

Evaluating Potential Overlap Between Pack Stock and Sierra Nevada Bighorn Sheep (*Ovis canadensis sierrae*) in Sequoia and Kings Canyon National Parks, California

Open-File Report 2015–1102

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By Robert C. Klinger, Alexandra P. Few, Kathleen A. Knox, Brian E. Hatfield, Jonathan Clark, David W. German, and Thomas R. Stephenson

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Conversion Factors

Inch/Pound to International System of Units

Multiply	By	To obtain
Area		
acre	4,047	square meter (m ²)
acre	0.4047	hectare (ha)

International System of Units to Inch/Pound

Multiply	By	To obtain
Length		
meter (m)	3.281	foot (ft)
Area		
square centimeter (cm ²)	0.001076	square foot (ft ²)
square meter (m ²)	0.0002471	acre
square meter (m ²)	10.76	square foot (ft ²)
hectare (ha)	2,471	acre

Datums

Vertical coordinate information is referenced to the North American Vertical Datum of 1988 (NAVD 88).

Elevation, as used in this report, refers to distance above the vertical datum.

Abbreviations

ANOVA	analysis of variance
AIC _c	Bias-corrected Akaike Information Criterion
DbRDA	Distance-based Redundancy Analysis
GIS	geographic information system
GPS	Global Positioning System
GLMM	Generalized Linear Mixed Model
NDVI	Normalized Difference Vegetation Index
PCA	Principal Components Analysis
<i>r</i>	correlation coefficient
SEKI	Sequoia and Kings Canyon National Parks
SNBS	Sierra Nevada bighorn sheep
USGS	U.S. Geological Survey
<i>w</i> AIC _c	AIC _c weights

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Evaluating Potential Overlap Between Pack Stock and Sierra Nevada Bighorn Sheep (*Ovis canadensis sierrae*) in Sequoia and Kings Canyon National Parks, California

By Robert C. Klinger¹, Alexandra P. Few², Kathleen A. Knox², Brian E. Hatfield^{1,2}, Jonathan Clark¹, David W. German², and Thomas R. Stephenson²

Abstract

Pack stock (horses, mules, burros, llamas, and goats) are frequently assumed to have negative effects on public lands, but there is a general lack of data to be able to quantify the degree to which this is actually the case. Sequoia and Kings Canyon National Parks have received complaints that pack stock may affect Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; SNBS), a federally endangered subspecies that occurs in largely disjunct herds in the Sierra Nevada Range of California. The potential effects are thought to be displacement of SNBS from meadows on their summer range (altered habitat use) or, more indirectly, through changes in SNBS habitat or forage quality. Our goals were to conduct an association analysis to quantify the degree of potential spatial overlap in meadow use between SNBS and pack stock and to compare differences in vegetation community composition, structure, and diversity among meadows with different levels of use by bighorn sheep and pack stock. For the association analysis, we used two approaches: (1) we quantified the proportion of meadows that were within the herd home ranges of bighorn sheep and were potentially open to pack stock, and, (2) we used Monte Carlo simulations and use-availability analyses to compare the proportion of meadows used by bighorn sheep relative to the proportional occurrence or area of meadows available to bighorn sheep that were used by pack stock. To evaluate potential effects of pack stock on meadow plant communities and SNBS forage, we sampled vegetation in 2011 and 2012 at 100 plots to generate data that allowed us to compare:

1. Herbaceous plant species composition, structure, and diversity in plots with different combinations of use by pack stock and SNBS;
2. Cover of bare ground in plots with different combinations of use by pack stock and SNBS; and,
3. Total cover, diversity, and species composition of SNBS forage species in plots with different combinations of use by pack stock and SNBS.

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The association analyses indicated the potential for overlap between pack stock and SNBS was minimal; only 1 percent of the potential meadow area in the SNBS herd home ranges overlapped that of pack stock meadows. There were no systematic differences in overall vegetation structure or composition, or in diversity, cover, or composition of forage species, that indicated pack stock were altering SNBS habitat or affecting their nutrition. Variation in plant species composition was influenced primarily by random differences among meadows and environmental gradients, and there was little evidence that pack stock use contributed in meaningful ways to this variation. The few differences among meadows with different levels of use by bighorn sheep and pack stock either were minor or were not in a direction consistent with negative effects of pack stock on SNBS. We conclude that the current plan for managing pack stock grazing has been successful in minimizing significant negative effects on Sierra Nevada bighorn sheep at Sequoia and Kings Canyon National Parks.

Introduction

Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; referred to hereon as “SNBS”) are a federally endangered subspecies that occurs in the Sierra Nevada Range of California. Although they feed on shrubs and subshrubs, SNBS are recognized primarily as grazers (Wehausen, 1980; Schroeder and others, 2010). Most of their diet is comprised of graminoids (grasses, sedges, and rushes) and forbs that provide adequate forage to meet their nutritional demands. During summer, SNBS primarily are present in steep, rocky areas characterized by a low density of vegetation, but they often move into meadows adjacent to rocky areas to feed. Meadows frequently have a relatively dense cover of highly nutritious herbaceous species (Wehausen, 1980). Thus, although SNBS spend most of their time in rocky areas, they likely get a disproportionate amount of their nutrition from the limited time they spend in meadows.

Of the herd units identified in the Recovery Plan for Sierra Nevada bighorn sheep (U.S. Fish and Wildlife Service, 2007), 10 of 16 (62.5 percent) lie partially or wholly within Sequoia and Kings Canyon National Parks (SEKI). Therefore, maintaining the integrity of habitats within SEKI is essential for recovery of SNBS. However, the National Park Service has received complaints that pack stock (horses, mules, burros, llamas, and goats) use the same habitats as SNBS and may be having negative effects on SNBS recovery. Unlike in many other western national parks, pack stock are allowed to graze in many of the wilderness meadows of SEKI. Pack stock use in high-elevation habitats occurs near trail systems throughout much of SEKI (McClaren, 1989), and particular concern has been expressed about the effect of such use on meadows. These herbaceous-dominated communities often are focal areas for wildlife and human activities (McClaren and Cole, 1993; Ostojka and others., 2014), but they are a limited resource in the Sierra Nevada; only an estimated 6–12 percent of the landscape in the alpine and subalpine zones of the Sierra Nevada is considered meadow (Robert C. Klinger, U.S. Geological Survey, unpub. data, 2012). Nevertheless, the importance of meadows to SNBS as well as other wildlife species greatly exceeds their land area (Allen, 1987). Currently, 219 meadows (totaling 753 acres) are open to grazing, with additional meadows open to smaller pack animals such as llamas (*Lama glama*) and burros (*Equus africanus*).

Despite the potential for negative effects on SNBS (Papouchis and others, 2001; Ostoja and others, 2014), documented evidence of the degree to which pack stock or how pack stock might effect SNBS has been unavailable. Potential negative effects include disease transmission, habitat destruction or alteration, behavioral displacement, or excessive removal of forage. With the exception of goats (*Capra aegagrus*), pack stock are unlikely to pose a disease risk to SNBS. Experimental studies that examined the co-pasturing of bighorn sheep with llamas and horses (*Equus ferus*) did not identify any evidence of disease transmission or morbidity and mortality associated with such contact (Foreyt, 1994; Foreyt and Lagerquist, 1996). Conversely, domestic goats have been associated with negative effects of disease following contact with bighorn sheep (Jansen and others, 2006). The risk associated with the use of packing goats is recognized and has resulted in their exclusion from SEKI and much of SNBS range.

In SEKI, potential effects by pack stock are most likely to be associated with influences on the foraging efficiency and forage supply for SNBS. Trampling by pack stock could have numerous effects on the structure of meadows through a combination of soil compaction, erosion, and destruction of vegetation (Cole and others, 2004). Additionally, grazing by pack stock could modify meadow structure because of excessive biomass removal (Ostoja and others, 2014).

Pack stock also could have negative effects on SNBS through behavioral interactions. For example, Ostermann-Kelm and others (2008) observed that desert bighorn avoided water sources when horses were nearby, and Brown and others (2010) noted that bighorn sheep foraged less efficiently in the presence of livestock, specifically cattle. Shrestha and Wegge (2008) observed that grazing by livestock in areas overlapping with wild sheep habitat likely resulted in competition for forage.

Cole and others (2004) observed that horses and mules preferred graminoids, and consequently modified the species composition in Sierra Nevada meadows that were grazed. Although SNBS consume a combination of grasses, forbs, and shrubs, graminoids typically compose the largest proportion of the diet during summer (Wehausen, 1980) and winter (Schroeder and others, 2010). Thus, the potential exists for pack stock to compete with bighorn sheep for forage when using the same areas. However, grazing can have positive or negative effects on plant growth and production depending on the level of removal (McNaughton, 1983; Belsky, 1986).

In order for SNBS to be negatively affected by pack stock, there must be spatial overlap in habitat use that negatively affects habitat quality, habitat use, or forage acquisition by SNBS. Therefore, the study objectives were to:

1. Conduct an association analysis to quantify the degree of potential spatial overlap in meadow use between SNBS and pack stock;
2. Analyze differences in vegetation community composition and structure among meadows with different levels of use by bighorn sheep and pack stock; and
3. Compare cover, diversity, and species composition of summer forage with different levels of use by SNBS and pack stock.

Methods

Study Area

The study focused on the Sawmill Canyon, Mount Baxter, Bubbs Creek, Mount Williamson, and Mount Langley herds. Situated within SEKI north to south along the Sierra Nevada escarpment, these five populations represent approximately 69 percent of all SNBS (Stephenson and others, 2012). SNBS spend summers in the alpine and subalpine zones, and winters either in the same summer habitats or on low-elevation winter ranges, typically east of the crest at the base of the escarpment (U.S. Fish and Wildlife Service, 2007). Pack animals are present in SNBS habitat in SEKI in the summer months, but are not present in the SNBS winter range. Therefore, we restricted our analysis to summer habitat for SNBS.

Spatial Data Sources

The primary source of SNBS spatial data included 25,510 locations collected between 2005 and 2012 in the five herd units within the boundaries of SEKI (table 1). SNBS locations were collected from Global Positioning System (GPS) and radio telemetry collars and digitized into geographic information system (GIS) shapefiles.

Meadows were delineated from a GIS layer provided by SEKI. This layer included a field that identified whether a meadow was open or closed to use by pack stock.

Table 1. Number of Sierra Nevada bighorn sheep locations collected from Global Positioning System and radio telemetry collars in five herd units within Sequoia and Kings Canyon National Parks, California.

[Start year and End year are the years of first and last collection of data, respectively]

Herd unit	Number of locations	Start year	End year
Mount Baxter	5,505	2008	2012
Bubbs Creek ¹	1,619	2010	2011
Mount Langley	8,224	2005	2012
Sawmill Creek	8,212	2005	2012
Mount Williamson ¹	1,950	2008	2012

¹These herd units did not encompass any meadows open to pack stock, so they were not included in any analyses.

Association Analyses

Two approaches were used to quantify potential overlap in meadow use. The first approach was based on the proportion of meadows in the parks that was within the herd home ranges of bighorn sheep and that was potentially open to pack stock. In the second approach, we compared the proportion of meadows used by bighorn sheep relative to the proportional area of meadows available to bighorn sheep that were used by pack stock. The first approach allowed us to evaluate the potential for overlap of bighorn sheep and pack stock based on the number of meadows at the landscape scale, whereas the second approach allowed us to evaluate the potential for overlap after accounting for availability based on meadow area.

Number and Proportion of Area of Meadows Within Herd Home Ranges of Bighorn Sheep

Pack stock are legally constrained to a subset of meadows within the parks, and bighorn sheep are biologically constrained to areas near escape terrain (defined as areas with slopes of $31^\circ > x > 70^\circ$). These constraints created four mutually exclusive meadow classes:

1. Not used by SNBS or pack stock,
2. Used by SNBS but not pack stock,
3. Used by pack stock but not SNBS, and,
4. Used by SNBS and pack stock.

We used GIS to generate minimum convex polygons from all locations within each herd unit, and then calculated the number of meadows that intersected or were within each herd unit polygon as well as the area (in hectares) of meadows within each of the herd unit polygons. Additionally, we calculated the number and area of the meadows open to pack stock grazing that were outside of the herd unit polygons.

Bighorn Sheep Use and Availability of Meadows in Different Classes of Pack Stock Use

Although a meadow could be within a herd unit polygon, this did not necessarily mean it was available to bighorn sheep because of their strong tendency to be near escape terrain. Despite the large number of bighorn sheep locations, less than 2.5 percent (N=566) occurred within mapped meadows (N=92). Many other locations were near meadows, however, and it was reasonable to assume that SNBS were using many of those meadows. Moreover, more SNBS locations likely would be recorded in larger meadow polygons. Therefore, the first step was to establish a justifiable definition of meadow availability to SNBS. To do this, we used a Generalized Linear Mixed Model (GLMM) to analyze the relationship between the number of SNBS locations and distance from escape cover and meadow area. The model included a Poisson error structure and log link with herd unit as a random factor. The GLMM estimated potential availability; therefore, we classified the number of predicted SNBS locations at distances from escape terrain of 50 m (a conservative estimate of availability), 100 m (a moderate estimate of availability), and 250 m (a liberal estimate of availability). We then calculated the percentiles of the predicted locations from the GLMM that occurred within each distance class.

Two methods were used to compare potential use of meadows by SNBS relative to pack stock use. The first method allowed us to account for potential use relative to availability after accounting for differences in meadow area. The second method allowed us to account for SNBS and pack stock not having equal probability of occurring in the meadows because of the distribution of the meadows within the herd units. The potential for overlap between pack stock and SNBS would be greatest if the number of meadows available to SNBS and open to grazing by pack stock was higher than would be expected based on their proportional area on the landscape. Meadows open to grazing by pack stock but not available for potential use by SNBS, meadows not open to pack stock but available for potential use by SNBS, and meadows not open to pack stock and not available for potential use by SNBS would provide reference levels relative to those meadows potentially used by both SNBS and pack stock.

The first method consisted of a use-availability analysis where availability was based on the area (in hectares) of meadows in each of the four meadow use classes, and potential use by SNBS was based on the number of meadows in each of the use classes. A log-likelihood χ^2 statistic first was used to evaluate evidence of overall differences in potential use among the classes. If the χ^2 statistic was significant then simultaneous confidence intervals were constructed for each class; classes with confidence intervals not overlapping available area were considered to have the potential to be used more or less than their availability based on their proportional area (Manly and others, 2002).

The second method consisted of a series of Monte Carlo simulations where we calculated the actual (“observed”) proportion of meadows within each of the three distance from escape terrain classes (determined from the GLMM). We then drew 10,000 random samples of meadows from within each of the three classes. To account for potential sample-size bias, we repeated this for samples based on 50, 60, 70, and 80 percent of the total number of meadows within each of the three distance classes. We constructed frequency distributions of proportional use in each of the distance/sample size combinations (N=15), and then compared the actual proportion in each use class to the distribution of simulated values. If the actual proportion was less than the 5th percentile or greater than the 95th percentile, we considered this evidence of disproportionately lesser or greater chance of overlap, respectively, than expected by chance.

Meadow Community and Forage Analysis

Evidence of the potential for displacement of bighorn sheep by pack stock would represent a direct negative effect, but pack stock could have indirect negative effects due to habitat alteration or changes in forage quantity. By conducting an analysis of meadow vegetation composition and structure, we could infer the likelihood that potential indirect effects were occurring and, if so, how strong they were. Similarly, by analyzing forage cover, diversity, and species composition, we could infer the likelihood that pack stock were affecting SNBS nutrition.

Sampling

We used a GIS to randomly select 21 meadows within the herd home ranges of Mount Baxter, Mount Langley, and Sawmill Creek herd units. We randomly located 3–14 plots in each meadow (N=100 plots total) and classified each plot into one of the four SNBS/pack stock use classes (table 2). Each plot was 0.25 ha in area and consisted of four 25-m transects originating from a center point, with each transect oriented in one of the four cardinal directions. Ocular estimates of cover and measurements of height were made for all herbaceous species (forbs, grasses, and sedges) in five randomly selected 1-m² quadrats along each transect (fig. 1). Cover and height of woody and herbaceous species and cover of rock were estimated with point-intercept sampling (points evenly spaced at 0.5-m intervals) along each transect. Woody plants were identified to species level, whereas herbaceous species were placed in one of three classes; forb, grass, or sedge. Woody density was estimated from species-specific counts in a 5-m belt transect (2.5 m on either side of each transect). Herbaceous biomass (identified as forb, grass, or sedge) was collected from three 100-cm² subplots on each transect. Data were collected from July through August in 2011 and 2012.

Analysis

The cover data were used to derive Hill's series of diversity numbers (Hill, 1973; Jost, 2006), as well as Simpson's index of evenness ($E_{1/d}$), for all herbaceous species and all herbaceous forage species. Hill's series of diversity numbers is based on an order of mathematically related diversity indices. As the order of the series increases, the indices are less influenced by rare species (or, conversely, have increasing sensitivity to the dominant species in an assemblage). One of the most appealing characteristics of the series is that the numbers are interpreted as the effective number of species—that is, the number of species that would be expected if all had equal abundances (Chao and others, 2012, 2014). We used three indices: N_0 (species richness), N_1 (e^H , where H =Shannon's diversity index), and N_2 ($1/d$, where d =Simpson's diversity index). Hill's series and $E_{1/d}$ allowed us to measure diversity in the four bighorn sheep/pack stock use classes and then evaluate the degree to which they differed in the total number of species (N_0), the effective number of more common species (N_1 and N_2), and relative abundance of the species ($E_{1/d}$).

Table 2. Number of meadows, number of plots, and area in four combinations of use by Sierra Nevada bighorn sheep and pack stock within Sequoia and Kings Canyon National Parks, California, 2011–2012.

