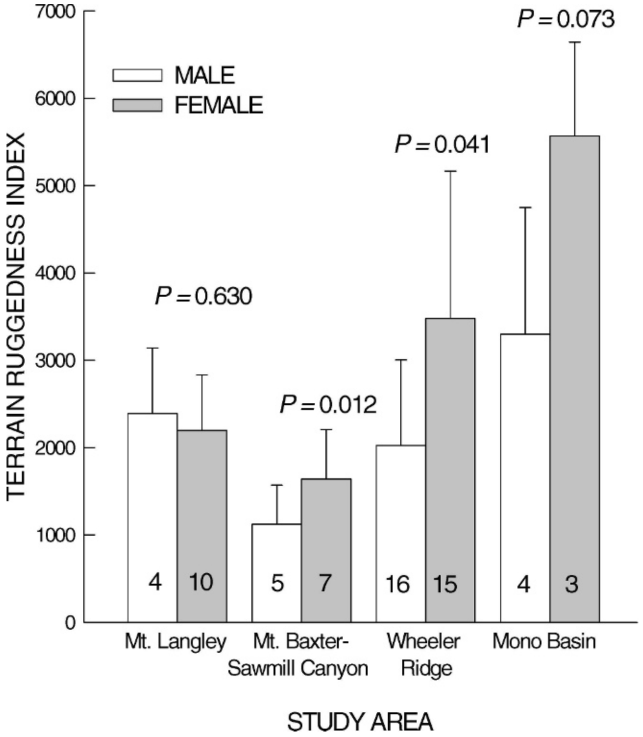

**FIGURE 7. Mean (+SE) use of rugged terrain during winter by subpopulations of bighorn sheep in the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2005 and 2006. Ruggedness values, as indexed by variation in slope and aspect, are presented with samples sizes inside bars. *P*-values are between-sex comparisons for each subpopulation.**

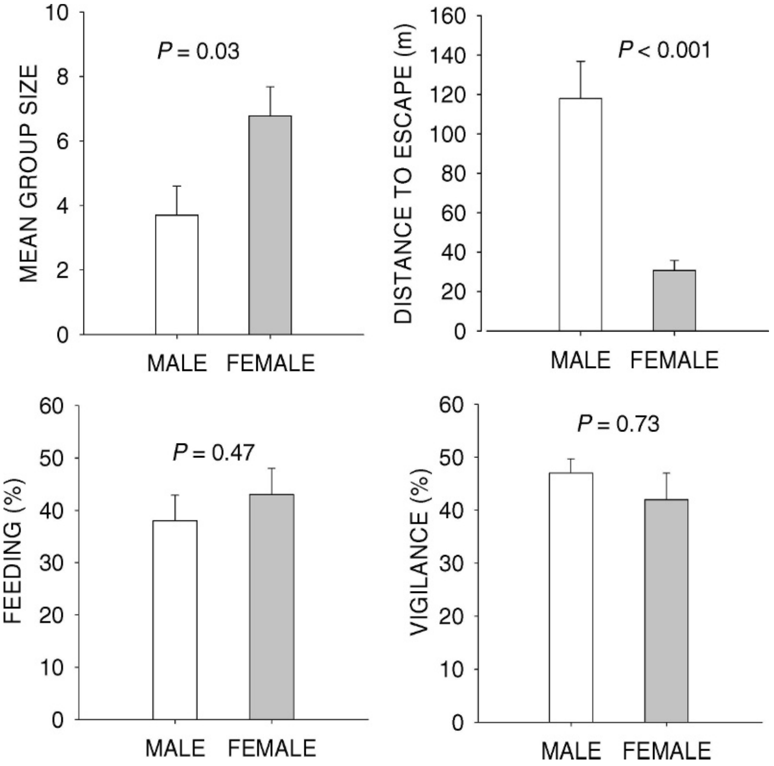

**FIGURE 8. Mean group size (+SE), distance to escape terrain (m), and percentage of time spent feeding and being alert (vigilance) for male ($n = 15$) and female ($n = 14$) bighorn sheep in the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2005 and 2006.**

addition, differing strategies by the sexes are at the forefront of conservation issues relative to the maintenance of viable populations of large herbivores across increasingly fragmented landscapes (e.g., Bleich et al., 1997; Bowyer, 2004; Rubin and Bleich, 2005). Indeed, management plans implemented to enhance habitat for ungulates may inadvertently benefit one sex at the expense of the other (Bowyer et al., 2001; Stewart et al., 2003). Our results, derived specifically from research on one of the most endangered ungulates worldwide, provide additional insights into the evolutionary significance of sexual segregation, while simultaneously providing directions for implementing conservation strategies.

