

OVERLAP IN DIET AND HABITAT BETWEEN THE MULE DEER (*ODOCOILEUS HEMIONUS*) AND FERAL ASS (*EQUUS ASINUS*) IN THE SONORAN DESERT

JASON P. MARSHAL,* VERNON C. BLEICH, PAUL R. KRAUSMAN, MICKEY-LYNN REED, AND ALEX NEIBERGS

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa (JPM)
Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, 407 West Line Street,
Bishop, CA 93514 (VCB)

Boone and Crockett Program in Wildlife Conservation, University of Montana, Missoula, MT 59812 (PRK)

School of Natural Resources, University of Arizona, Tucson, AZ 85721 (MLR)

Bureau of Land Management, 300 South Richmond Road, Ridgecrest, CA 93555 (AN)

Present address of VCB: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209

**Correspondent: jason.marshal@wits.ac.za*

ABSTRACT—We studied use of habitats and diets of mule deer (*Odocoileus hemionus*) and feral asses (*Equus asinus*) by comparing vegetation (i.e., normalized-difference-vegetation index, normalized-difference-vegetation-index rate), elevation, slope, and distances to water-catchments, roads, rivers and canals, and washes used by each species. Distribution was similar with respect to distances to roads, catchments, and rivers and canals in winter, normalized-difference-vegetation index and distance to catchments in spring, distance to rivers and canals in summer, and slope in autumn. Diets (from microhistological analysis of feces) revealed biologically significant overlap during the abundant-forage season (simplified Morisita index >0.60). Diets of mule deer had high proportions of browse (76–85%) in all seasons and low proportions of grasses (1–2%) and forbs (4–8%); whereas, diets of feral asses contained less browse (65–72%) and more grasses (12–16%) and forbs (13–20%).

RESUMEN—Investigamos el uso de hábitat y las dietas del venado bura (*Odocoileus hemionus*) y el burro feral (*Equus asinus*) por comparar la vegetación (es decir, el índice de diferencias-normalizadas de la vegetación, tasa del índice de diferencias-normalizadas de la vegetación), la elevación, la inclinación y las distancias hacia aguas artificiales, caminos, ríos y canales, y arroyos usados por cada especie. La distribución fue similar con respecto a las distancias a caminos, aguas artificiales y ríos y canales en el invierno, el índice de diferencias-normalizadas de la vegetación y las distancias hacia aguas artificiales en la primavera, las distancias a ríos y canales en el verano, y la inclinación en el otoño. Las dietas (por el análisis microhistológico de fecas) revelaron una similitud biológicamente significativa durante la estación con el forraje abundante (el índice de Morisita simplificado >0.60). La dieta del venado bura tuvo proporciones altas de las especies leñosas (76–85%) en todas las estaciones y proporciones bajas de los pastos (1–2%) y de las especies de plantas de hojas anchas (4–8%), mientras que la dieta del burro feral contuvo menos especies leñosas (65–72%) y más pastos (12–16%) y especies de plantas de hojas anchas (13–20%).

Feral equids in the western USA originated as pack animals introduced to the Americas by Spanish colonists in the 1500s. The Wild and Free Roaming Horses and Burros Act, enacted by Congress in 1971, mandates protection of those animals (Douglas and Leslie, 1996). Detrimental impacts on arid ecosystems and native herbivores (e.g., bighorn sheep *Ovis canadensis*, mule deer *Odocoileus hemionus*) have been blamed on a subsequent increase in abundance of feral equids (Berger, 1985; Bleich and Andrew, 2000). Overlap in use of range and diet, as a consequence of common use of habitat (Dunn and Douglas, 1982) and forage (Ginnett

and Douglas, 1982), have raised concerns among wildlife managers about possible competition between feral asses (*Equus asinus*) and bighorn sheep. Only recently, however, has evidence suggested that population-level effects occur in bighorn sheep as a consequence of overlaps in habitat or diet with feral asses (Marshal et al., 2008).