Use class	Meadows	Plots	Area (hectares)
No bighorn sheep and no pack stock	10	29	37
Bighorn sheep and no pack stock	8	46	39
Pack stock and no bighorn sheep	3	13	37
Bighorn sheep and pack stock	4	12	40

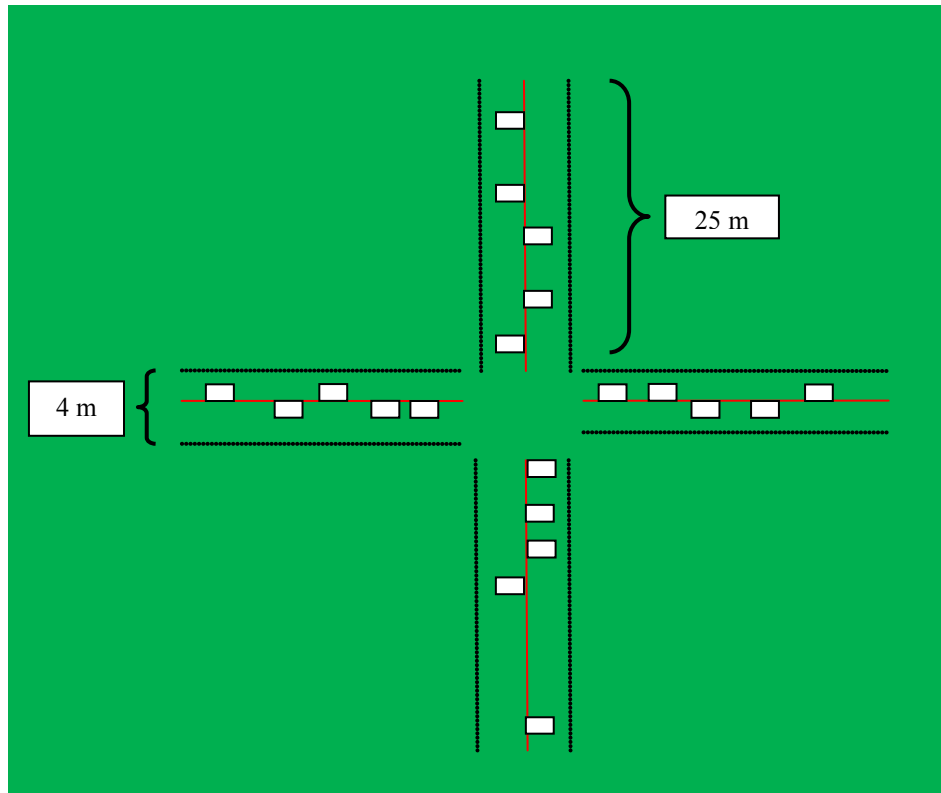


Figure 1. Layout of plots used to sample meadow vegetation in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by Sierra Nevada bighorn sheep or pack stock; (2) used by Sierra Nevada bighorn sheep but not pack stock; (3) used by pack stock but not Sierra Nevada bighorn sheep; and (4) used by Sierra Nevada bighorn sheep and pack stock. The four solid center lines were used for point-intercept sampling of woody species cover. Counts of woody species were done in four 100-square-meter belts (outer dashed lines). Rectangles represent 1-square-meter quadrats. See text (Subsection “Sampling” on page 6) for details on sampling protocols.

We used GLMMs to analyze differences in diversity among the meadow use classes, with meadow as a random effect. The analysis for N_0 had a Poisson error structure and log link, the analyses for N_1 and N_2 had a Gaussian error structure and identity link, and the analysis of $E_{1/d}$ had a binomial error structure and logit link. We used GLMMs with a binomial error structure and logit link to analyze differences in bare ground and total cover of forage species among the meadow use classes. Meadow was a random effect in the models. Forage species for SNBS on their summer range were based on Wehausen (1980).

We derived two models for each GLMM—a model with a term for meadow use classes and a model without the meadow use class term (null model). We used the bias-corrected Akaike Information Criterion (AIC_c) and AIC_c weights ($wAIC_c$) to compare the models and to evaluate the relative level of support for each model (Burnham and Anderson, 2002).

Principal Components Analysis (PCA) was used to derive gradients of vegetation structure from the total cover (summed across species) of forbs, grasses, sedges, bare ground, and litter. Analysis of variance (ANOVA) then was used to compare differences in vegetation structure (the PCA axes) among the meadow use classes. Meadow was coded as a block factor in the ANOVA.

We analyzed differences in species composition among the four meadow use classes with Distance-based Redundancy Analysis (DbRDA; Legendre and Anderson, 1999). DbRDA is a constrained version of PCA conducted on a distance matrix of dissimilarities. Continuous and categorical predictor variables can be included in the model, as can random effects. The importance of the predictor variables and ordination axes are evaluated from permutation tests, and the proportion of variance accounted for by the gradients can be calculated relative to the total variation in the model (“unconstrained variation”) or just the total variation accounted for by the predictor variables (“constrained variation”). We used a Hellinger transformation (Legendre and Gallagher, 2001) of the percent cover data to derive a Euclidean distance matrix among plots. We derived three models—the first model included eight environmental variables as well as the meadow use classes, the second model included only the eight environmental variables, and the third model included only the meadow use classes. In each model, we conditioned the permutation tests ($N=1,000$) on meadow (that is, meadow was a random factor). In combination, the three models allowed us to evaluate the proportion of variance in species composition that was explained by meadow use class relative to the environmental variables and the random effect of individual meadows. The environmental variables were divided into three classes—topography, vegetation, and climate (table 3). We started with 10 environmental variables, but highly correlated variables can lead to overestimates of the variation explained by DbRDA axes. Therefore we examined the pairwise correlations among the variables prior to running the analysis. We eliminated one of any pair with a correlation coefficient (r) >0.70 . This resulted in retaining eight of the variables in the models (table 3).

We analyzed differences in forage species composition among the four meadow use classes with pairwise similarity measures (Jost, 2007). The pairwise similarity analysis takes advantage of Hill’s numbers by calculating similarity indices based on N_0 (Sorenson’s index), N_1 (Horn’s index), and N_2 (Morisita-Horn index). This approach permits an evaluation of similarity along a gradient of the indices sensitivity to dominant species. Estimates of the indices and their standard errors were derived from 1,000 bootstrap samples. Differences in similarity among the four meadow use classes were evaluated by overlap in the error bars.

Table 3. Variables used in a Distance-based Redundancy Analysis (DbRDA) of species composition of meadow vegetation in Sequoia and Kings Canyon National Parks, California.

[Vegetation data were collected July–August in 2011 and 2012. **Model:** Yes means the variable was included in the DbRDA; No means the variable had a strong correlation with another variable ($r > 0.70$) and was not used in the DbRDA. **Class:** The general group into which variables were classified]

Variable	Abbreviation	Model	Class
Elevation	Elevation	No	Topography
Slope	Slope	No	Topography
Aspect (cosine transform)	Aspectcos	Yes	Topography
Topographic Roughness Index	TRI	Yes	Topography
Peak Normalized Difference Vegetation Index ¹	NDVIPeak	Yes	Vegetation
Photosynthetically Active Radiation	PRR	Yes	Vegetation
Hillshade Index	Hillshade	Yes	Vegetation
Annual Precipitation ²	Precip	Yes	Climate
July Maximum Temperature ³	Tmax07	Yes	Climate
January Minimum Temperature ³	Tmin01	Yes	Climate
Meadow use class	Occurcode	Yes	Pack stock

¹ Mean peak NDVI from June through September 1990 through 2010.

² Mean total annual precipitation from 1950 through 2000.

³ Climate layer source: Alvarez and others (2013).

Results

Association Analyses

A total of 5,892 meadows have been mapped within the borders of SEKI. Of those, 2,780 (47.2 percent) are open to pack stock grazing. However, only 621 meadows (10.5 percent of all meadows, 22.3 percent of grazed meadows) occur in the five occupied bighorn sheep herd unit polygons that are within the boundaries of the parks (table 1). Moreover, the Bubbs Creek and Mount Williamson herds do not have any meadows open to grazing. Thus, meadows (N=57) in these herd units were not included in any of the analyses.

The five herd units within the boundaries of the parks comprise 58,378 ha, and the herd unit polygons comprised 40,415 ha. The total area of the 621 meadows within the herd units was 660 ha (1.1 percent of the herd unit area and 1.6 percent of the herd unit polygon area). Thus, even before further filtering for distance from escape terrain, this was a strong indication that there is very little overlap at the landscape scale between bighorn sheep and pack stock.

There was a strong negative relationship between the number of bighorn sheep locations and distance of the meadow from escape terrain (fig. 2a). The 50-m distance from escape terrain class represented the 76th percentile of predicted locations, whereas the 100-m and 250-m distance classes represented the 89th and 97th percentiles, respectively. The number of bighorn sheep locations was highest for meadows ranging in area from 7 to 17 ha (fig. 2b).

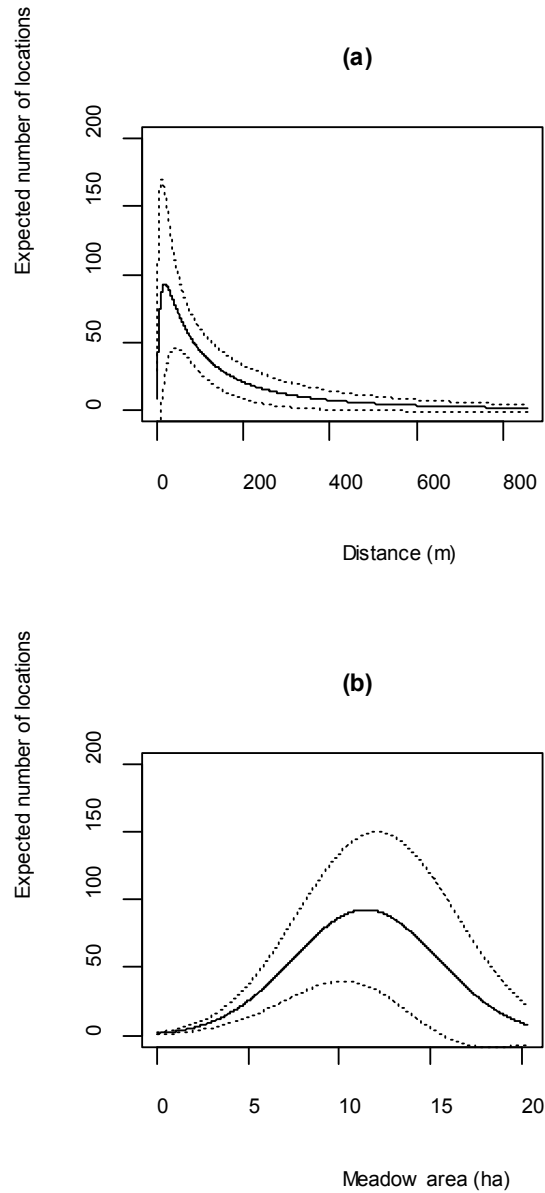


Figure 2. Relationship between the estimated number of Sierra Nevada bighorn sheep locations and distance from escape terrain (a) and size of meadows (b) in Sequoia and Kings Canyon National Parks, California, 2011–2012. Dashed lines are 95-percent confidence intervals. Locations are from Global Positioning System and radio telemetry fixes collected between 2005 and 2012 (N=25,510).

A total of 407 meadows in the Mount Langley, Mount Baxter, and Sawmill Creek herd units were not open to pack stock (referred to hereon as “ungrazed”; table 4). A total of 157 meadows within these herd units were open to pack stock (referred to hereon as “grazed”; table 4). Most grazed meadows generally were nearly 400 m from escape terrain, whereas ungrazed meadows were within 225 m from escape terrain (fig. 3). There were few grazed meadows in the 50 and 100-m distance classes (N=1 and 4, respectively), whereas 42 grazed meadows were in the 250-m distance class and potentially were used by SNBS (table 4). In contrast, 24 and 61 ungrazed meadows were in the 50 and 100-m distance classes, whereas 265 ungrazed meadows were in the 250-m distance class.

The analysis of use-availability based on meadow area indicated that grazed meadows available to SNBS occurred in proportion to their area on the landscape regardless of their distance from escape terrain (fig. 4). Proportional availability and potential use by SNBS was lowest for this use class on the landscape. Ungrazed meadows not available to SNBS comprised the greatest area of the landscape for the 50-m and 100-m distance classes; the number of meadows was proportional to meadow area in these distance classes (fig. 4). In contrast, ungrazed meadows not available to SNBS comprised less landscape area in the 250-m distance class, and the number of meadows in this class was significantly less than expected relative to their area (fig. 4). This was because there was a greater number and area of ungrazed meadows available to SNBS in the 250-m distance class (fig. 4); the number of meadows was significantly higher than expected in this class relative to their area. In the 50-m and 100-m distance classes, however, the proportion of ungrazed meadows available to SNBS sheep was less than 0.1 of the total landscape area and the number of meadows was proportional to their area on the landscape (fig. 4). Regardless of the distance class, the number of grazed meadows not available to SNBS was disproportionately lower than the area they comprised on the landscape (fig. 4).

Table 4. Number of meadows in two classes of use by pack stock and four classes of distance from Sierra Nevada bighorn sheep escape terrain in Sequoia and Kings Canyon National Parks, California, 2011–2012.

Use class	Distance class			
	50- meters	100- meters	250- meters	>250- meters
Closed to pack stock (ungrazed)	24	61	265	57
Open to pack stock (grazed)	1	4	42	110

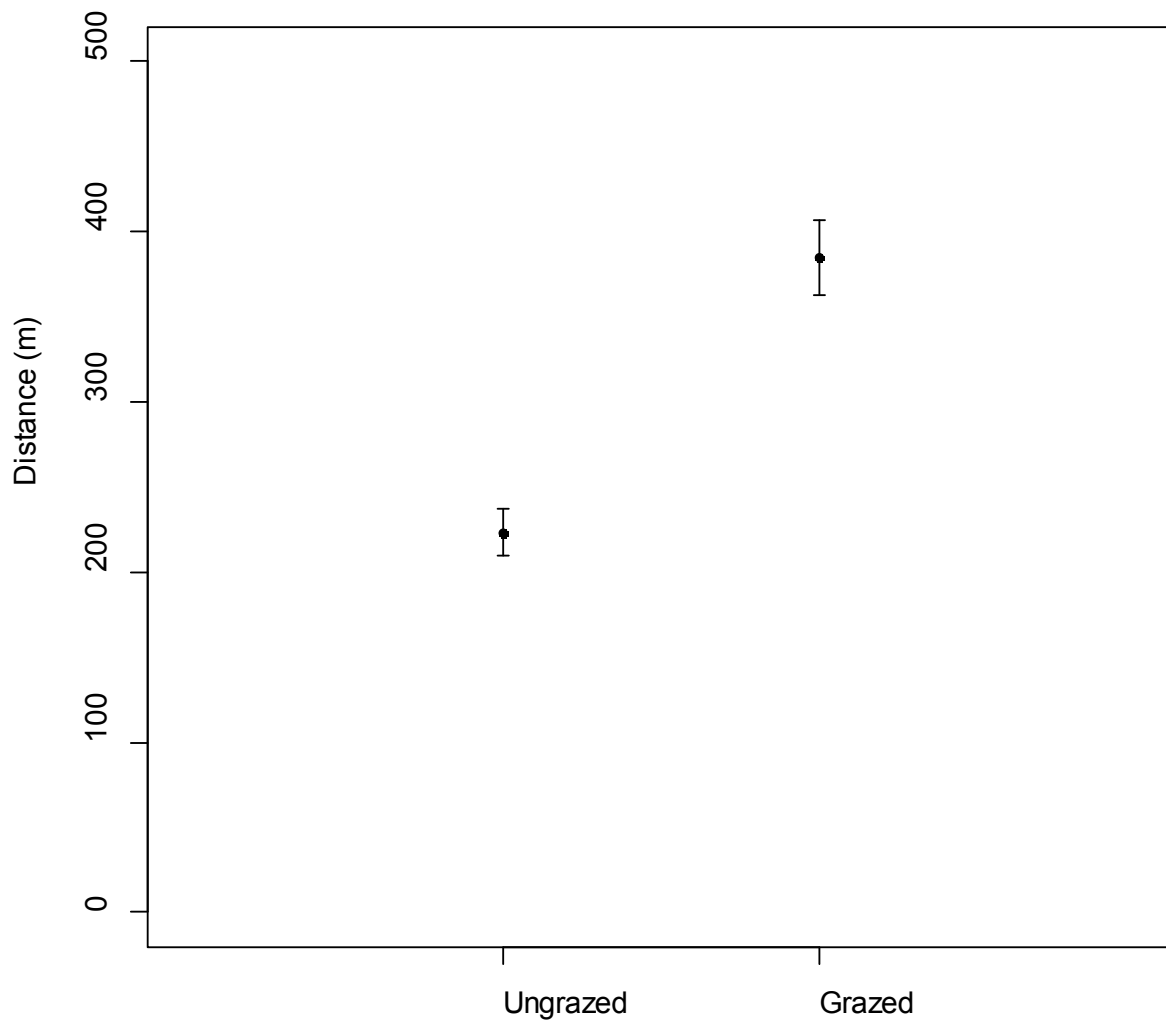


Figure 3. Relationship of the distance a meadow was from Sierra Nevada bighorn sheep escape terrain and whether a meadow was ungrazed or grazed closed or open to pack stock grazing, respectively in Sequoia and Kings Canyon National Parks, California, 2011–2012. Error bars are 95-percent confidence intervals.