Predictions from predation and gastrocentric hypotheses (Bowyer, 2004) were generally supported by results from this study of bighorn sheep (Table 4). These hypotheses need not be mutually exclusive but the predation and gastrocentric hypotheses are necessary to explain observed patterns of niche partitioning between sexes, especially where tradeoffs occur (Bowyer, 2004). Competing hypotheses exist (Bowyer, 2004; Main, 2008), but predation and the gastrocentric hypothesis are most fruitful of viable hypotheses for framing research questions because they make testable predictions (Bowyer, 2004; Long et al., 2009).

### *GASTROCENTRIC HYPOTHESIS*

Greater biomass of forage occurred at locations of males than those of females. Dietary separation between sexes, and male bighorn sheep traveling farther than females, also supported the gastrocentric hypothesis (Table 4). Predicted differences in fecal nitrogen, however, did not (Barboza and Bowyer, 2000, 2001). In addition, differences between sexes in daily distance traveled and bite rate potentially support both predation and gastrocentric hypotheses.

Although sample sizes were small, male bighorn sheep moved farther per day than did females. These larger daily movements may be explained by the need for males to acquire a greater amount of food per day than needed by females (Gross et al., 1996; Barboza and Bowyer, 2000, 2001). Male bighorn sheep, owing to their larger rumens, can use lower-quality forage with higher fiber content than can females (Barboza and Bowyer, 2000, 2001; Zimmerman et al., 2006). Further, allometric differences in digestive tract morphology between males and females predict

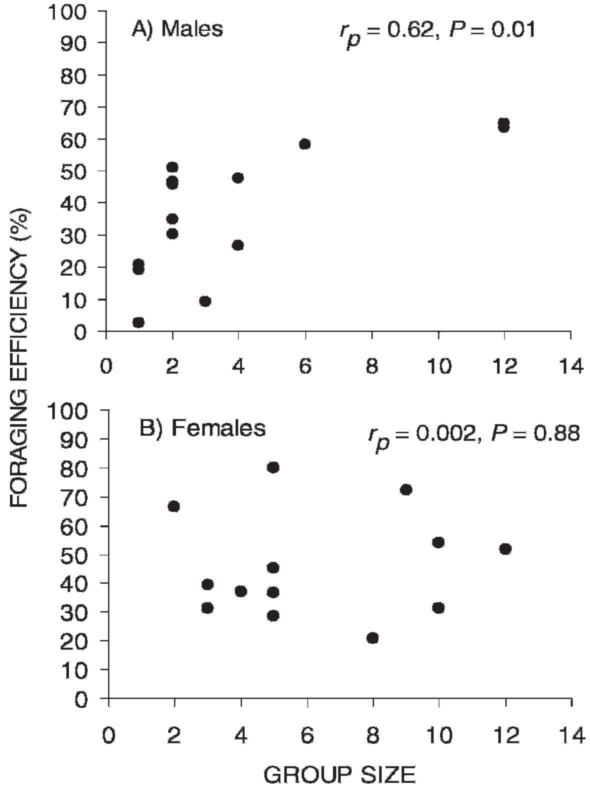

**FIGURE 9. Relationship between foraging efficiency (percentage of active time spent feeding) and group size for (a) male ($n = 15$) and (b) female ($n = 13$) bighorn sheep in the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2005 and 2006.**

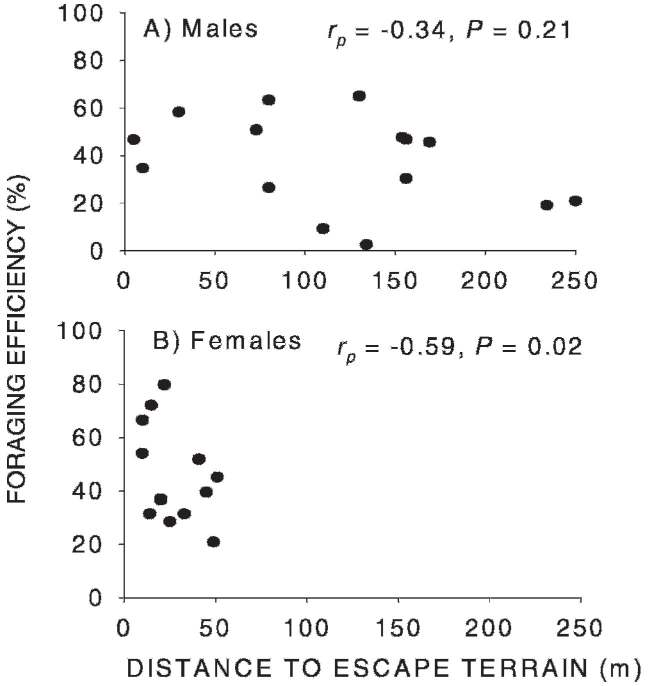

**FIGURE 10. Relationship between foraging efficiency (percentage of active time spent feeding) and the distance to nearest escape terrain (m) for (a) male ($n = 15$) and (b) female ($n = 13$) bighorn sheep in the Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter 2005 and 2006.**