Concerns about competition arise because of loss of partitioning of resources among herbivores when an exotic species is introduced to a new environment (Voeten and Prins, 1999). Partitioning of resources plays a central role in establishing niches among species using similar resources and in structuring communities that

contain those species (Putman, 1996). When there is overlap in use of a scarce but essential resource, competition for that resource should detrimentally affect demography of at least one of the competing species (Wiens, 1989). Thus, coexistence of sympatric species has been viewed to depend on temporal or spatial partitioning of resources (Schoener, 1974; Pianka, 1981). Partitioning of resources likely arises through evolution of mechanisms in species that have been sympatric over many generations. Where an exotic herbivore is introduced to a system, however, those mechanisms likely do not occur (Ilse and Hellgren, 1995; Douglas and Leslie, 1996; Voeten and Prins, 1999). As a consequence, there is greater potential for introduced and native herbivores to use the same limited resources.

Concerns about competition also arise because of foraging strategies among herbivores. Bighorn sheep and mule deer are selective browsers and ruminants with four-chambered stomachs that facilitate digestion of plants through fermentation (Kie and Czech, 2000; Krausman and Shackleton, 2000). The requirement that particles of plants be small (<1 mm) to pass from the rumenoreticulum to the omasum limits capacity of ruminants to vary rate of passage through the digestive tract according to nutritional quality of forage (Spalinger, 2000). Thus, rate of intake and time for passage must be low enough to permit sufficient digestion of consumed plants, and quality of forage must be above a minimum limit to meet nutritional requirements (Janis, 1976). In contrast, equids are bulk foragers and hind-gut fermenters with an enlarged caecum (Janis, 1976). They vary rate of intake and passage when quality of available forage is low; thus, equids can partially compensate for poor quality of forage (Douglas and Leslie, 1996). A rate of passage higher than that for typical ruminants means poorer digestive efficiency (Spalinger, 2000), but equids are more effective at using diets high in fiber (Janis, 1976). As a consequence, diet of feral asses can incorporate higher-quality forage, such as that used by ruminants, when it is available, but focus on lower-quality forage, unsuitable for ruminants, during periods of scarcity. This might allow feral asses a competitive advantage in highly variable, arid environments.

Unlike for bighorn sheep, degree of overlap on resources remains unknown for feral asses and mule deer in the Sonoran Desert. There is strong potential for competition between feral asses and bighorn sheep (Seegmiller and Ohmart, 1981; Douglas and Leslie, 1996), and because of similarity in size, digestive morphology, and foraging behavior between mule deer and bighorn sheep, competitive interactions between feral asses and mule deer also are possible. Thus, our objective was to evaluate degree of overlap in resources between mule deer and feral asses via comparison of use of habitat and diet.

MATERIALS AND METHODS—Data were collected in a 1,100-km² area in the Sonoran Desert, Imperial County, California, during May 1999–June 2004. The area was hot and arid, with summer high temperatures >45°C and average annual precipitation <100 mm (Imperial Irrigation District, Imperial, California). We used biological seasons defined according to behavior of mule deer and their responses to changes in rainfall and temperature (Marshal et al., 2006a). Winter (cool-rainy) began with the rut ca. 1 January. Spring (hot-dry) began during April or May when mule deer moved to <5 km of sources of water. Summer (hot-rainy) began when mule deer moved >5 km from sources of water, which coincided with the first monsoonal rains ca. 1 July. Autumn (cool-dry) began after the last rains in summer, ca. 1 October. Onset of seasons varied among years (Marshal et al., 2006a).

Mountainous areas supported creosotebush (*Larrea tridentata*), brittle-bush (*Encelia farinosa*), burro-weed (*Ambrosia dumosa*), and ocotillo (*Fouquieria splendens*). Vegetation in riparian areas adjacent to the Colorado River included salt cedar (*Tamarix*), cattails (*Typha domingensis*), and arrowweed (*Pluchea sericea*; Andrew, 1994). Of biomass of plants away from the river, >90% occurred in xeroriparian associations along dry desert washes (Marshal et al., 2005a), which contained desert ironwood (*Olneya tesota*), palo verde (*Parkinsonia florida*), honey mesquite (*Prosopis glandulosa*), and catclaw (*Acacia greggii*; Andrew et al., 1999).

Several sources of water were available to mule deer and feral asses: Colorado River, All-American Canal, and 17 watering sites for wildlife (i.e., catchments) at an average density of 1/35 km². Most catchments were surrounded by fences to permit use by mule deer and bighorn sheep but prevent use by feral asses (Andrew et al., 1997). There also were natural rock basins and springs, most of which became dry during the hot-dry season.