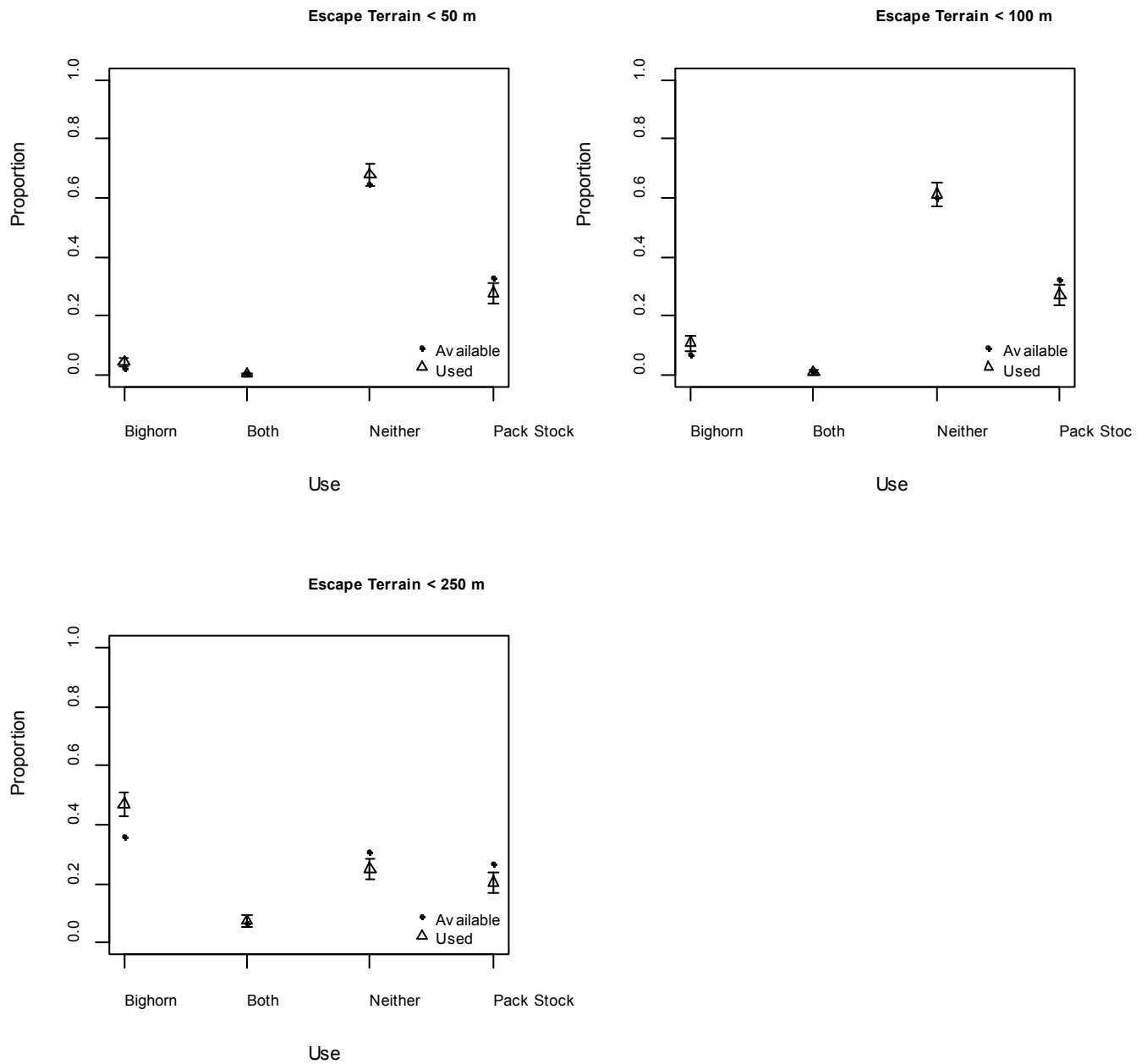
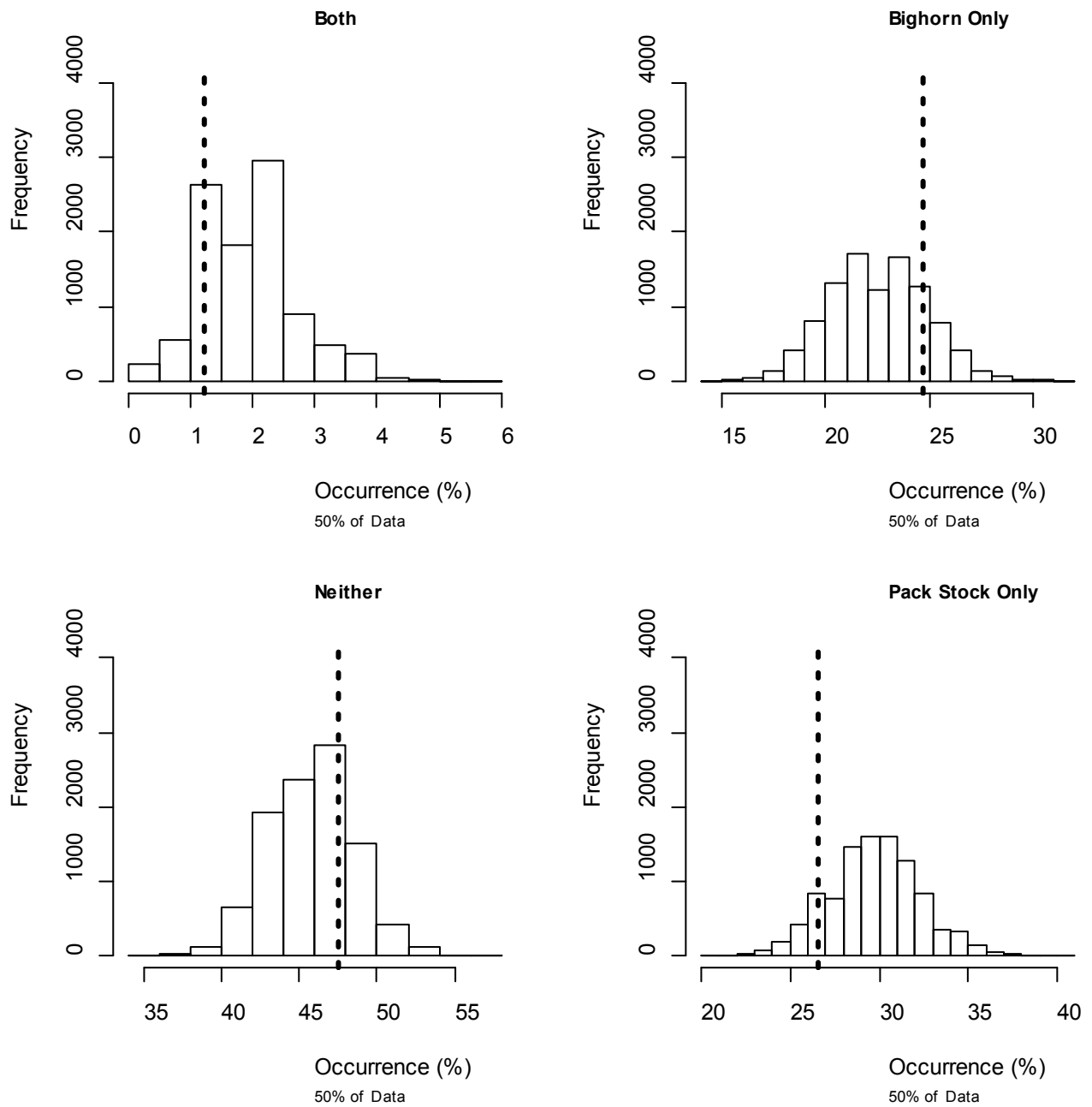


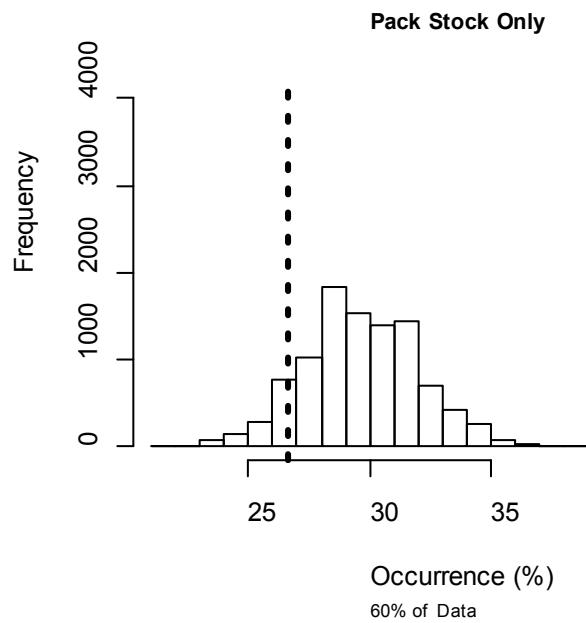
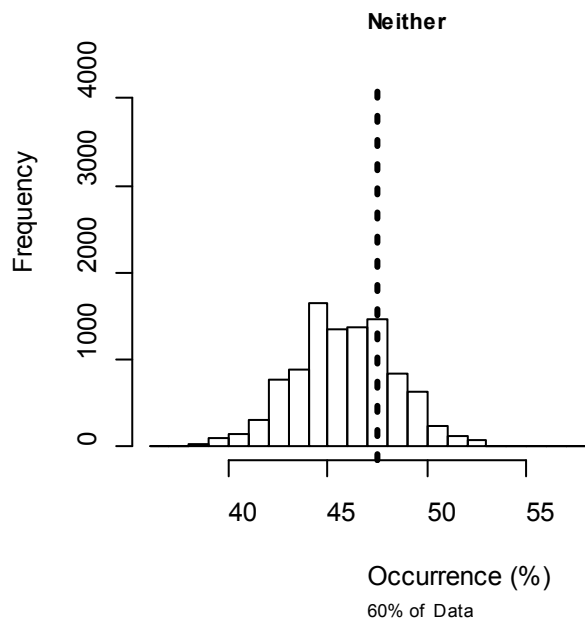
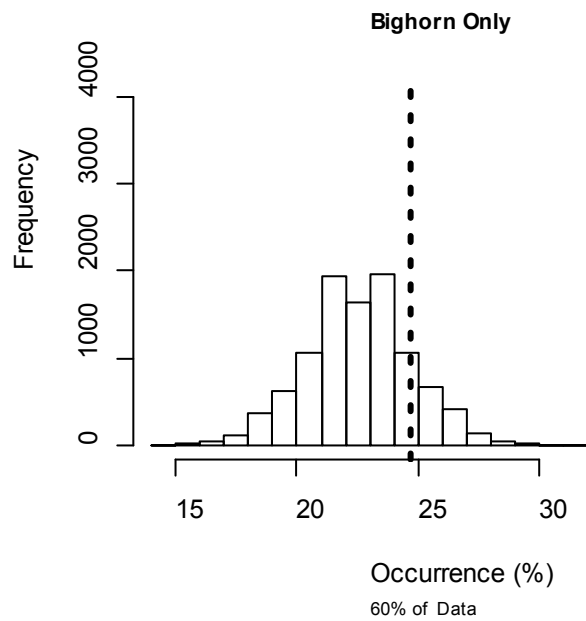
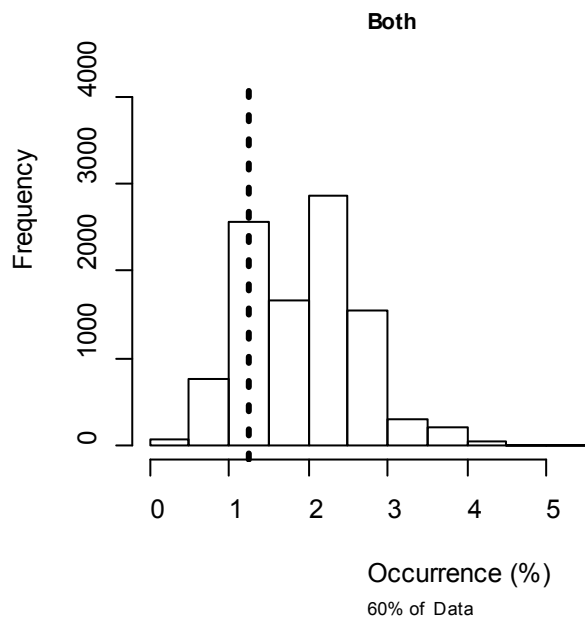
Figure 4. Analysis of potential use-availability of meadows in four Sierra Nevada bighorn sheep and pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. Use and availability were defined as meadows within 50, 100, and 250 m of bighorn sheep escape terrain. Error bars are 95-percent confidence intervals.

Results from the Monte Carlo simulations were similar to those of the analyses of potential use and availability based on area of the meadows (figs. 5–7). When a conservative estimate of availability was used (50 m), the estimate of availability was well within the 2.5 and 97.5 percentiles regardless of how large of a sample (that is, 50, 60, 70, and 80 percent) of the meadows was used in the simulations (fig. 5). When a moderate estimate of availability was used (100 m), the estimate of availability was well within the 2.5 and 97.5 percentiles for all classes except ungrazed meadows available to SNBS; more meadows occurred in that class than expected based on the random samples of their distribution on the landscape (fig. 6). When a liberal estimate of availability was used (250 m), the estimate of availability was well outside the 2.5 and 97.5 percentiles for all use classes (fig. 7). A greater proportion of grazed meadows was available to SNBS than expected based on random samples of their distribution on the landscape; however, this use class comprised less than 4 percent of the meadows on the landscape. A much greater proportion of ungrazed meadows available to SNBS occurred on the landscape than expected based on random samples of their distribution. This use class comprised more than 30 percent of the meadows on the landscape (fig. 7). Ungrazed meadows not available to SNBS as well as grazed meadows not available to SNBS occurred less than expected on the landscape (fig. 7). These two classes comprised 31–35 percent and 23–24 percent of the landscape area, respectively.



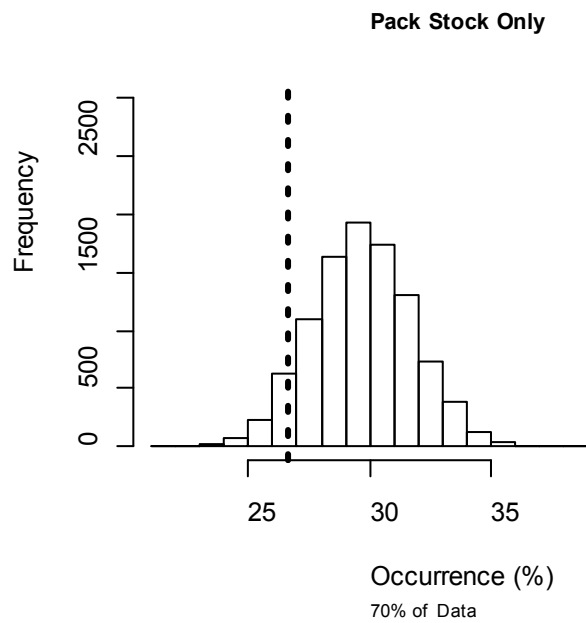
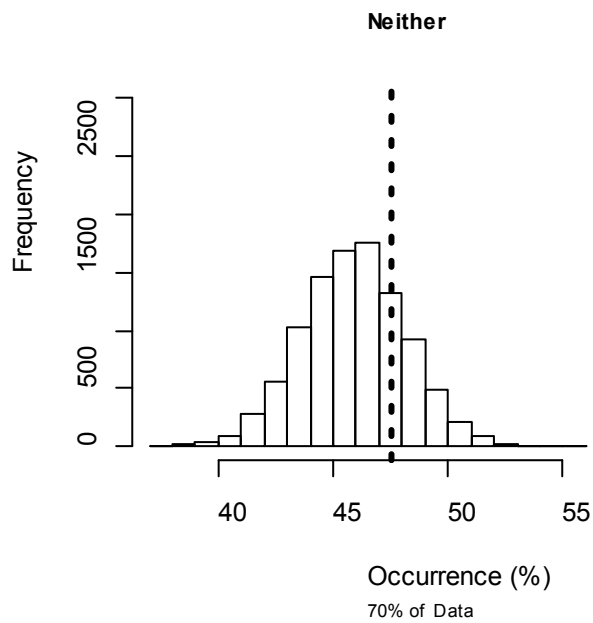
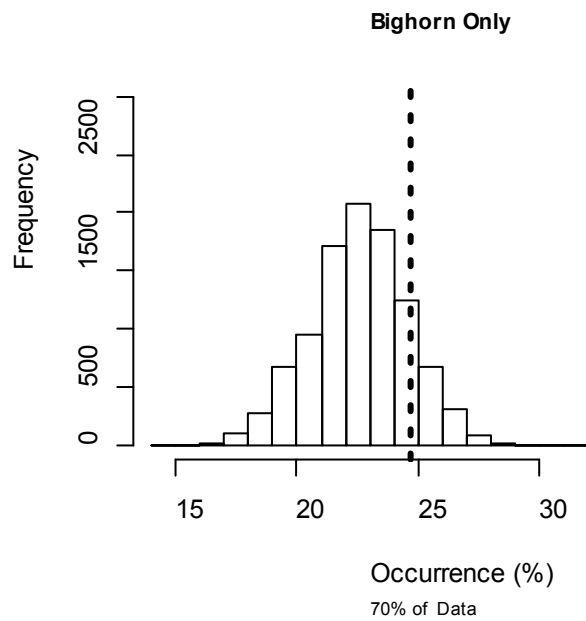
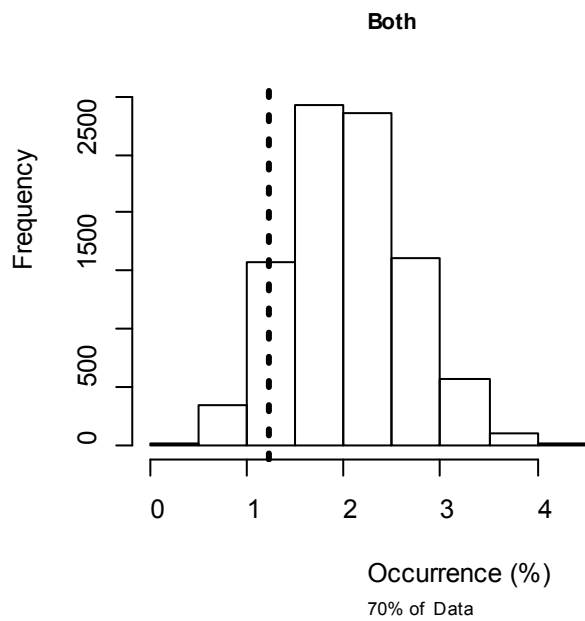
A. 50 percent of the meadows within 50 meters of bighorn sheep escape terrain.

Figure 5. Results of Monte Carlo simulations of potential use-availability of meadows in four Sierra Nevada bighorn sheep and pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. Randomizations were conducted for 50, 60, 70, and 80 percent (%) of the meadows within 50 meters of bighorn sheep escape terrain. Vertical dashed lines are the actual proportion in each use class.



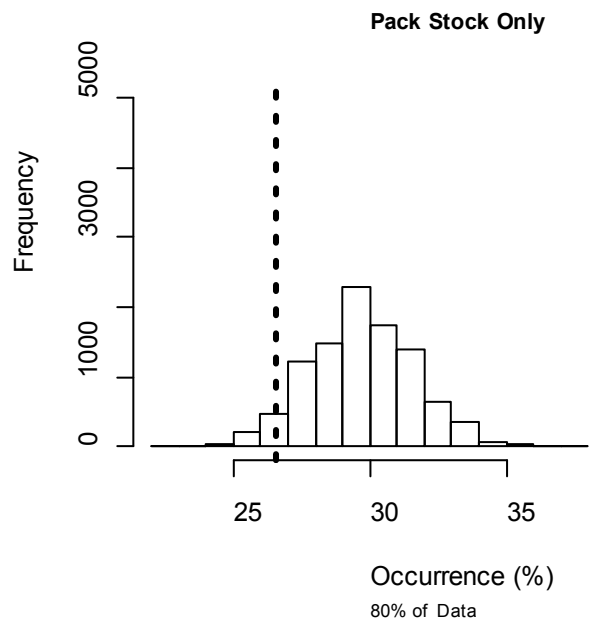
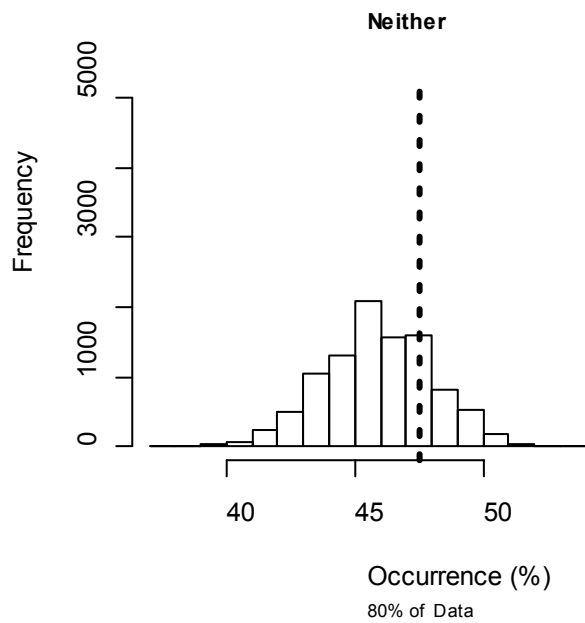
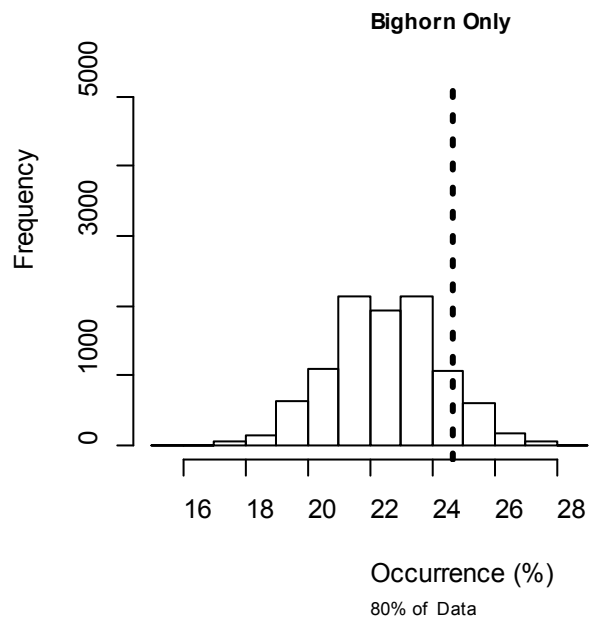
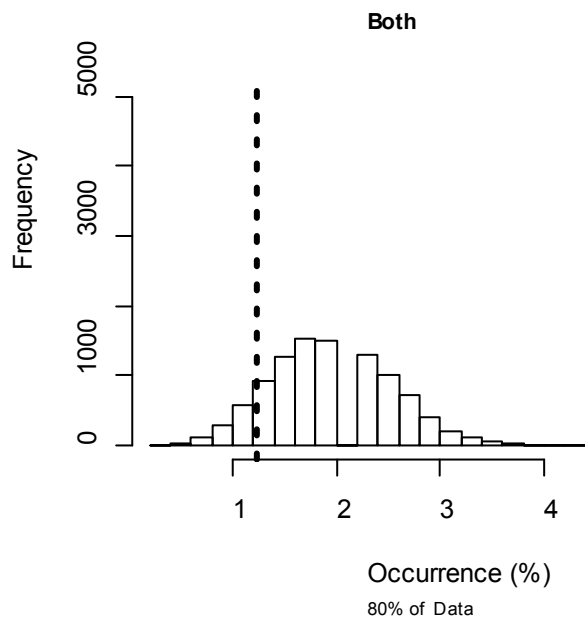
B. 60 percent of the meadows within 50 meters of bighorn sheep escape terrain.