male ruminants require longer periods of non-activity for rumination (Demment and Van Soest, 1985; Jenks et al., 1994; Ruckstuhl, 1998; Barboza and Bowyer, 2000, 2001). Adult female bighorn sheep are approximately 60% the weight of adult 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 nutritional requirements (including males possessing a larger rumen than females) and sparsely vegetated winter ranges in alpine zones of the Sierra Nevada offer a reasonable explanation for why male bighorn sheep moved greater distances per day than did females.

As noted previously, diets of male and female bighorn sheep did not differ in diet quality during winter (as indexed by fecal nitrogen). No difference in diet quality between sexes may not be a reasonable conclusion because of previous contradictory results (Barboza and Bowyer, 2000, 2001; Bowyer, 2004, for reviews) and the large differences in the dietary niches of male and female bighorn sheep (Fig. 6). Results for fecal nitrogen may be confounded by the role that sexual dimorphism and resultant differences in allometry play in digesting forages of varying fibrosity and quality (Jenks et al., 1994; Barboza and Bowyer, 2000, 2001). Females, because of changes in gut morphology associated with late gestation, may be better at extracting nitrogen from forage than are males (Jenks et al., 1994; Zimmerman et al., 2006; J. A. Jenks, personal communication). Differences in fecal nitrogen, however, occurred between subpopulations of bighorn sheep (Table 1, Fig 2), indicating that fecal nitrogen was reflecting overall changes in diet quality. For instance, diet quality in the Mono Basin was significantly lower than for all other subpopulations, likely a result of bighorn sheep in the Mono Basin occupying high elevations with low-quality forages during winter. Although levels of fecal nitrogen (1.2 to 2.4%) were lower for bighorn sheep occupying the Mono Basin than for other subpopulations, those levels are within the range or higher than other published values reported for bighorn sheep inhabiting the Rocky Mountains, U.S.A., during winter (0.8–3.2%, Irwin et al., 1993; 1.2–1.5%, Blanchard et al., 2003). Further, most fecal nitrogen levels were >1.3%, reported by Irwin et al. (1993) as necessary for a maintenance diet during winter, indicating bighorn sheep in the Mono Basin were not nutritionally deficient during winter 2005.

**TABLE 4**

**Predictions from the predation and gastrocentric hypotheses as related to variables sampled for bighorn sheep in Sierra Nevada, Inyo and Mono counties, California, U.S.A., during winter. na = not applicable.**

| Variables | Hypothesis | |
|---|---|---|
| | Predation | Gastrocentric |
| **Forage Based** | | |
| Fecal nitrogen | na | No |
| Biomass | na | Yes |
| Dietary niche | na | Yes |
| Bite rate | Yes | Yes |
| **Behavioral** | | |
| Daily distance traveled | Yes | Yes |
| Group size | Yes | na |
| Foraging efficiency | Yes | na |
| **Physical Attributes** | | |
| Visibility | Yes | na |
| Terrain ruggedness | Yes | na |
| Distance to escape terrain | Yes | na |

Principal Component Analysis indicated that diets of bighorn sheep from the two regions (Mono Basin and Southern Region) diverged markedly in forage composition (Fig. 5), probably a result of bighorn sheep foraging in differing plant communities associated with varying elevations. Bighorn sheep in the Mono Basin foraged mostly on plants characteristic of the alpine fell-fields community (Munz 1974), which included *Leptodactylon*, *Astragalus*, and *Carex*. Bighorn sheep in the Southern Region, however, foraged mostly on plants in the sagebrush-scrub community and included more *Artemisia*, *Achnatherum*, *Festuca*, and *Agropyron* in their diets during winter. Further, diets of male and female bighorn sheep in the Southern Region exhibited significant separation (Fig. 6); males had a broader dietary niche (PC2) than those of females and tended to eat more shrubs such as *Artemisia*, whereas females tended to eat more graminoids including *Achnatherum*, *Poa*, and *Festuca*. In the Mono Basin, diets of males were more characteristic of lower-elevation communities (PC1) in the Southern Region and contained more *Artemisia*, *Achnatherum*, *Poa*, *and Festuca*, whereas diets of females in the Mono Basin were associated with higher elevations and contained mostly *Leptodactylon*, *Astragalus*, and *Carex*.