Mule deer occurred at low density in the study area (0.05–0.13 deer/km²; Thompson and Bleich, 1993; Marshal et al., 2006b). An aerial survey of feral asses produced an estimate of 0.38/km² (Bureau of Land Management), and density of bighorn sheep was estimated at 0.38/km² (California Department of Fish and Game). In addition to large herbivores, medium-sized herbivores included the black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), and desert tortoise (*Gopherus agassizii*).

Mule deer were captured as part of a concurrent study (Marshal et al., 2006a). We used a net-gun fired from a helicopter, as described by Krausman et al. (1985), to capture adult female mule deer and adult feral asses of both sexes. Duration of chase for each animal was <5 minutes. Upon capture, we blind-folded and hobbled each animal to facilitate handling (Jessup et al., 1986), attached a VHF radiocollar with mortality sensor (6-h delay; MOD-500, Telonics, Mesa, Arizona), and released the animal at site of capture.

We conducted weekly flights with a fixed-wing aircraft (Cessna 185) equipped with two H-type antennas, one on each wing to locate radiocollared animals. When we located a collared animal, the aircraft slowed and circled until we achieved the strongest possible signal, as described by Krausman et al. (1984), but we did not fly low enough for visual observations for safety reasons (Bleich et al., 2001). We recorded location in degrees latitude and longitude on a global-positioning-system (GPS) receiver and downloaded geographic

coordinates directly to a computer for analysis. Average error of locations was 380 m (95% CI = 308–451; Marshal et al., 2006a).

We collected 20 groups of fecal pellets monthly for mule deer and for feral asses. We collected samples opportunistically throughout the study area, with most samples coming from dry desert washes near xeroriparian vegetational associations. Pellets were fresh (i.e., <1 week old), air-dried at room temperature, and stored in paper bags until analysis. We identified fresh pellets by their dark-brown, sometimes shiny, exterior and green interior; older pellets had a faded, paler brown or gray appearance (Marshal et al., 2004). Plants in diets were identified by microhistological analysis of epidermal fragments (Vavra and Holechek, 1980). Because of cost, we used monthly composites of fecal samples. We used two pellets from each individual sample of feces from mule deer and ca. 20 cm³ from each individual sample of feces from feral asses. We used a compound microscope at 100× to examine three slides/composite. We computed frequencies of each species of plant from 20 fields/slide; each containing ≥7 identifiable particles. Frequencies were converted to density of particles (Fracker and Brischle, 1944) and then to relative density (Sparks and Malechek, 1968).

We used geographic-information-system (GIS) models of landscape and ARC/INFO software (Environmental Systems Research Institute, Redlands, California) to develop a model of habitat for mule deer, which included raster models of indices of vegetation, attributes of terrain, and distances to features of points or lines. We used eight GIS layers to represent components of resources or habitat. Sources of data were GIS Data Depot (<http://data.geocomm.com/>) and Cal-Atlas Geospatial Clearinghouse (<http://www.atlas.ca.gov/>).

Elevations came from 30-m resolution, digital-elevation, raster models (United States Geological Survey); we derived slope from elevation. We used line-vector coverage of roads for Imperial County to develop a distance-to-roads layer. Washes (i.e., stream beds that were dry most of the year) were digitized as polygons from 1-m-resolution, digital, satellite photos (digital-orthographic-quarter quadrangles, United States Geological Survey) to develop a distance-to-wash layer. We measured locations of catchments with a GPS unit and used those data to develop a point-vector layer. We used existing polygon-vector coverage of rivers and canals (i.e., both features combined) for California to derive a distance-to-river layer that included the Colorado River and All-American Canal. For each distance-to-layer, we converted each model of vectors into a 30-m raster model and then calculated distances from the center of each cell to the center of those containing the feature represented in the original vector layer.

We used the Advanced Very High Resolution Radiometer normalized-difference-vegetation index, a remote-sensing imagery having a resolution of 1 km, as an index of wet biomass of forage (Tucker, 1979). Source of imagery was the University of Arizona School of Arid Lands Studies. We calculated differences between consecutive, biweekly, normalized-difference-vegetation-index layers to determine normalized-difference-vegetation-index rate (Parker, 2003), an index to growth and die-back of forage and, thus, to nutritional quality of forage (Marshal et al., 2005b). The normalized-difference-vegetation-index layers have a standard 0–1 range in values for surfaces of land; however, those used in our model had been converted to an eight-bit color scale to conserve computing resources. As a result, values were integers without units that had a range of 0–

200 (Wallace, 2002); typical values from our study area had a smaller range (ca. 100–150). Values for normalized-difference-vegetation-index rate could be positive or negative, depending on whether the value for a pixel increased or decreased between biweekly periods. Locations of animals and normalized-difference-vegetation-index layers were date-specific; thus, analysis required associating each location with the appropriate biweekly normalized-difference-vegetation index or normalized-difference-vegetation-index-rate layer.