Figure 5.—Continued.



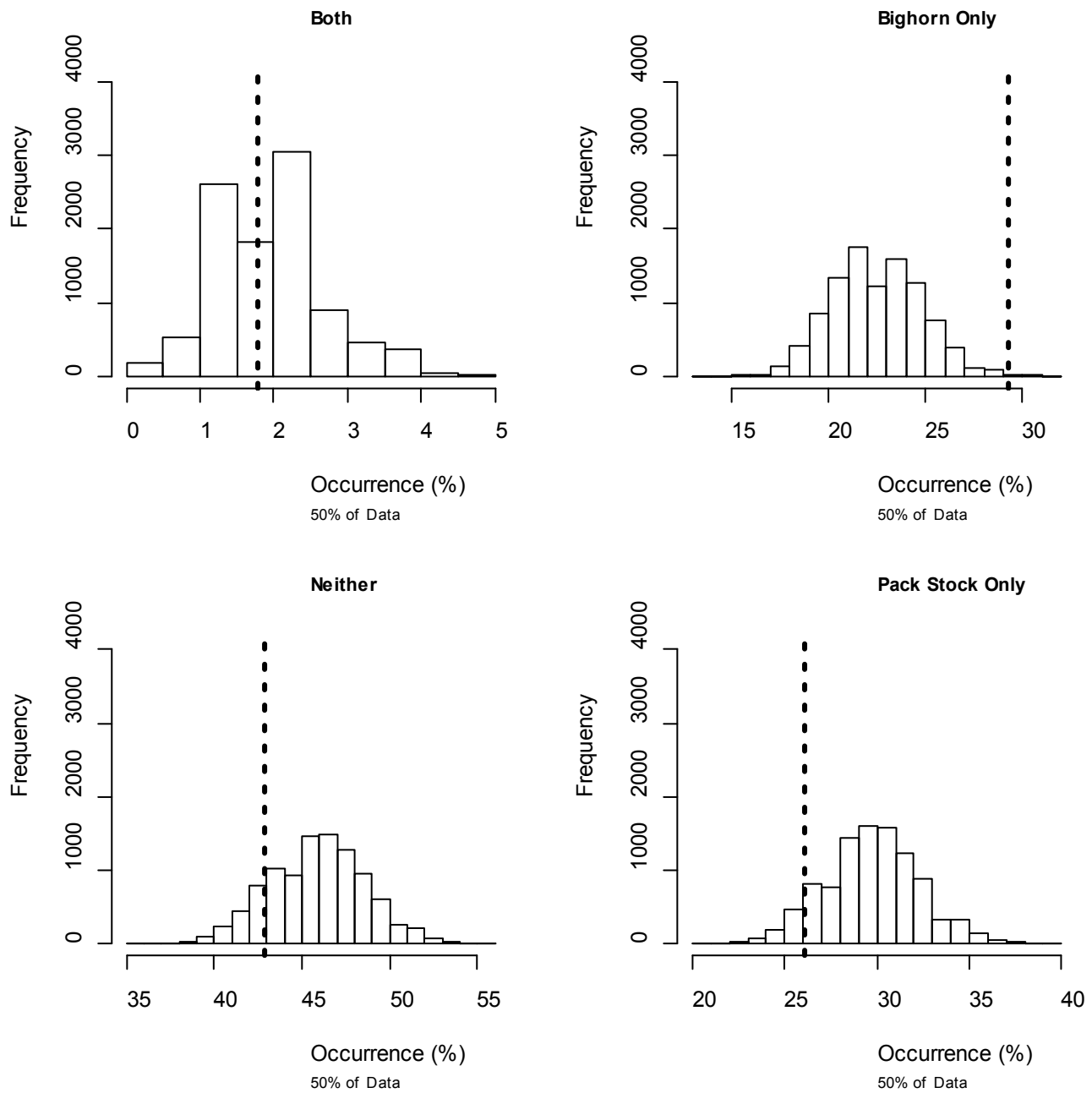
C. 70 percent of the meadows within 50 meters of bighorn sheep escape terrain.

Figure 5.—Continued.



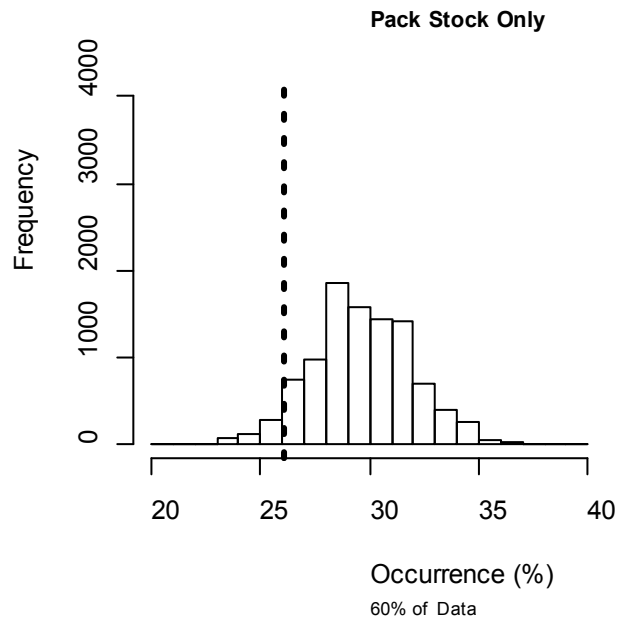
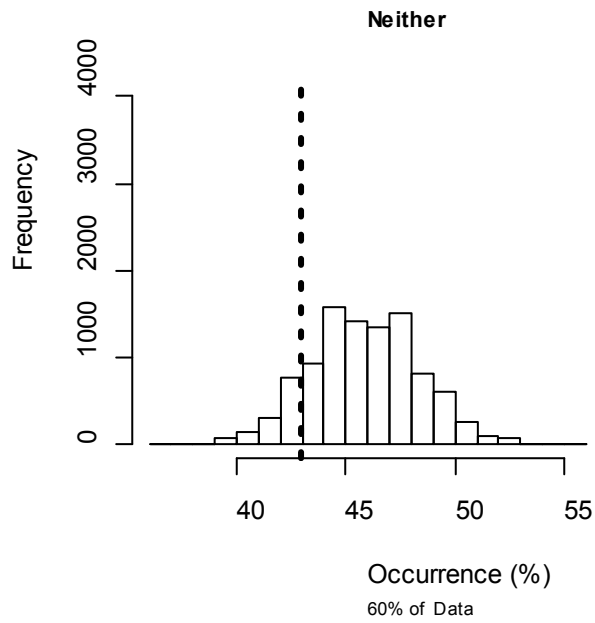
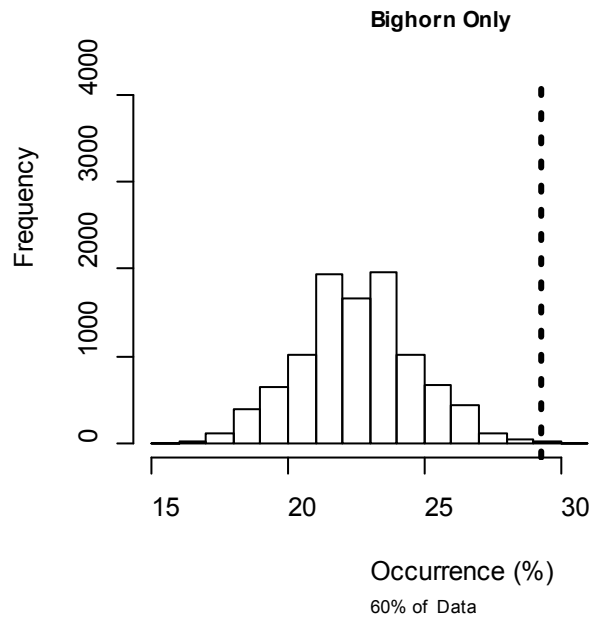
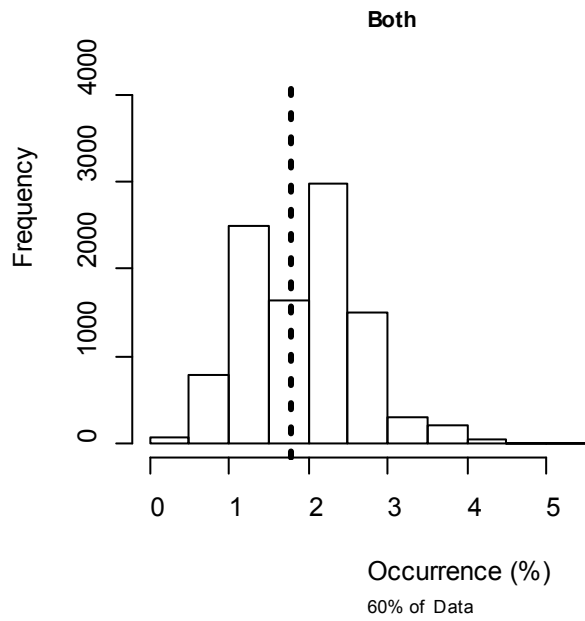
D. 80 percent of the meadows within 50 meters of bighorn sheep escape terrain.

Figure 5.—Continued.



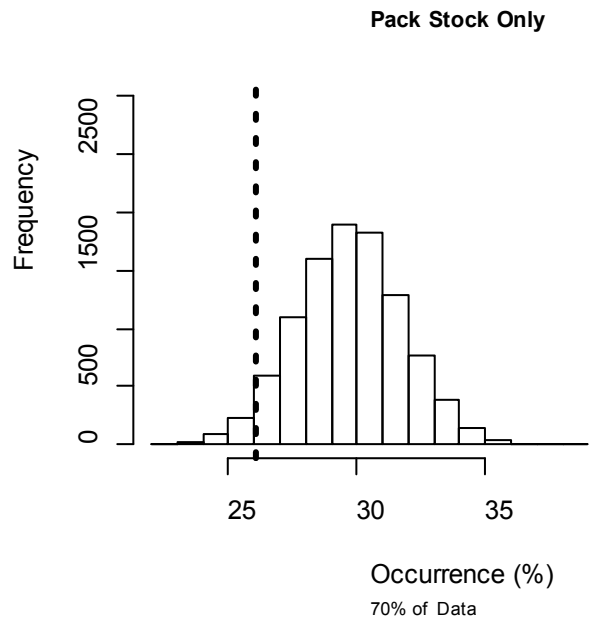
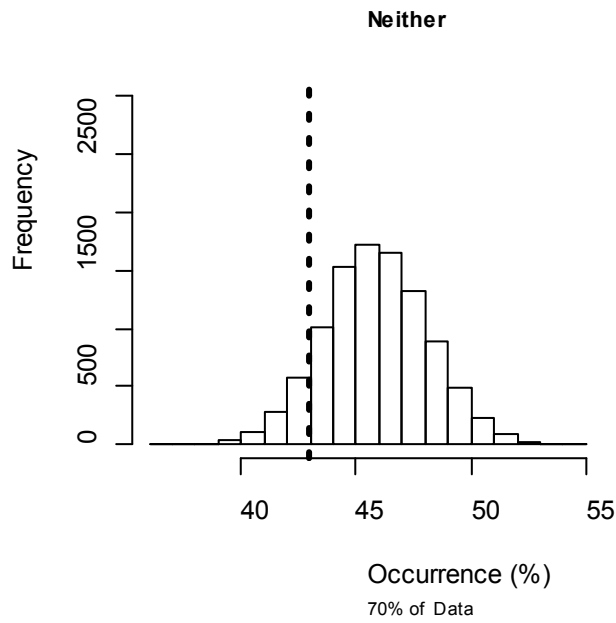
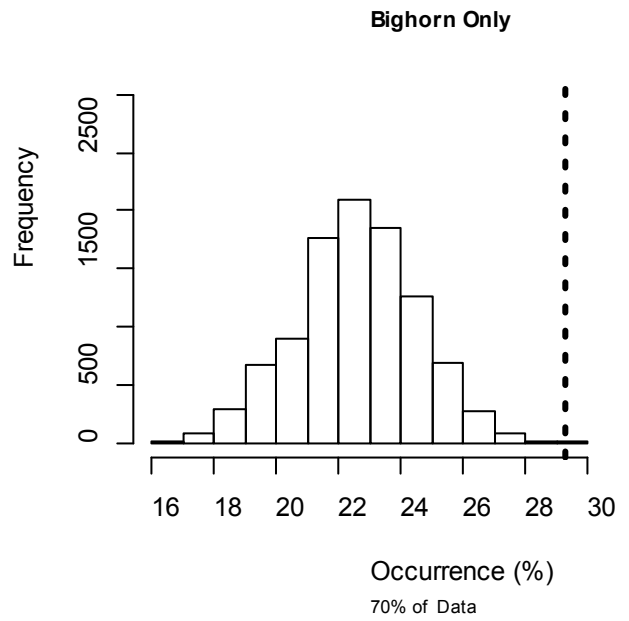
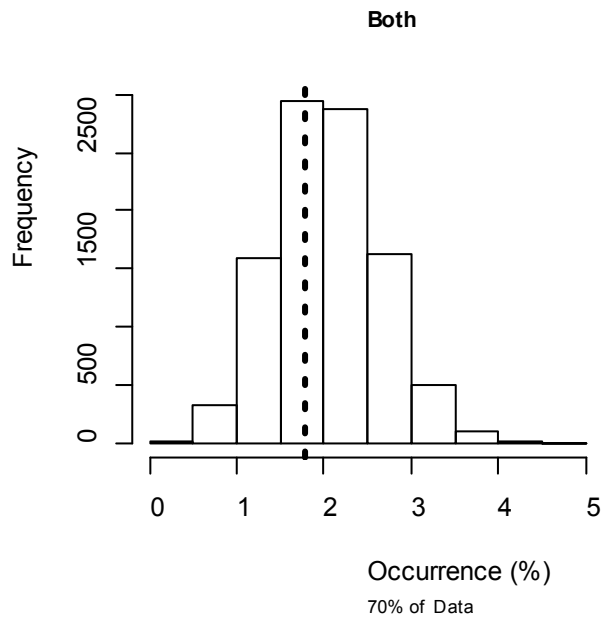
A. 50 percent of the meadows within 100 meters of bighorn sheep escape terrain.

Figure 6. Results of Monte Carlo simulations of potential use-availability of meadows in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. Randomizations were conducted for 50, 60, 70, and 80 percent (%) of the meadows within 100 meters of bighorn sheep escape terrain. Vertical dashed lines are the actual proportion in each use class..



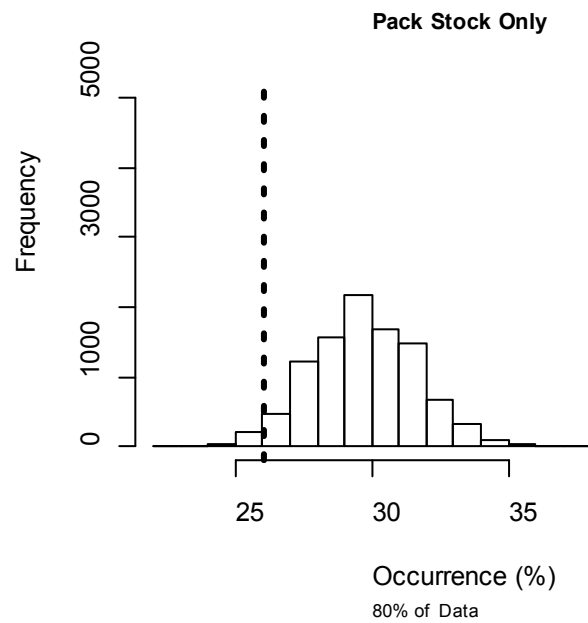
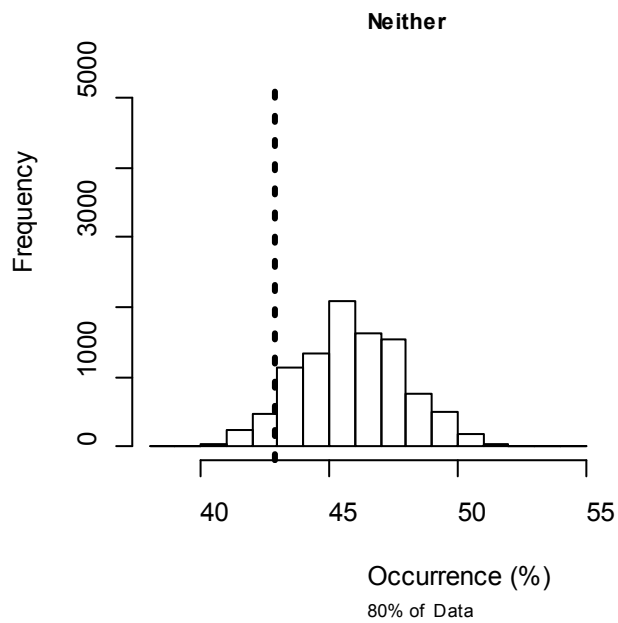
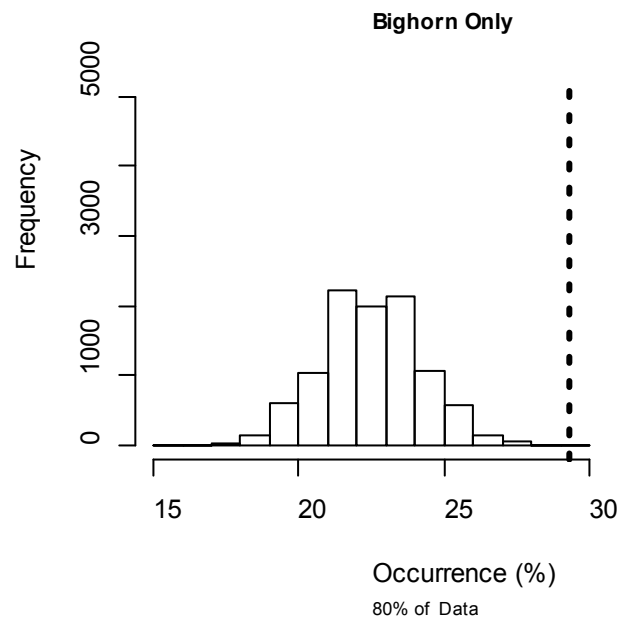
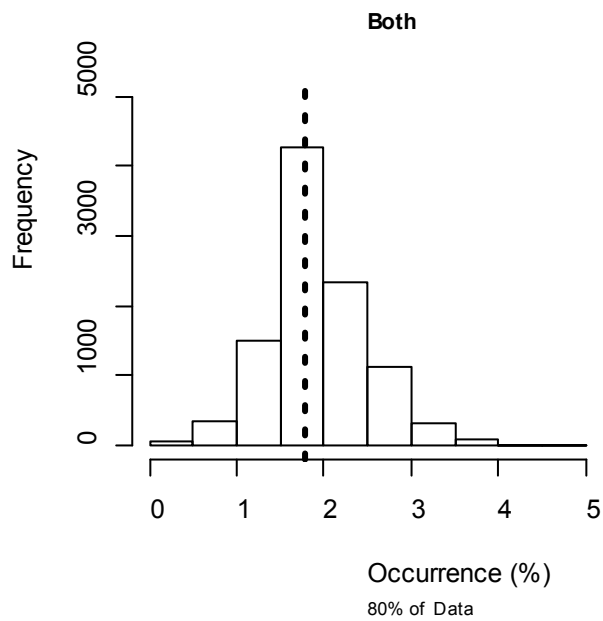
B. 60 percent of the meadows within 100 meters of bighorn sheep escape terrain.