Differences in diet composition between sexes of bighorn sheep are consistent with a niche-based approach to understanding sexual segregation (Kie and Bowyer, 1999; Bowyer, 2004; Bowyer and Kie, 2004), where overlap on one niche axis is accompanied by avoidance on another. Spatial separation of sexes in both the Mono Basin and the Southern Region were documented. There was, however, more spatial (differential use of rugged terrain by sexes) and less dietary separation between sexes in the Mono Basin than in the Southern Region. Conversely, the sexes of bighorn sheep in the Southern Region exhibited less separation in use of rugged terrain, with considerably less overlap on the dietary niche axis than for bighorn sheep occupying the Mono Basin. These results are consistent with previous studies where dietary and spatial niches between sexes resulted in overlap on one niche axis being accompanied by avoidance on another (Kie and Bowyer, 1999; Stewart et al., 2003). These outcomes also provide additional support for the concept that the sexes of dimorphic ungulates should be managed as if they were coexisting species (Kie and Bowyer, 1999; Bowyer et al., 2001; Stewart et al., 2003; Bowyer, 2004; Rubin and Bleich, 2005).

### *PREDATION HYPOTHESIS*

Observations concerning the behavior of sexes of bighorn sheep that supported the predation hypothesis included differences in the distance sexes occurred from escape terrain, variation in group size by sex, differential visibility and ruggedness of terrain for habitats occupied by males and females, and sexual differences in foraging efficiency (Table 4). Females occurring in areas with less forage but forming larger groups than males indicated that predation risk rather than resources were responsible for this pattern of group formation in females. Others have reported that males foraged in smaller groups than females (Mooring et al., 2003). In addition, males foraged farther from escape terrain than did females (Fig. 8), which also was reported by Berger (1991) for bighorn sheep inhabiting a desert environment.

Females occupied more rugged terrain than did males (Fig. 7). Bleich et al. (1997) similarly reported that females used more rugged terrain, and that males occupied gentler slopes (and even flat terrain) when foraging. Terrain ruggedness was significantly different across geographic locations but, with the exception of the Mt. Langley subpopulation, the pattern of females using more rugged terrain than males was consistent. We hypothesize that females used more rugged terrain to reduce the risk of predation and for protection of their vulnerable offspring, which has been reported by others (Berger, 1991; Bleich et al., 1997; Bleich, 1999; Mooring et al., 2004).

Males foraged in areas with significantly lower visibility (56%) than areas where females foraged (74%). Visibility and distance to escape terrain influence how bighorn sheep allocate foraging time and time spent vigilant for detecting predators. Females typically select more open habitats than do males (Berger, 1991; Bleich et al., 1997). Further, because there was more variation in visibility in habitats used by males, we hypothesize that those individuals were willing to occupy sites with a greater risk of predation, but with abundant forage, to obtain the food necessary for maintenance of body reserves during winter. Indeed, a larger proportion of male bighorn sheep than females have been killed by mountain lions in the Sierra Nevada (California Department of Fish and Game, unpublished data). In addition, Bleich et al. (1997) reported that males occupied areas with more predators than did females when the sexes were spatially segregated.

Foraging efficiency was positively correlated with group size for males, but not for females (Fig. 9). Foraging efficiency was negatively influenced by distance from escape terrain for females, but not for males (Fig. 10). Females, regardless of group size, remained much closer to escape terrain than did males. These observations are unique to this study and emphasize the need to fully understand habitat requirements of the sexes. Others also have reported that foraging efficiency was positively related to group size (Berger, 1978; Rachlow and Bowyer, 1998) and negatively related to distance from escape terrain (Risenhoover and Bailey, 1985), but those authors did not differentiate between sexes. Indeed, Bleich et al. (1997) noted that proximity to escape terrain was more important in defining habitat selection by female than male bighorn sheep.

Female mountain sheep use steep, rocky terrain with good visibility ostensibly to detect and evade predators (Festa-Bianchet, 1988; Berger, 1991; Bleich et al., 1997; Rachlow and Bowyer, 1998; Bleich, 1999; Mooring et al., 2004). Consequently, females remain closer to escape terrain than do males. Males venture farther from escape terrain, and such movements likely increase the rate at which they encounter new foraging areas (Mysterud et al., 2001), 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). Differences in daily movements between sexes of bighorn sheep also might 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 than do females (Barboza and Bowyer, 2000, 2001).

### *OTHER TRADEOFFS*

Female bighorn sheep had higher bite rates than males for all classes of forage (Fig. 4). We hypothesize that the higher bite rates detected in females likely occurred because of smaller bite sizes taken by females than by males, which may result in reduced handling time (i.e., mastication and rumination; Ruckstuhl et al., 2003). Females also may have exhibited higher bite rates because of the tradeoff between foraging efficiency and predation risk. Increasing bite rates combined with a more rapid rate of digestion by females (Barboza and Bowyer, 2000, 2001) would allow them to spend less time with the head in a foraging position, and thereby increase the chance of detecting a predator (Berger, 1978, 1991; Ruckstuhl et al., 2003). Females, however, were not significantly more vigilant than males, perhaps because they occurred in areas with greater visibility than did males.

Female bighorn sheep also may increase bite rates in late spring when energy requirements are higher because of costs of late gestation (Gross et al., 1996). Indeed, female ungulates of sexually dimorphic species typically take smaller bites and forage more selectively than do males (Miquelle et al., 1992; Spaeth et al., 2004). Additionally, males may be less selective for particular parts of plants because they can digest low-quality forage more easily than can females (Barboza and Bowyer, 2000, 2001); hence, males take larger bites with a concomitant increase in the amount of the time needed to masticate and break down plant tissue (or spend more time ruminating).

### *IMPLICATIONS FOR CONSERVATION*

Several important differences in the foraging behavior and habitat use of male and female bighorn sheep inhabiting alpine areas of the Sierra Nevada were documented. Those differences provide conservationists and land managers with detailed knowledge of sex-specific habitat requirements for these endangered herbivores. Further, behavioral differences exist in mountain ungulates that could be used in population-level decisions for management and monitoring. For instance, male bighorn sheep used ranges with more shrub and overall biomass of vegetation than ranges used by females in winter. Additionally, females used more open habitats, whereas males used areas with lower visibility.

Group size and escape terrain should be considered when making some management decisions because of their effects on foraging behavior of bighorn sheep (Risenhoover and Bailey, 1985). Our results indicated that group size has a greater effect on foraging efficiency of males, but that proximity to escape terrain may be a more important factor increasing foraging efficiency of females. These differences could be meaningful when determining a minimum number of animals to be translocated or when deciding if potential translocation sites provide adequate habitat (e.g., escape terrain for females, abundant forage for males). In addition, locating and developing water sources for bighorn sheep in more arid landscapes than the Sierra Nevada might inadvertently favor one sex over the other (Whiting et al., 2009, 2010). Only 41 of 100 populations of bighorn sheep that were translocated in the western United States from 1923 to 1997 were successful (Singer et al., 2000). Considering behavioral and ecological differences between sexes may improve this record.

Habitat loss, protection, and management are key issues for the conservation of many wildlife species (Rubin and Bleich, 2005; Wearmouth and Sims, 2008), especially for bighorn sheep inhabiting alpine environments. Nonetheless, land managers traditionally have considered habitat needs of males and females to be identical (Bowyer et al., 2001; Stewart et al., 2003; Bowyer, 2004). The current recovery plan for the bighorn sheep in the Sierra Nevada does not make a distinction between the habitat requirements of the sexes (U.S. Fish and Wildlife Service, 2008). Our research indicated that critical habitat requirements are specific to each sex. For instance, protection of alpine meadow systems containing an abundance of forbs and grasses that are located immediately adjacent to escape terrain could be beneficial for female bighorn sheep to enhance foraging efficiency and reduce risk of predation. Habitat treatments that are designed with sex-specific considerations, such as removal of overstory vegetation (i.e., pinyon juniper and other conifers) adjacent to escape terrain, may be useful for enhancing habitat on winter ranges used by female bighorn sheep. In the Sierra Nevada, however, the use of fire as a 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. Fires prescribed in areas occupied by male bighorn sheep initially may reduce the overall biomass of vegetation and reduce shrub cover. Even short-term detriments could be important in the conservation these rare alpine ungulates. Nonetheless, management that favors females may be prudent because of the polygynous mating system and the need to enhance population growth for recovery of bighorn sheep in the Sierra Nevada.

Recovery could be enhanced by implementation of management strategies that incorporate differential niche requirements of sexes of bighorn sheep. For example, proposals for translocation should consider 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. Males in our study exhibited much larger daily rates of movement than did females. 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 bighorn sheep (DeCesare and Pletscher, 2006).

Male and female ruminants use space differently during segregation, and this behavior has implications for wildlife biologists seeking to improve methods for population estimation (Bleich et al., 1997; Bowyer, 2004; Rubin and Bleich, 2005). During winter, bighorn sheep are sexually segregated, which may affect estimates of male to female ratios if one sex or the other is undercounted during surveys because of their disjunct distributions (Bleich et al., 1997). We demonstrated that females generally occupy more rugged terrain, which could affect visibility and cause a bias associated with population estimates. Estimating the number of males in a population also could be problematic if bighorn sheep are more likely to move greater distances on a daily basis, and thereby exacerbate the potential for double counting or under-estimation if surveys are not properly designed. Bighorn 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 alpine-dwelling ungulate if they are to be successful.