Figure 6.—Continued.



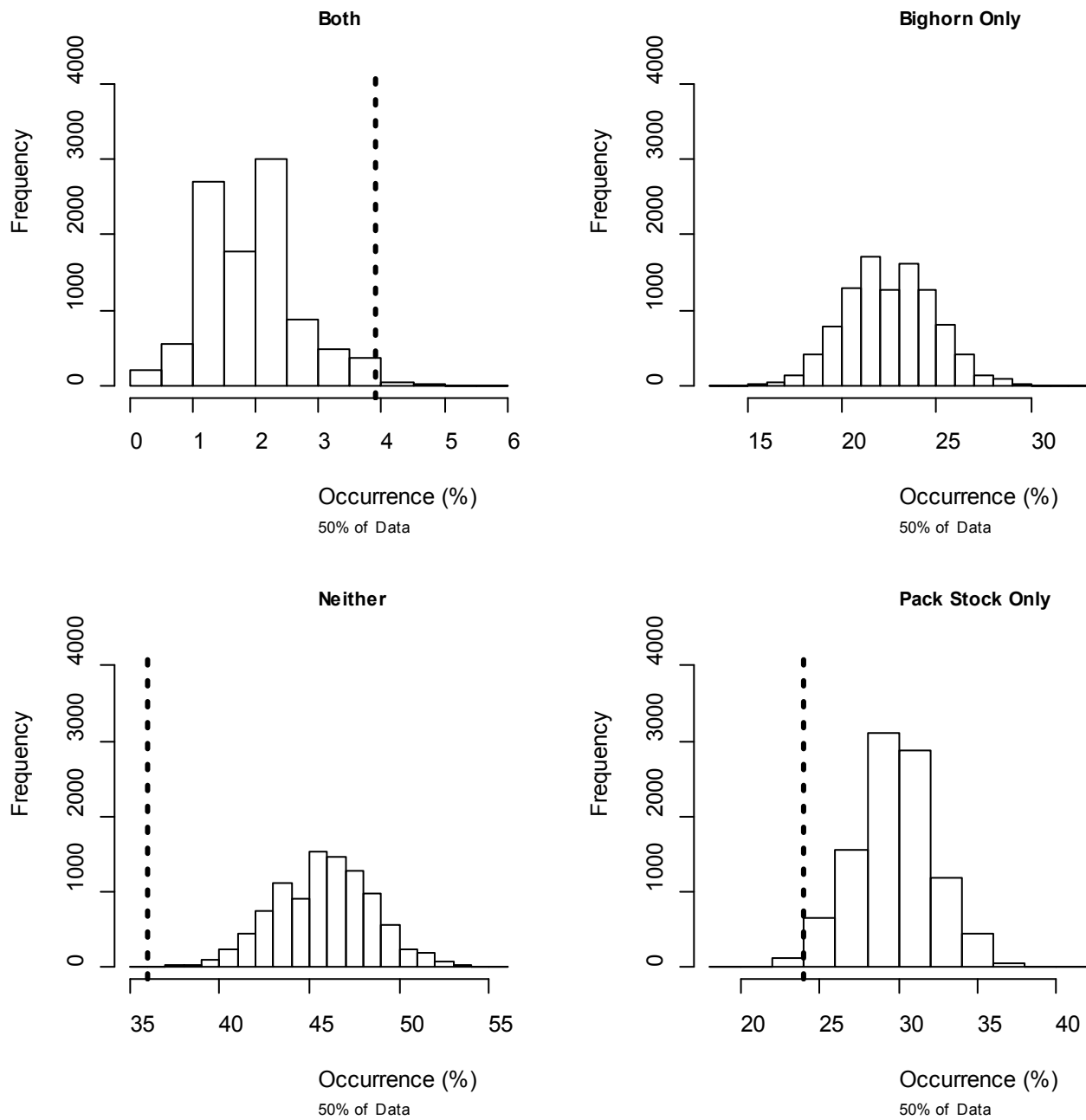
C. 70 percent of the meadows within 100 meters of bighorn sheep escape terrain.

Figure 6.—Continued.



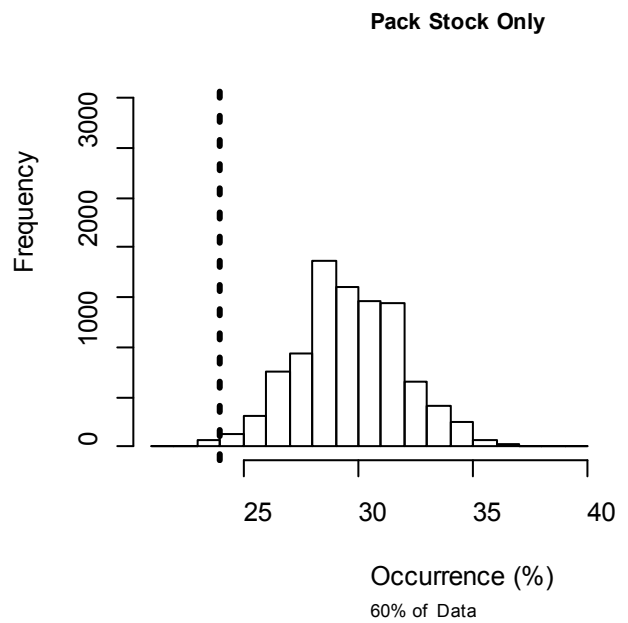
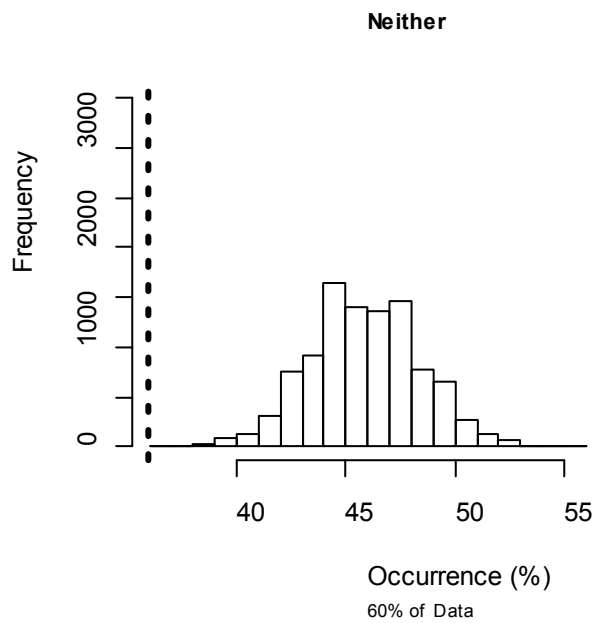
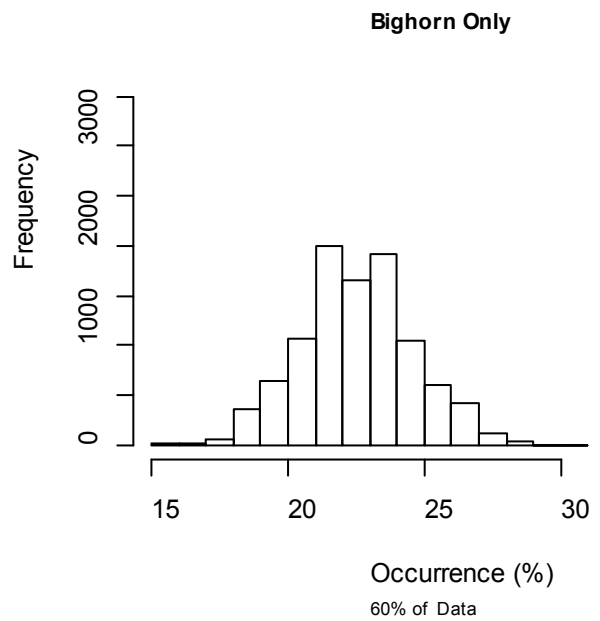
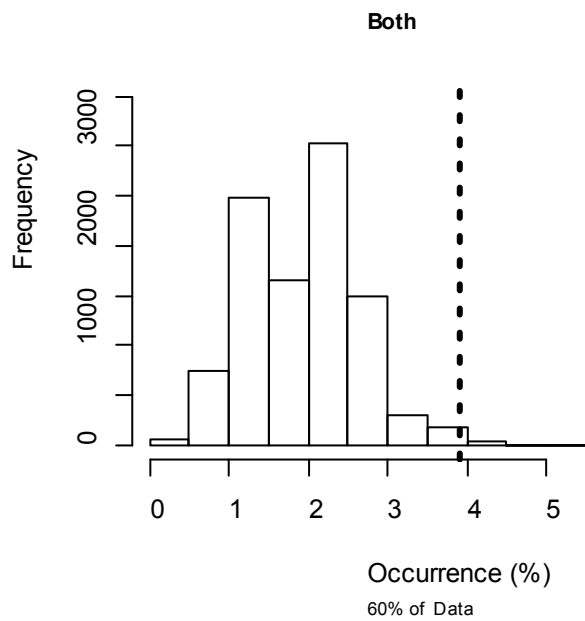
D. 80 percent of the meadows within 100 meters of bighorn sheep escape terrain.

Figure 6.—Continued.



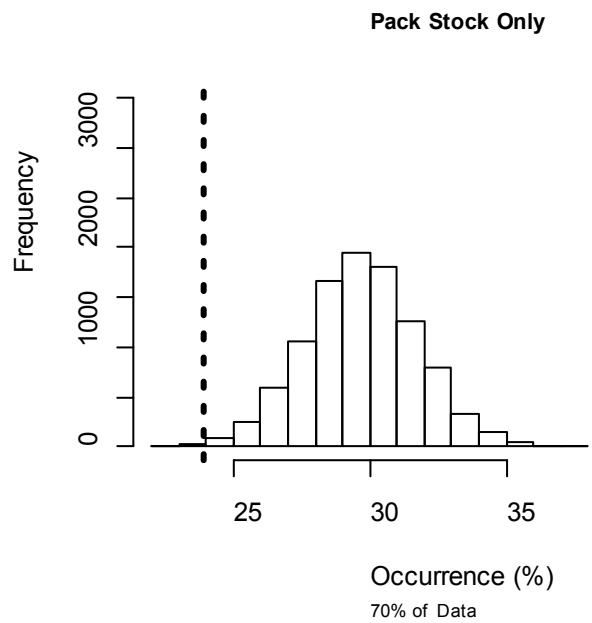
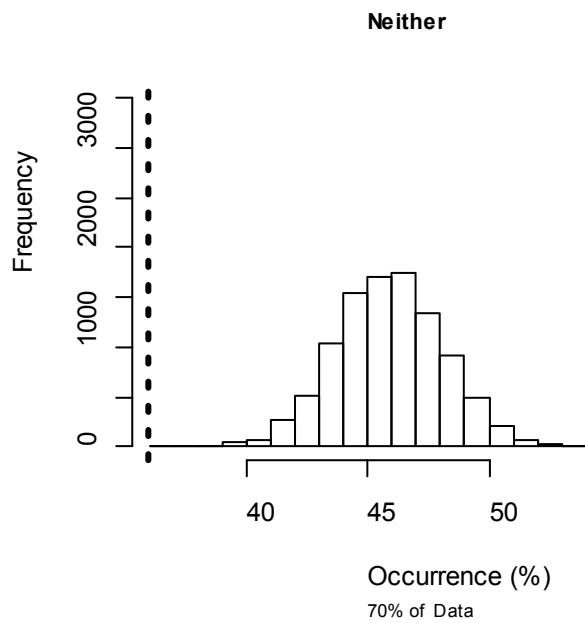
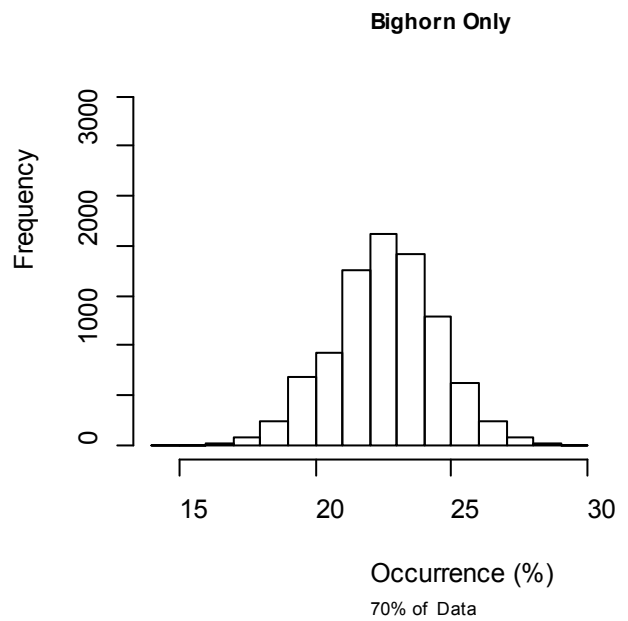
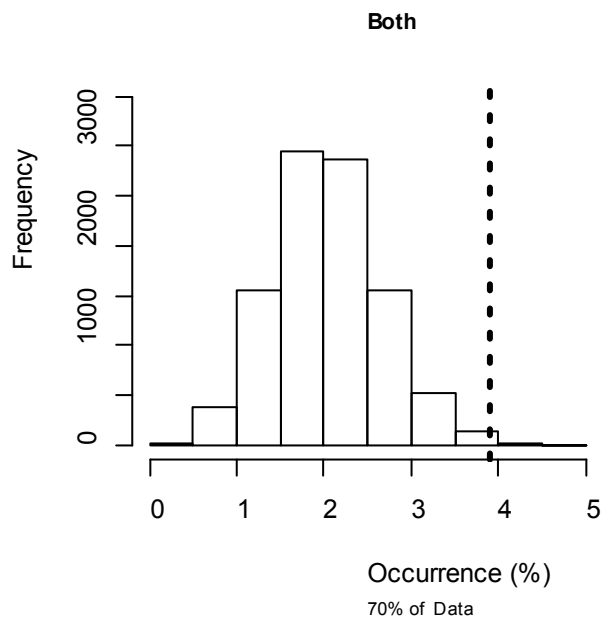
A. 50 percent of the meadows within 250 meters of bighorn sheep escape terrain.

Figure 7. Results of Monte Carlo simulations of potential use-availability of meadows in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. Randomizations were conducted for 50, 60, 70, and 80 percent (%) of the meadows within 250 meters of bighorn sheep escape terrain. Vertical dashed lines are the actual proportion in each use class.



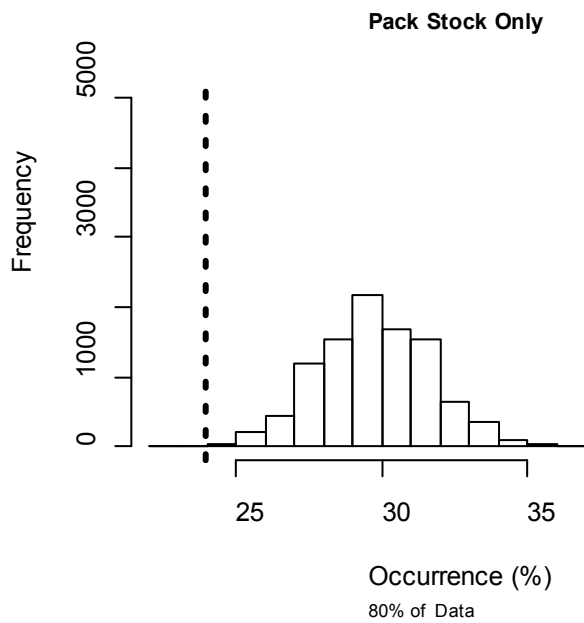
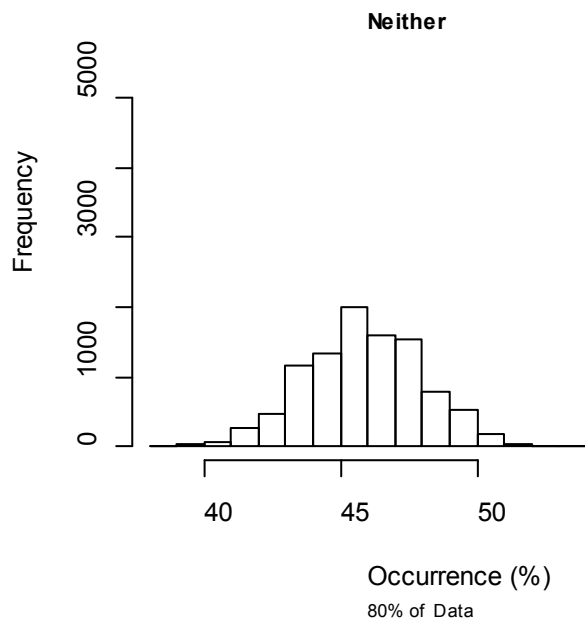
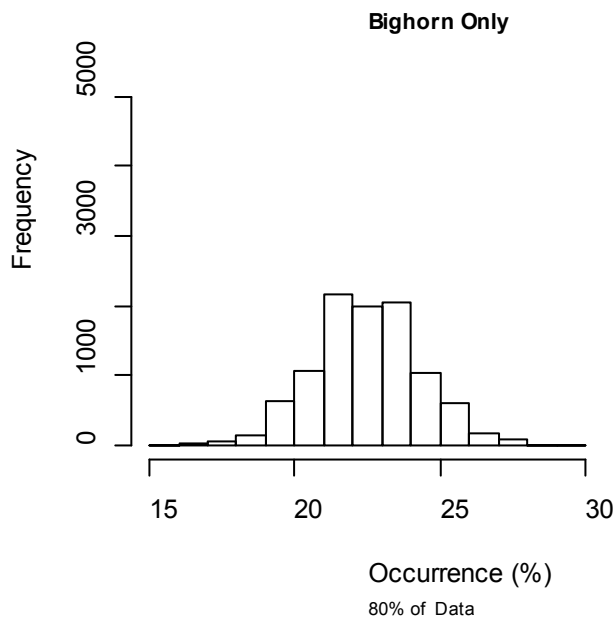
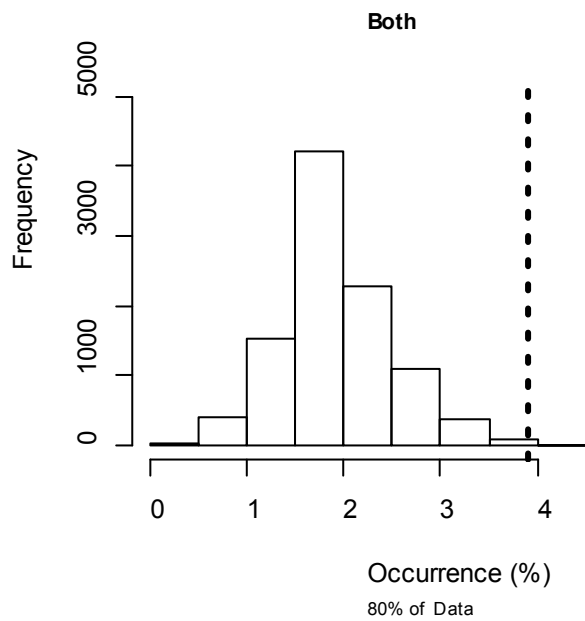
B. 60 percent of the meadows within 250 meters of bighorn sheep escape terrain.