## Acknowledgments

This project was funded by California Department of Fish and Game (CDFG), the California Chapter of the Foundation for North American Wild Sheep, and the Department of Biological Sciences at Idaho State University. The CDFG provided field equipment, logistical support, and access to maps and some data used in analyses. D. German, H. Johnson, D. Jensen, J. Wehausen, L. Bowermaster, J. Villepique, and B. Pierce provided support and helped develop ideas for this research. K. M. Stewart, P. Murphy, J. G. Kie, D. J. Delehanty, K. L. Monteith, J. C. Whiting, and P. Atwood assisted with data analysis and reviewed this manuscript. This is a contribution from the CDFG Mountain Sheep Conservation Program, and is Professional Paper 066 from the Eastern Sierra Center for Applied Population Ecology.

## References Cited

Altmann, J., 1974: Observational study of behavior: sampling methods. *Behaviour*, 49: 227–276.

Barboza, P. S., and Bowyer, R. T., 2000: Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy*, 81: 473–489.

Barboza, P. S., and Bowyer, R. T., 2001: Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces*, 37: 275–292.

Barten, N. L., Bowyer, R. T., and Jenkins, K. J., 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., Festa-Bianchet, M., Gaillard, J.-M., and Jorgenson, J. T., 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., 1999: Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy*, 80: 283–289.

Bleich, V. C., Hargis, C. D., Keay, J. A., and Wehausen, J. D., 1991: Interagency coordination and the restoration of wildlife populations. *In* Edelbrock, J., and Carpenter, S. (eds.), *Natural Areas and Yosemite: Prospects for the Future*. Denver, Colorado: U.S. National Park Service, Denver Service Center, 277–284.

Bleich, V. C., Bowyer, R. T., and Wehausen, J. D., 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., 1986: Habitat selection by southern mule deer. *California Fish and Game*, 72: 153–169.

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 Kie, J. G., 2004: Effects of foraging activity on sexual segregation in mule deer. *Journal of Mammalogy*, 85: 498–504.

Bowyer, R. T., Kie, J. G., and Van Ballenberghe, V., 1998: Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *Journal of Mammalogy*, 79: 415–425.

Bowyer, R. T., Van Ballenberghe, V., Kie, J. G., and Maier, J. A. K., 1999: Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy*, 80: 1070–1083.

Bowyer, R. T., Pierce, B. M., Duffy, L. K., and Haggstrom, D. A., 2001: Sexual segregation in moose: effects of habitat manipulation. *Alces*, 37: 109–122.

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, 157 pp.

Coggins, V. L., and Matthews, P. E., 1992: Lamb survival and herd status of the Lostine bighorn herd following a *Pasteurella* die-off. *Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council*, 8: 147–154.

DeCesare, N. J., and Pletscher, D. H., 2006: Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. *Journal of Mammalogy*, 87: 531–538.

Demment, M. W., and Van Soest, P. J., 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 Apollonio, M., 2003: *Animal Behavior and Wildlife Conservation*. Washington, D.C: Island Press.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., and Toigo, C., 2000: Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, 31: 367–393.

Gannon, W. L., Sikes, R. S., the Animal Care and Use Committee of the American Society of Mammalogists, 2007: Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 88: 809–823.

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

Griffith, B., and Youtie, B. A., 1988: Two devices for estimating foliage density and hiding cover. *Wildlife Society Bulletin*, 16: 206–210.

Gross, J. E., Alkon, P. U., and Demment, M. W., 1996: Nutritional ecology of dimorphic herbivores: digestion and passage rates in Nubian ibex. *Oecologia*, 107: 170–178.

Hay, D. T., Cross, P. C., and Funston, P. J., 2008: Trade-offs of predation and foraging explain sexual segregation in African buffalo. *Journal of Animal Ecology*, 77: 850–858.

Hill, M., 1975: *Geology of the Sierra Nevada*. Berkeley: University of California Press.

Hodgman, T. P., Davitt, B. B., and Nelson, J. R., 1996: Monitoring mule deer diet quality and intake with fecal indices. *Journal of Range Management*, 49: 215–222.

Illius, A. W., and Gordon, I. J., 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>.

Irwin, L. L., Cook, J. G., McWhirter, D. E., Smith, S. G., and Arnett, E. B., 1993: Assessing winter dietary quality in bighorn sheep via fecal nitrogen. *Journal of Wildlife Management*, 57: 413–421.

Jenks, J. A., Leslie, D., Jr., Lochmiller, R. L., and Melchiors, M. A., 1994: Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. *Journal of Mammalogy*, 75: 1045–1053.

Jones, F. L., 1950: A survey of the Sierra Nevada bighorn. *Sierra Club Bulletin*, 35(6): 29–76.

Kie, J. G., and Bowyer, R. T., 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 Bowyer, R. T., 2003: Mountain sheep (*Ovis canadensis and O. dalli*). *In* Feldhamer, G. A., Thompson, B. C., and Chapman, J. A. (eds.), *Wild Mammals of North America: Biology, Management, and Conservation*. Baltimore: The Johns Hopkins University Press, 105–118.

Krausman, P. R., Hervert, J. J., and Ordway, L. L., 1985: Capturing deer and mountain sheep with a net-gun. *Wildlife Society Bulletin*, 13: 71–73.

LeBlanc, M., Festa-Bianchet, M., and Jorgenson, J. T., 2001: Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Canadian Journal of Zoology*, 79: 1661–1670.

Leslie, D. M., Jr., Bowyer, R. T., and Jenks, J. A., 2008: Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. *Journal of Wildlife Management*, 72: 1420–1433.

Little, R. C., Milliken, G. A., Stroup, W. W., and Wolfinger, R. D., 1996: *SAS System for Mixed Models*. Cary, North Carolina: SAS Institute.

Loison, A., Gaillaird, J.-M., Pleabon, C., and Yoccoz, N. G., 1999: What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research*, 1: 611–633.

Long, R. A., Rachlow, J. L., and Kie, J. G., 2009: Sex-specific responses of North American elk to habitat manipulation. *Journal of Mammalogy*, 90: 423–432.

Main, M. B., 2008: Reconciling competing hypotheses for sexual segregation in ungulates. *Ecology*, 89: 693–704.

Main, M. B., Weckerly, F. L., and Bleich, V. C., 1996: Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy*, 77: 449–461.

McGarigal, K., Cushman, S., and Stafford, S., 2000: *Multivariate Statistics for Wildlife and Ecology Research*. New York: Springer.

Miquelle, D. G., Peek, J. M., and Van Ballenberghe, V., 1992: Sexual segregation in Alaskan moose. *Wildlife Monographs*, 122: 1–57.

Molvar, E. M., and Bowyer, R. T., 1994: Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy*, 75: 621–630.

Mooring, M. S., Fitzpatrick, T. A., Benjamin, J. E., Fraser, I. C., Nishihira, T. T., Reisig, D. D., and Rominger, E. M., 2003: Sexual segregation in desert bighorn sheep (*Ovis canadensis mexicana*). *Behaviour*, 140: 183–207.

Mooring, M. S., Fitzpatrick, T. A., Nishirira, T. T., and Reisig, D. D., 2004: Vigilance, predation risk, and the Allee effect in desert bighorn sheep. *Journal of Wildlife Management*, 68: 519–532.

Munz, P. A., 1974: *A Flora of Southern California*. Berkeley: University of California Press.

Mysterud, A., Perez-Barberia, F. J., and Gordon, I. J., 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, Nevada, U.S.A. <http://www.wrh.noaa.gov/vef/regionalclimate.php>.

Nicholson, M. C., Bowyer, R. T., and Kie, J. G., 1997: Habitat selection and survival of mule deer: tradeoffs associated with migration. *Journal of Mammalogy*, 78: 483–504.

Oehler, M. W., Sr., Bowyer, R. T., and Bleich, V. C., 2003: Home ranges of female mountain sheep, *Ovis canadensis nelsoni*: effects of precipitation in a desert ecosystem. *Mammalia*, 67: 385–401.

Oehler, M. W., Sr., Bleich, V. C., Bowyer, R. T., and Nicholson, M. C., 2005: Mountain sheep and mining: implications for conservation and management. *California Fish and Game*, 91: 149–178.

Onderka, D. K., Rawluk, S. A., and Wishart, W. D., 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., Gordon, I. J., and Pagel, M., 2002: The origins of sexual dimorphism in body size of ungulates. *Evolution*, 56: 1276–1285.

Pierce, B. M., Bleich, V. C., and Bowyer, R. T., 2000a: Social organization of mountain lions: does a land-tenure system regulate population size? *Ecology*, 81: 1533–1543.

Pierce, B. M., Bleich, V. C., and Bowyer, R. T., 2000b: Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. *Journal of Mammalogy*, 81: 462–472.