Figure 7.—Continued.



C. 70 percent of the meadows within 250 meters of bighorn sheep escape terrain.

Figure 7.—Continued.



D. 80 percent of the meadows within 250 meters of bighorn sheep escape terrain.

Figure 7.—Continued.

Meadow Community and Forage Analysis

The DbRDA indicated that differences in species composition in the plots were primarily due to random effects within the meadows and environmental gradients (fig. 8). Relative to the amount of unconstrained variation, the predictor variables in the model that included the eight environmental variables and the meadow use classes accounted for 17.5 percent of the variation in species composition (table 5), whereas the variation in the models with just the eight environmental variables and just the meadow use classes was 15.0 and 3.9 percent, respectively. The variation explained by random effects within meadows was 22.1 percent. The first three constrained axes in the model with the eight environmental variables and the meadow use classes had meaningful contributions to variation in species composition ($P < 0.01$). The first axis primarily was a topographic roughness and photosynthetically active radiation gradient (38.0 percent variation explained). The second axis was a gradient characterized by peak NDVI and the amount of shading in a plot (27.7 explained), and the third axis was a gradient of peak NDVI and meadow use class (10.9 percent explained). Compared to the environmental gradients, however, there was very little turnover in species composition among the meadow use classes, with the centroids of the four classes all clustered near the origin of the ordination space (fig. 8). Moreover, the permutation tests indicated only marginal support for meaningful levels of variation in species composition among the meadow use classes ($P = 0.071$; table 6). Finally, plots in ungrazed and grazed meadows not used by SNBS were very similar in species composition (fig. 8).

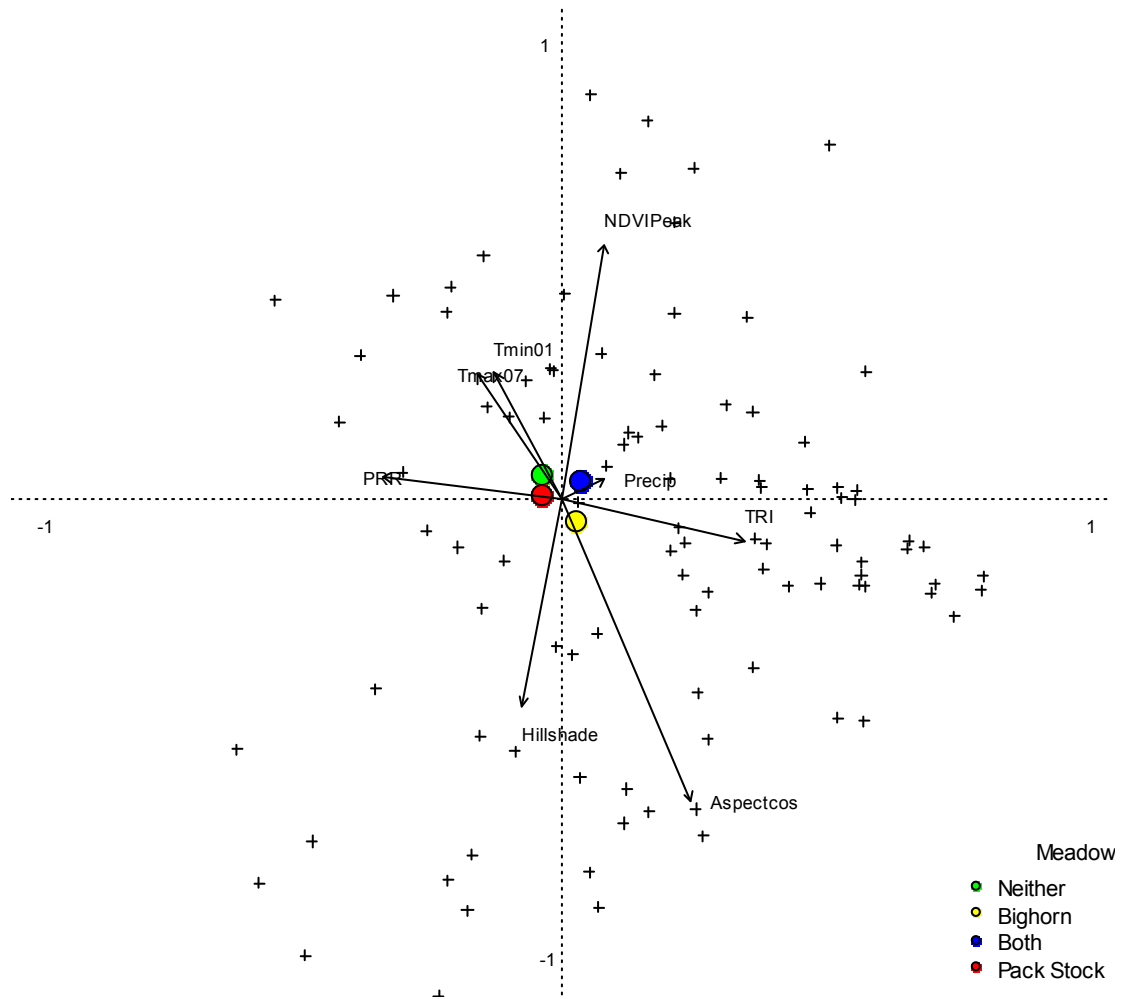


Figure 8. Biplot of the results from a Distance-based Redundancy Analysis of species composition in meadows in four Sierra Nevada bighorn sheep and pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by bighorn sheep and pack stock (Both), and (4) used by pack stock but not bighorn sheep (Packstock). Circles represent the centroids of the use classes, and crosses represent position of the species in ordination space.

Table 5. Statistics from a Distance-based Redundancy Analysis (DbRDA) of meadow vegetation species composition in Sequoia and Kings Canyon National Parks, California.

[Vegetation data were collected July–August in 2011 and 2012. λ = Variation. See table 3 for definitions of variables]

Source of variation	λ	Percent	
Environmental	0.6250	17.5	
Meadow (random)	0.7903	22.1	
Unexplained	2.1600	60.4	
Total	3.5753	100.0	
Variable	Axis 1	Axis 2	Axis 3
Bighorn only ¹	0.2567	-0.4620	-0.0266
Pack stock only ¹	-0.1558	0.0430	0.0376
Bighorn and pack stock ¹	0.1253	0.1579	-0.6084
Aspectcos	0.2830	-0.6581	-0.1332
PRR	-0.3943	0.0490	-0.0229
Hillshade	-0.0886	-0.4499	-0.2718
TRI	0.3991	-0.0896	0.1378
NDVIPeak	0.0924	0.5579	-0.6325
Precip	0.0934	0.0449	-0.0053
Tmax07	-0.1873	0.2736	0.0324
Tmin01	-0.1485	0.2786	0.0312
Variation explained			
Unconstrained (percent)	8.5	6.2	2.4
Constrained (percent)	38.0	27.7	10.9
<i>Meadow Use Centroids</i>			
Class	Axis 1	Axis 2	Axis 3
No use by bighorn sheep or pack stock	-0.1739	0.2460	0.2966
Bighorn sheep only	0.1206	-0.2171	-0.0125
Pack stock only	-0.1748	0.0482	0.0422
Bighorn sheep and pack stock	0.1472	0.1855	-0.7146

¹Meadow use class.

Table 6. Tests of the importance of eight environmental variables in a Distance-based Redundancy Analysis (DbRDA) of turnover in meadow plant species composition in Sequoia and Kings Canyon National Parks, California.

[Vegetation data were collected July–August in 2011 and 2012. See table 3 for definitions of variables. DF = degrees of freedom, *F* = F-ratio, *p* = probability based on 1000 Monte Carlo simulations]

Variable	DF	Variance	<i>F</i>	<i>P</i>
Meadow Use Class ¹	3	0.1414	1.877	0.071
Aspectcos	1	0.0925	3.681	0.011
PRR	1	0.0664	2.645	0.022
Hillshade	1	0.0973	3.873	0.010
TRI	1	0.0503	2.003	0.029
NDVIPeak	1	0.0630	2.509	0.031
Precip	1	0.0501	1.997	0.113
Tmax07	1	0.0224	0.890	0.415
Tmin01	1	0.0417	1.659	0.109

¹Meadow use classes: not used by pack stock or Sierra Nevada bighorn sheep, used by bighorn sheep but not pack stock, used by pack stock but not bighorn sheep, and used by both

The PCA indicated a high degree of overlap in vegetation structure among the four use classes (fig. 9). Meadows open to grazing by pack stock and meadows open to grazing by pack stock and available to SNBS had greater cover of grasses and sedges than the other two use classes. The ANOVA of the PCA scores indicated that the only significant difference in structure was between grazed meadows available to SNBS and ungrazed meadows available to SNBS ($P=0.029$), primarily because of greater sedge cover in grazed meadows and available to SNBS (fig. 9).

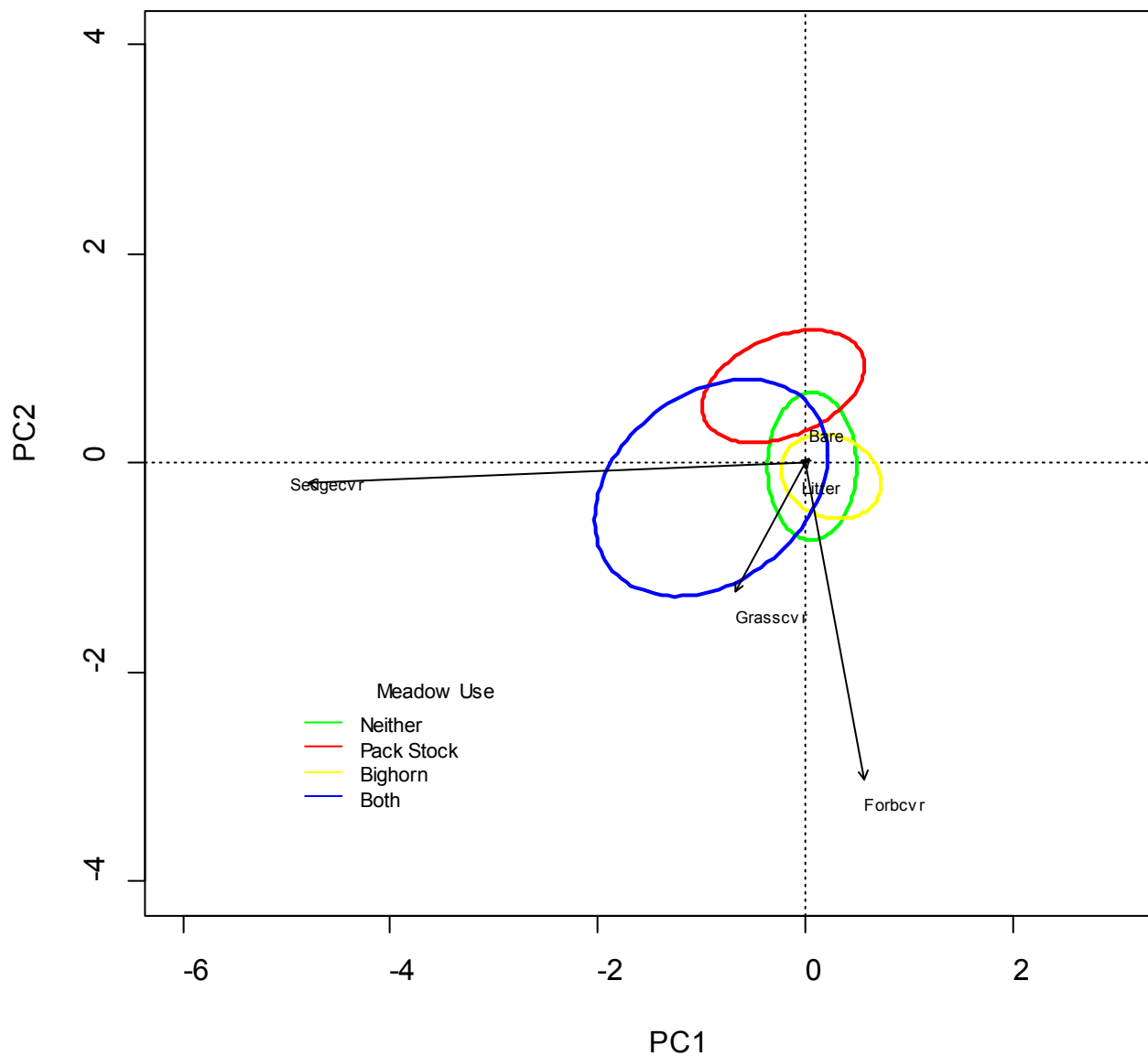


Figure 9. Principal Components Analysis biplot of vegetation structure in meadows in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by pack stock but not bighorn sheep (Packstock), (3) used by bighorn sheep but not pack stock (Bighorn), and (4) used by bighorn sheep and pack stock (Both).

There was virtually no evidence of differences in N_0 ($\Delta AIC_c=6.27$; $wAIC_c=0.96$) or N_1 ($\Delta AIC_c=2.69$; $wAIC_c=0.79$) for herbaceous species diversity among the meadow use classes. The null model for N_2 also had the greatest support, but the evidence was weaker ($\Delta AIC_c=1.04$; $wAIC_c=0.63$). The diversity profiles clearly showed, however, that any differences among the use classes were ecologically trivial (fig. 10). Evenness was low in all meadow use classes, but there was overwhelming evidence that $E_{1/d}$ differed among them ($\Delta AIC_c=9.67$; $wAIC_c=0.99$). This was because of relatively higher values of $E_{1/d}$ in plots used just by SNBS (fig. 11), but the differences were small and probably biologically irrelevant. There was no evidence of meaningful differences in $E_{1/d}$ among the other use classes (fig. 11).

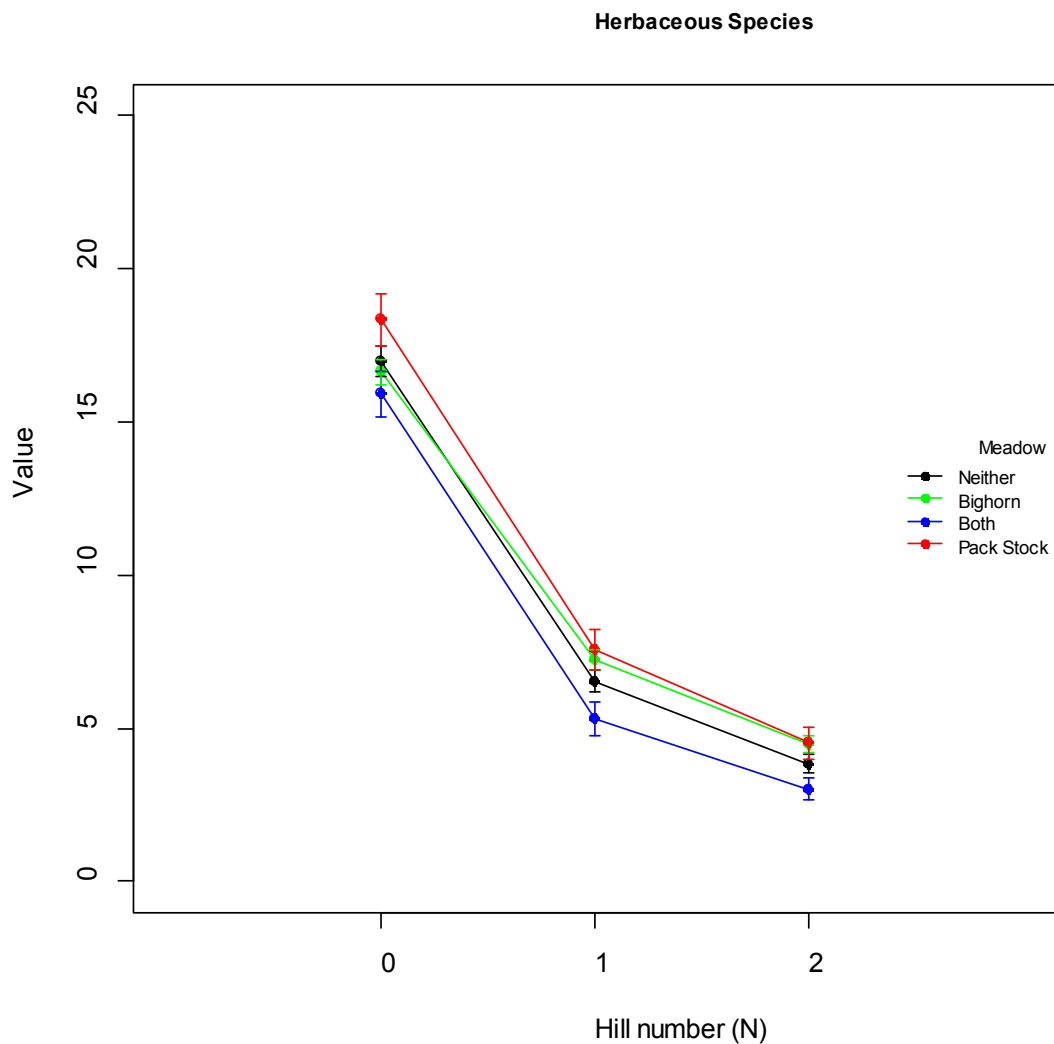


Figure 10. Profiles of herbaceous species diversity for meadows in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by bighorn sheep and pack stock (Both), and (4) used by pack stock but not bighorn sheep (Packstock). N_0 = species richness, N_1 = the exponentiation of Shannon’s index, and N_2 = the inverse of Simpson’s index. Error bars are 95-percent confidence intervals.

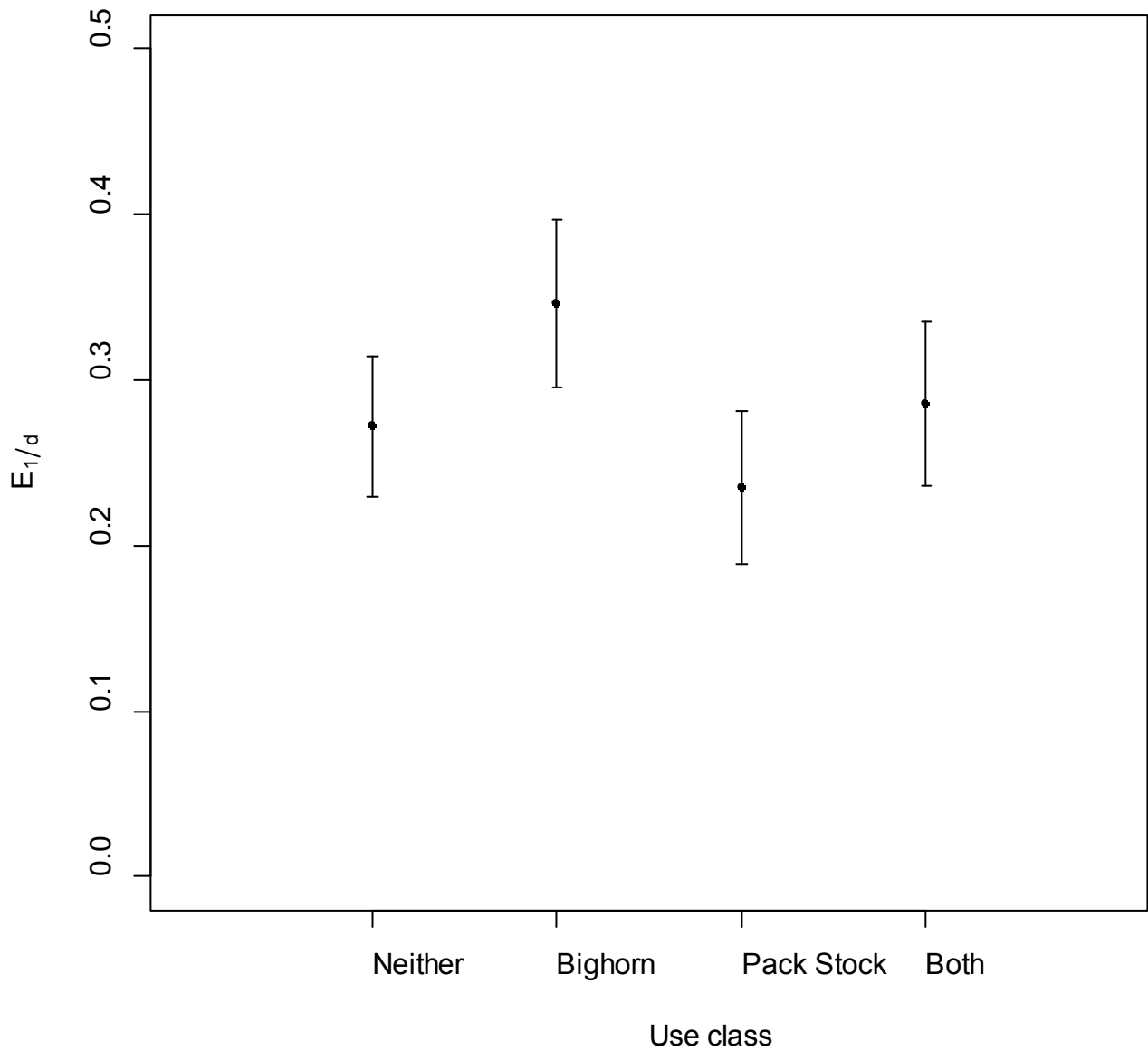


Figure 11. Simpson's index of evenness ($E_{1/d}$) in meadows in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by pack stock but not bighorn sheep (Packstock), and (4) used by bighorn sheep and pack stock (Both). Error bars are 95-percent confidence intervals.

Wehausen (1980) described 54 herbaceous forage species used by SNBS. Of these, 27 (50 percent) were recorded in our plots. There was overwhelming evidence that total cover of these forage species differed among the meadow use classes ($\Delta AIC_c=176.6$; $wAIC_c=1.00$). Cover was approximately two times greater in plots used just by pack stock than in plots used just by SNBS or those not used by pack stock or SNBS, and it was approximately three times greater than in plots used by both (fig. 12).

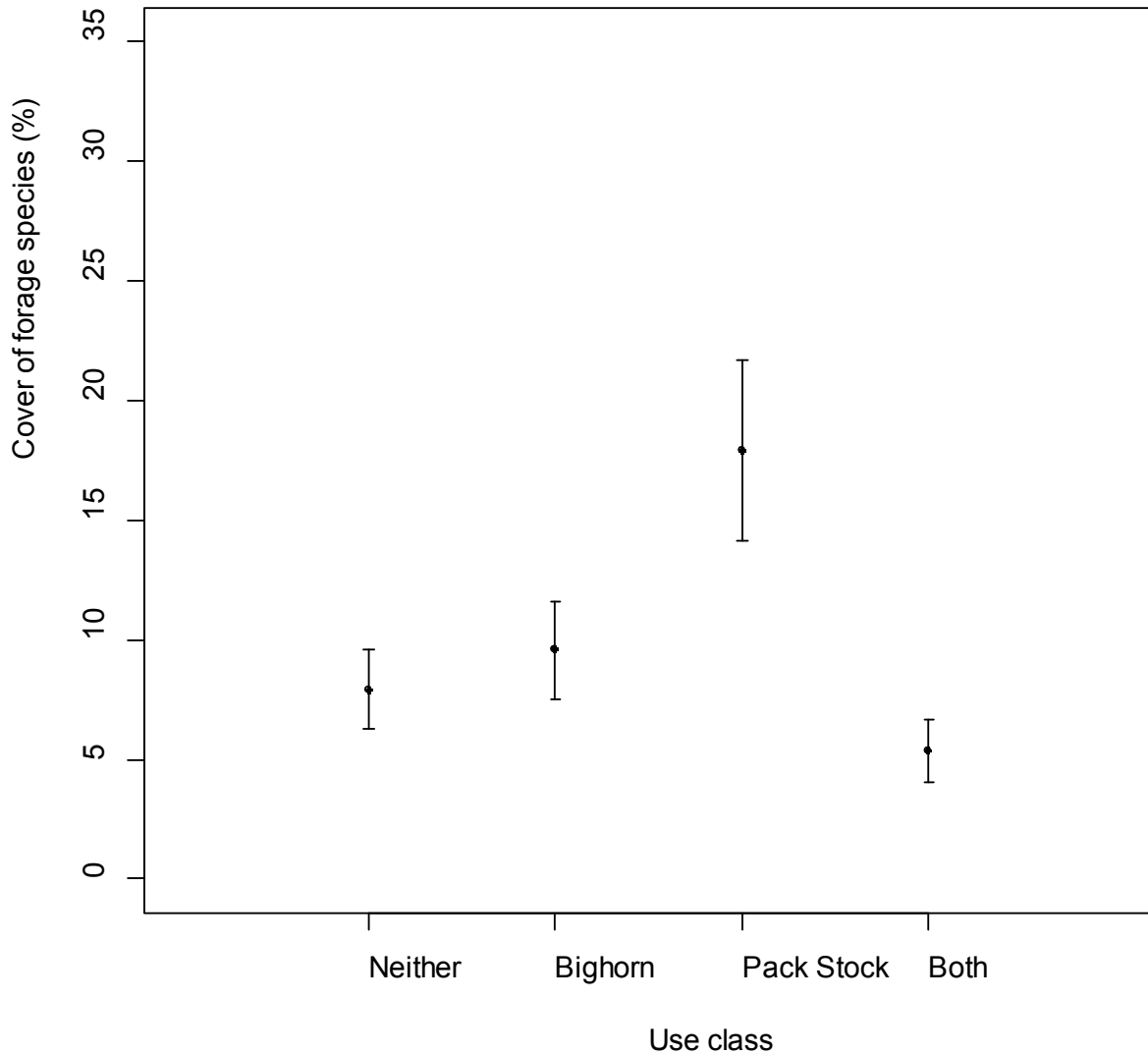


Figure 12. Percentage (%) cover of herbaceous forage species for meadows in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by pack stock but not bighorn sheep (Packstock), and (4) used by bighorn sheep and pack stock (Both). Error bars are 95-percent confidence intervals.

There was virtually no evidence of differences in N_0 ($\Delta AIC_c=6.02$; $wAIC_c=0.95$), N_1 ($\Delta AIC_c=4.88$; $wAIC_c=0.92$), or N_2 ($\Delta AIC_c = 4.94$; $wAIC_c = 0.92$) for forage species diversity among the meadow use classes (fig. 13). Evenness was moderate in all meadow use classes, but there was overwhelming evidence that $E_{1/d}$ differed among them ($\Delta AIC_c=28.24$; $wAIC_c=1.00$). This was because of relatively higher values of $E_{1/d}$ in plots used just by both pack stock and SNBS (fig. 14). The differences in $E_{1/d}$ among the four classes were small, however, and probably biologically irrelevant.

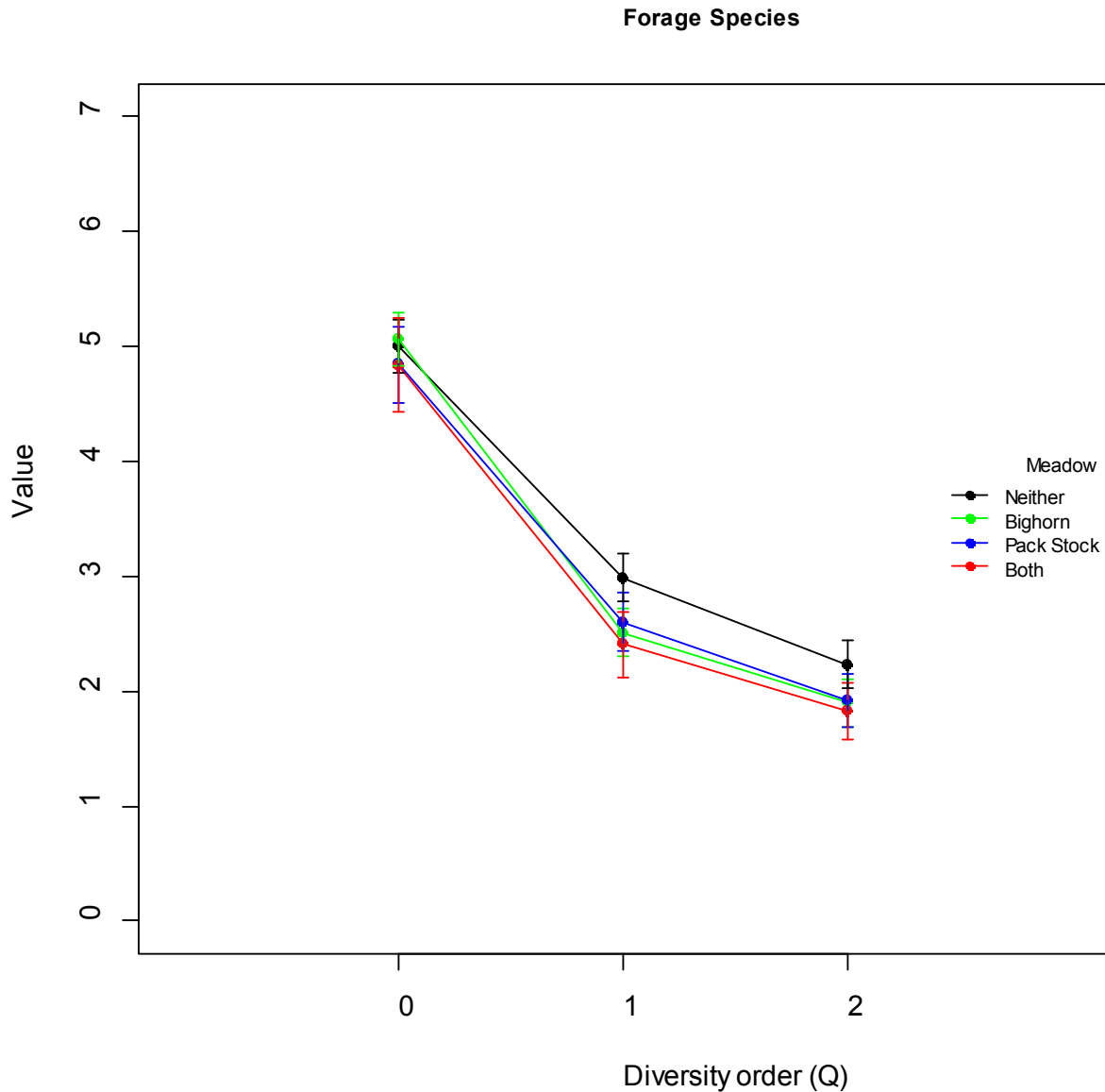


Figure 13. Profiles of herbaceous forage species diversity for meadows in four Sierra Nevada bighorn sheep and pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by bighorn sheep and pack stock (Both), and (4) used by pack stock but not bighorn sheep (Packstock). N_0 = species richness, N_1 = the exponentiation of Shannon’s index, and N_2 = the inverse of Simpson’s index. Error bars are 95-percent confidence intervals.

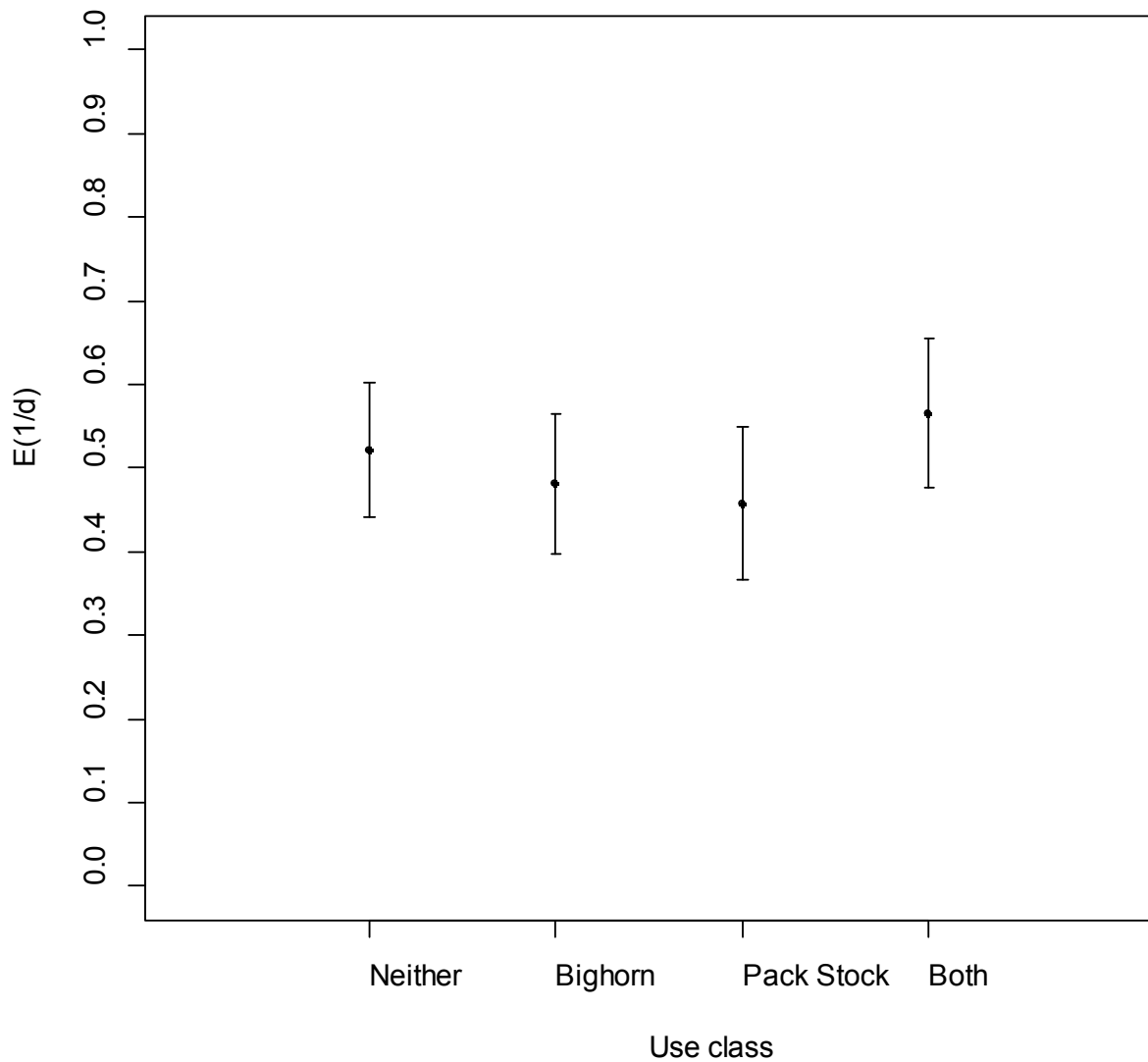


Figure 14. Simpson's index of evenness ($E_{1/d}$) in for herbaceous forage species in four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by pack stock but not bighorn sheep (Packstock), and (4) used by bighorn sheep and pack stock (Both). Error bars are 95-percent confidence intervals.

There was overwhelming evidence that bare ground was 10–11 percent greater in grazed plots not available to SNBS and ungrazed plots available to SNBS compared to plots not used by either or plots used by both ($\Delta AIC_c=24.88$; $wAIC_c=1.00$). There was no evidence that bare ground differed in any ecologically meaningful way among plots not used by either pack stock or SNBS or plots used by both pack stock and SNBS (fig. 15).

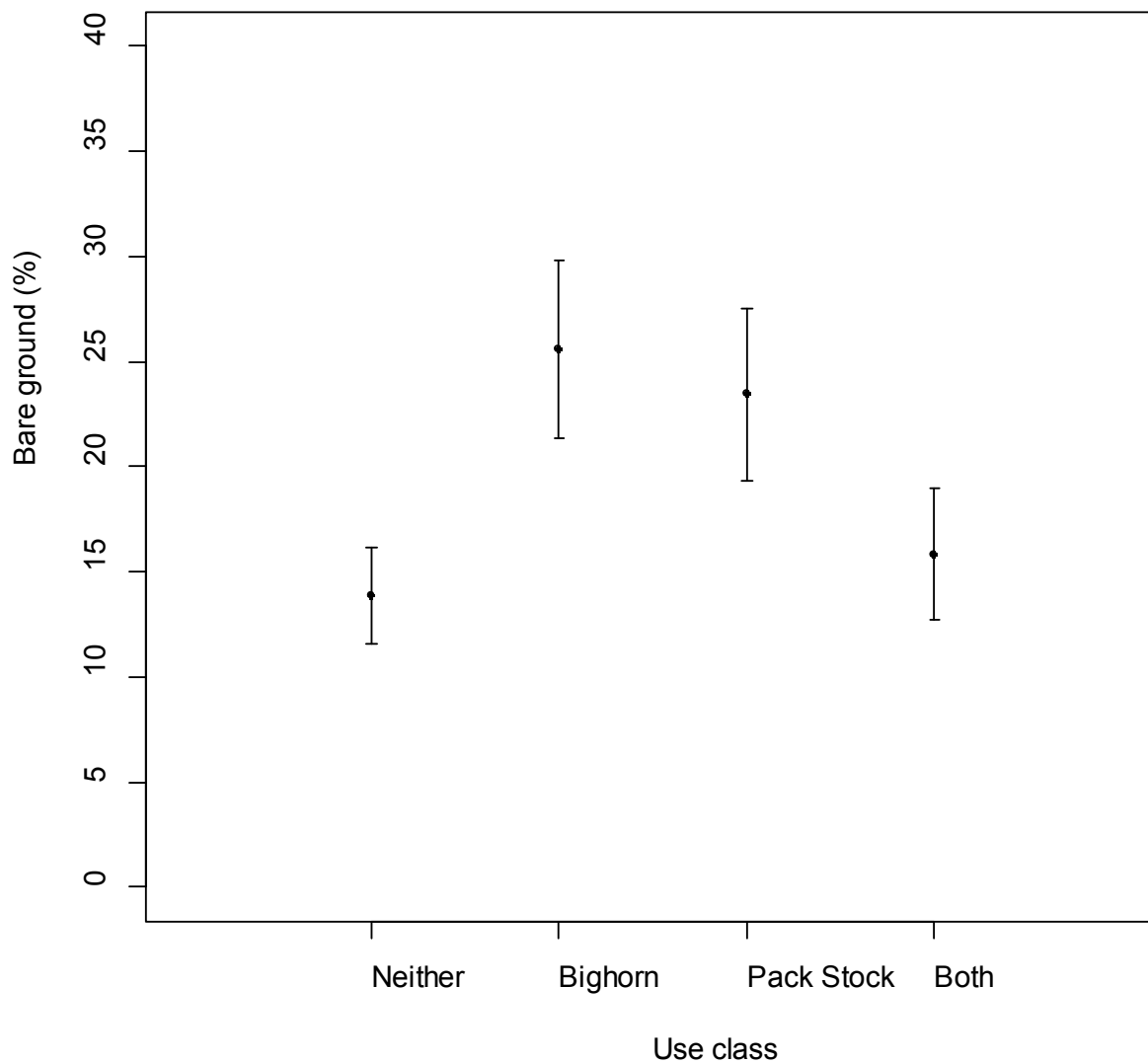


Figure 15. Percentage (%) cover of bare ground for meadows in four Sierra Nevada bighorn sheep and pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by pack stock but not bighorn sheep (Packstock), and, (4) used by bighorn sheep and pack stock (Both). Bare ground was defined as exposed soil other than rock. Error bars are 95-percent confidence intervals.