Pierce, B. M., Bowyer, R. T., and Bleich, V. C., 2004: Habitat selection by mule deer: forage benefits or risk of predation? *Journal of Wildlife Management*, 68: 533–541.

Rachlow, J. L., and Bowyer, R. T., 1991: Interannual variation in timing and synchrony of parturition in Dall's sheep. *Journal of Mammalogy*, 72: 487–492.

Rachlow, J. L., and Bowyer, R. T., 1994: Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? *Journal of Mammalogy*, 75: 328–337.

Rachlow, J. L., and Bowyer, R. T., 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., Bayne, R. L., and West, N. E., 1980: Evaluation of double-sampling estimators of subalpine herbage production. *Journal of Range Management*, 33: 300–306.

Reich, R. M., Bonham, C. D., and Remington, K. K., 1993: Technical notes: double-sampling revisited. *Journal of Range Management*, 46: 88–90.

Ricklefs, R. E., and Miller, G. L., 2001: *Ecology.* Fourth edition. New York: W. H. Freeman.

Risenhoover, K. L., and Bailey, J. A., 1985: Foraging ecology of mountain sheep: implications for habitat management. *Journal of Wildlife Management*, 49: 797–804.

Rodgers, A. R., and Carr, A. P., 1998: *HRE: the Home Range Extension for ArcView*. Thunder Bay, Ontario, Canada: Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research.

Rubin, E. S., and Bleich, V. C., 2005: Sexual segregation: a necessary consideration in wildlife conservation. *In* Ruckstuhl, K. E., and Neuhaus, P. (eds.), *Sexual Segregation in Vertebrates: Ecology of the Two Sexes*. Cambridge: Cambridge University Press, 379–391.

Ruckstuhl, K. E., 1998: Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour*, 56: 99–106.

Ruckstuhl, K. E., and Festa-Bianchet, M., 2001: Group choice by subadult bighorn rams: tradeoffs between foraging efficiency and predator avoidance. *Ethology*, 107: 161–172.

Ruckstuhl, K. E., and Neuhaus, P., 2001: Behavioral synchrony in ibex groups: effects of age, sex, and habitat. *Behaviour*, 137: 361–377.

Ruckstuhl, K. E., and Neuhaus, P., 2002: Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Review*, 77: 77–96.

Ruckstuhl, K. E., Festa-Bianchet, M., and Jorgenson, J. T., 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. Cary, North Carolina: SAS Institute.

Singer, F. J., Papouchis, C. M., and Symonds, K. K., 2000: Translocations as a tool for restoring populations of bighorn sheep. *Restoration Ecology*, 8: 6–13.

Spaeth, D. F., Bowyer, R. T., Stephenson, T. R., and Barboza, P. S., 2004: Sexual segregation in moose *Alces alces*: an experimental manipulation of foraging behavior. *Wildlife Biology*, 10: 59–72.

Sparks, D. F., and Malechek, J. C., 1968: Estimating percentage dry weight in diets using a microscopic technique. *Journal of Range Management*, 21: 264–265.

Stewart, K. M., Fulbright, T. E., Drawe, D. L., and Bowyer, R. T., 2003: Sexual segregation in white-tailed deer: responses to habitat manipulations. *Wildlife Society Bulletin*, 31: 1210–1217.

U.S. Fish and Wildlife Service, 2008: Recovery plan for the Sierra Nevada bighorn sheep *(Ovis canadensis californiana)*. Portland, Oregon: U.S. Fish and Wildlife Service.

Wearmouth, V. J., and Sims, D. W., 2008: Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology*, 54: 107–170.

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, 240 pp.

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 of the Northern 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.

Whiting, J. C., Bowyer, R. T., and Flinders, J. T., 2008: Young bighorn (*Ovis canadensis*) males: can they successfully woo females? *Ethology*, 114: 32–41.

Whiting, J. C., Bowyer, R. T., and Flinders, J. T., 2009: Annual use of water sources by reintroduced Rocky Mountain bighorn sheep: effects of season and drought. *Acta Theriologica*, 54: 127–136.

Whiting, J. C., Bowyer, R. T., Flinders, J. T., Bleich, V. C., and Kie, J. G., 2010: Sexual segregation and use of water by bighorn sheep: implications for conservation. *Animal Conservation*. doi:10.1111/j.1469-1795.2010.00370.x.

Zar, J., 1999: *Biostatistical Analysis.* Fourth edition. Upper Saddle River, New Jersey: Prentice Hall Inc.

Zimmerman, T. J., Jenks, J. A., and Leslie, D. M., Jr., 2006: Gastrointestinal morphology of female white-tailed and mule deer: effects of fire, reproduction, and feeding type. *Journal of Mammalogy*, 87: 598–605.

*MS accepted March 2010*