There was little evidence of differences in forage species composition among the meadow use classes (figs. 16–18). Similarity generally was high to moderately high regardless of the index, and the error bars generated from the bootstrap samples overlapped among all classes.

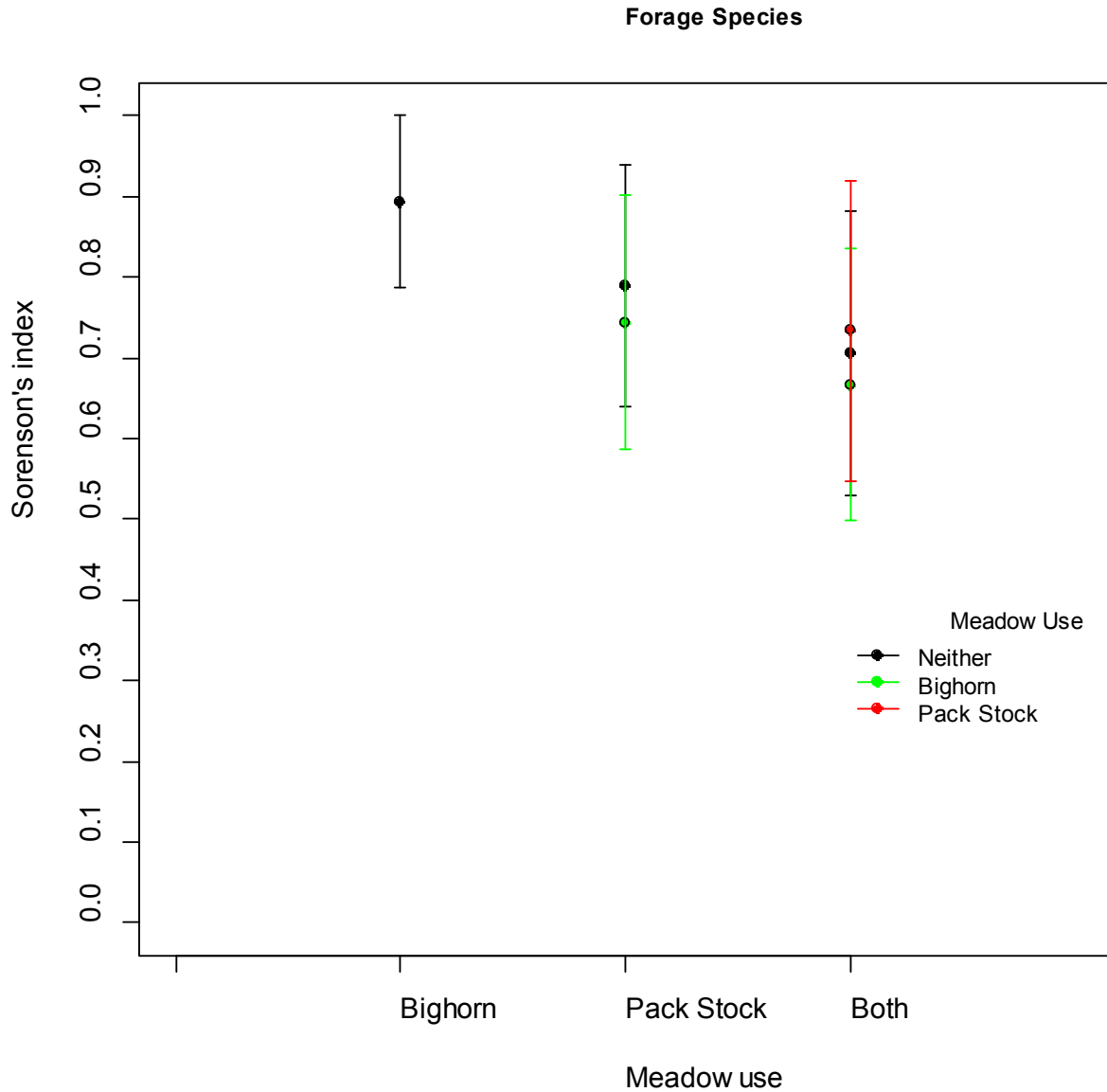


Figure 16. Pairwise similarity in herbaceous forage species composition among four Sierra Nevada bighorn sheep and pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn); (3) used by pack stock but not bighorn sheep (Packstock), and (4) used by bighorn sheep and pack stock (Both). Error bars are standard errors generated from 1,000 bootstrap samples.

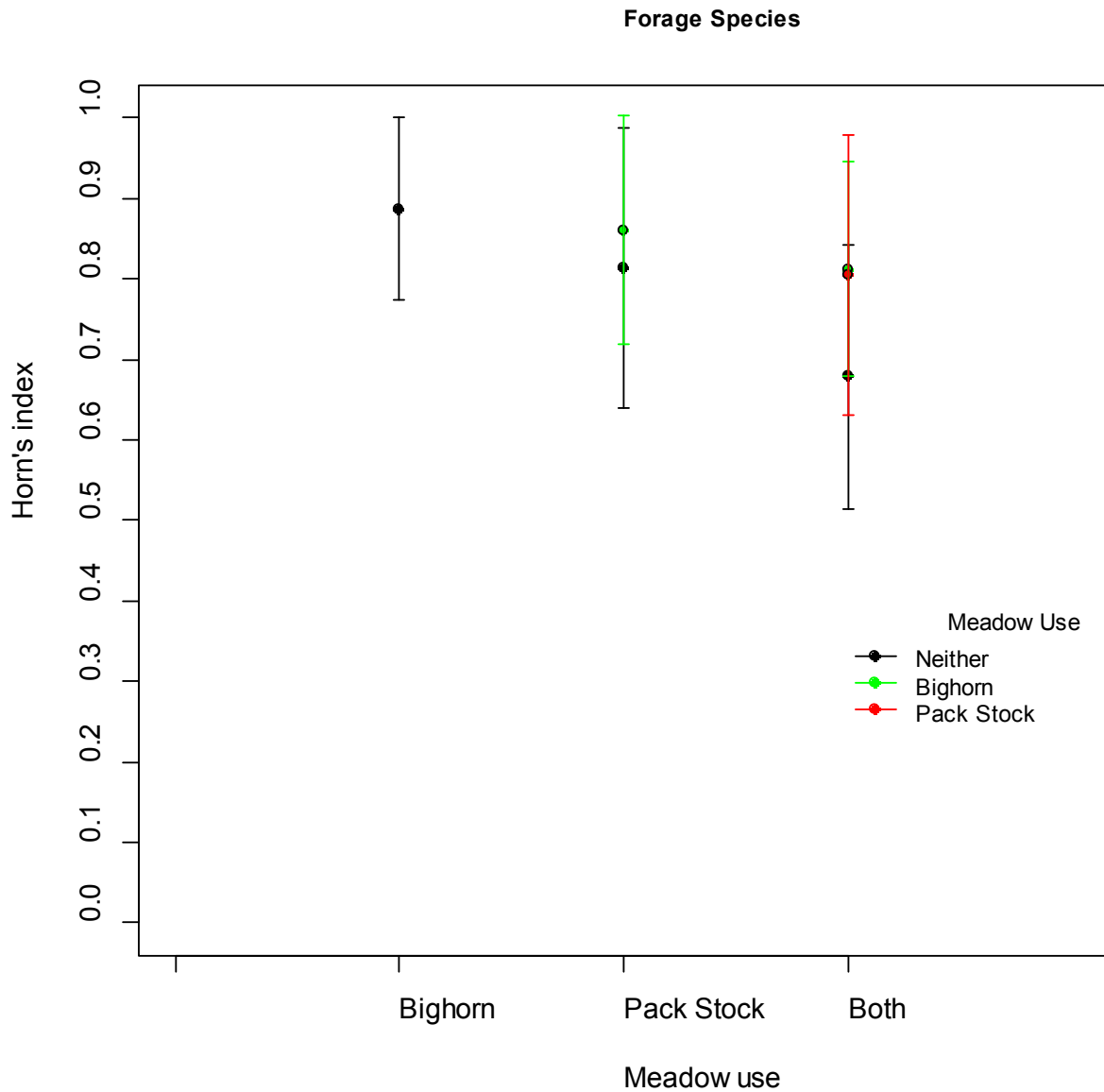


Figure 17. Pairwise similarity in herbaceous forage species composition among four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by pack stock but not bighorn sheep (Packstock), and (4) used by bighorn sheep and pack stock (Both). Error bars are standard errors generated from 1,000 bootstrap samples.

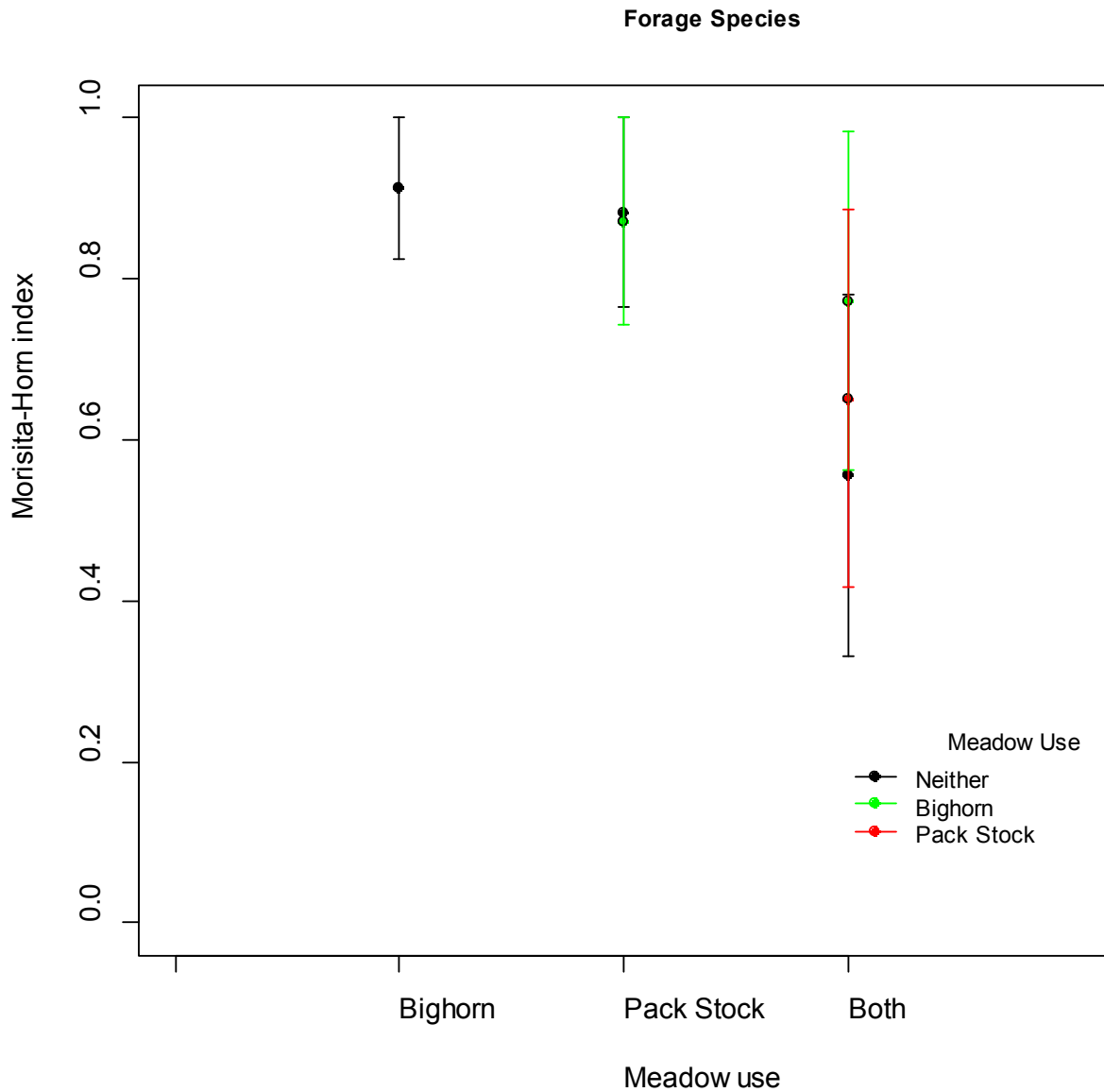


Figure 18. Pairwise similarity in herbaceous forage species composition among four Sierra Nevada bighorn sheep/pack stock use classes in Sequoia and Kings Canyon National Parks, California, 2011–2012. The use classes were (1) not used by bighorn sheep or pack stock (Neither), (2) used by bighorn sheep but not pack stock (Bighorn), (3) used by pack stock but not bighorn sheep (Packstock), and, (4) used by bighorn sheep and pack stock (Both). Error bars are standard errors generated from 1,000 bootstrap samples.

Discussion

Overall, the study indicated that there is little overlap in spatial use of meadows by SNBS and pack stock at SEKI. Meadows open to pack stock grazing generally were at large distances from SNBS escape terrain, and those relatively near SNBS escape terrain generally were not open to grazing by pack stock. Even when we used a very liberal definition of availability (250 m from escape terrain) a large proportion of meadows were closed to pack stock use. Furthermore, meadows open to grazing by pack stock and available to SNBS represented a very small proportion of all meadows on the landscape. These patterns were consistent regardless of whether availability was based on meadow area or distribution of meadows on the landscape. They were influenced minimally by sample sizes used in the analyses and simulations, and virtually all patterns were the opposite of patterns one would expect if pack stock were having negative effects on SNBS. Finally, relatively few meadows that were open to grazing by pack stock occurred within the herd unit polygons. However, the analyses for the 50 and 100-m distance classes in the use-availability and Monte Carlo simulations need to be interpreted with some caution because of the small number of meadows available to SNBS and open to grazing by pack stock. This largely reflected the reality of the use class designation. However, it also could be an artifact of SNBS frequently using small alpine meadows that typically are smaller than the mapping resolution used in this study. If this was the case, however, it would only increase the level of separation between SNBS and pack stock because these small meadows are not open to pack stock grazing.

Cole and others (2004) reported that horses and mules preferred graminoids and altered species composition in herbaceous assemblages in a field experiment conducted in Yosemite National Park. However, the grazing intensity in their study was artificially high and likely not representative of pack stock grazing regimes in SEKI. There was little evidence in our study indicating that pack stock grazing was having a consistent effect on plant community structure or species composition in meadows. Differences in species composition were most related to abiotic (topographic complexity and solar radiation) and biotic (vegetation production) factors. Variation in species composition among the meadow use classes was small compared to random variation among meadows and the influence of environmental variables. Structure did not vary among the use classes in a direction that would be expected if pack stock were having a significant effect on the relative abundance of forbs or graminoids. For instance, total cover of SNBS forage species was greatest in plots that were open to grazing by pack stock and not SNBS, and sedges, which are a favored diet item of pack stock and SNBS, were most common in plots open to pack stock and SNBS. The amount of bare ground was similar among plots not used by pack stock or SNBS and those potentially used by both, and it was almost twice as high in plots used just by pack stock or potentially just by SNBS compared to the other two classes. Moreover, there was no evidence that plant diversity was lower in meadows open to grazing by pack stock than in meadows not open to grazing. This was the case for overall herbaceous plant diversity and forage species alike. Finally there were no consistent differences in species identity or relative abundance of the SNBS forage assemblage suggesting negative effects by pack stock.

These patterns underscore two very important points that Ostoja and others (2014) made in their review of potential pack stock effects in meadows in the Sierra Nevada. First, meadows in the Sierra Nevada are heterogeneous; therefore, it is likely that such relatively fine-grained variation will override effects from low and moderate levels of grazing. This point is consistent with our finding that the greatest amount of variation in herbaceous species composition was explained by random effects of the meadows, as well as a lack of any consistent patterns of low plant cover, more bare ground, or low diversity in areas open to grazing by pack stock. Second, grazing by pack stock in the Sierra Nevada tends to be relatively intermittent and of low intensity. This also is the case with SNBS, which occur at low densities, seldom stay in an area for periods of time exceeding several hours, and spend the overwhelming amount of their time in rocky habitats. Thus, it is possible that such a grazing regime in meadows in the Sierra Nevada, by either pack stock or SNBS, may either increase herbaceous plant species diversity or at least have a neutral effect, as has been observed in other grazing systems (McNaughton, 1983; Belsky, 1986).

Our findings indicate that the current plan for managing pack stock grazing at SEKI (National Park Service, 1986) has been successful at minimizing the likelihood of significant negative effects on SNBS. A critical piece of information in evaluating potential effects of pack stock on SNBS is that there has been no observed decrease in population size of SNBS that could be attributed to interactions with pack stock. On the contrary, the population of bighorn sheep in the Sierra Nevada has increased since being listed as federally endangered in 1999 (Stephenson and others, 2012), and in particular the herds in this study have all had strong positive rates of population change since then (Runcie and others, 2014).

In conclusion, we stress that these analyses provided only an indirect measure of potential, not actual, overlap or impacts. Direct measurement of displacement of SNBS by pack stock would require an intensive observational study or a manipulative experiment, both of which likely would be time-consuming and costly. Instead of investing in such a costly study, our analyses allowed us to first assess how great the potential for displacement of SNBS by pack stock actually was and (or) if there was evidence of pack stock having a negative effect on SNBS forage. If our results indicated that the potential for these negative effects was high, then an investment in a more costly study would be justified. However, our results suggest that such an investment likely is not warranted.

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