We evaluated influence of environmental factors on distribution of mule deer and feral asses by comparing observed and random use for each species with resource-selection functions based on logistic-regression models (Manly et al., 2002). Because our interest was to evaluate common use of components of habitat where competition was most likely, we considered selection of habitat at the scale of location of animal within the home range (third-order selection; Johnson, 1980). We used minimum-convex polygons (Mohr, 1947) to identify seasonal home ranges for each animal. Using each minimum-convex polygon as a boundary, we generated one random location for every observed location, after establishing experimentally that more than one random location per observed location did not improve fit of the model (Gross et al., 2002). We buffered observed and random locations by 500 m to be certain that we accounted for the largest likely uncertainty in telemetric locations (Marshal et al., 2006a). We associated each location with the average value within the buffer for each GIS layer. Those averages became the data used to analyze distribution of mule deer and feral asses in logistic-regression analysis.

The global model with which we began to develop each seasonal resource-selection function contained landscape variables represented in the GIS model (screened initially for multicollinearity) of habitat, species, and all two-way interactions between species and variables of landscape as explanatory variables, and whether location was used or random as the response variable. Two-way interactions tested whether there was evidence of overlap in use of habitat. If significant, those interactions would indicate aspects of habitat that were used differently by mule deer and feral asses. Lack of significance for an interaction would suggest similar use of the component of habitat represented in the interaction. Data based on locations of all individuals were combined for each seasonal analysis; to account for repeated observations on each radiomarked individual, a variable identifying each individual was included in each seasonal model as a random effect (Gillies et al., 2006). Fitting models of resource-selection functions in a mixed-effects framework has two main advantages over fitting such models with standard, fixed-effects methods. First, it treats levels within the random effect (e.g., individual animals in our study) as sampling units that represent a broader population (i.e., one parameter is estimated for all levels of random effect instead of separate parameters for each level). Second, it is a convenient way to deal with repeated measures, where multiple observations for the same individual are not independent. Thus, for our study, mixed-effects models allowed inferences to be based on individual mule deer and feral asses as sampling units representing their respective populations, rather than on samples of observed locations of animals. Sexes of feral asses were combined after establishing that there was no evidence of different use of habitat.

We arrived at a final reduced model for interpretation

following methods in two stages. First, selection of variables occurred by the recursive-backward, one-at-a-time elimination of variables with the highest P -values. Once the resulting model contained variables for which there was some evidence of an effect ($P < 0.10$), the second stage investigated influence of those remaining variables by removing each variable individually, refitting the model, and comparing that model to the original global model using the likelihood-ratio test (Manly et al., 2002; Ramsey and Schafer, 2002). A nonsignificant value for the likelihood-ratio test at this stage indicated that the removed variable was not important for explaining variation in the dataset. Thus, our final reduced model was that with the fewest number of variables where variation explained in the dataset by the final model was not significantly different from variation explained by the global model. We conducted logistic-regression analysis in R (R Development Core Team, Vienna, Austria) with function LMER in package LME4 (D. Bates, <http://r-project.org/>).

We evaluated overlap in diet with the simplified Morisita index (Horn, 1966), which ranges from 0 (no overlap) to 1 (complete overlap), with substantial overlap indicated when the index is >0.60 (Zaret and Rand, 1971). This index has relatively low bias and is appropriate for studies in which selection of resources is reported as a proportion of total resources used by the animal (Krebs, 1989). We calculated an index of overlap for each monthly composite using proportion of each identified taxon of plants as categories. Then we plotted indices by month to determine how overlap varied seasonally and during which months overlap was >0.60 .

RESULTS—We analyzed data from 44 female mule deer (Marshal et al., 2006a) and 44 feral asses (24 male, 20 female). We obtained 2,000 locations for mule deer (winter, 490; spring, 570; summer, 544; autumn, 396) and 945 for feral asses (winter, 276; spring, 193; summer, 148; autumn, 328). During no season was there evidence for an effect of sex of feral ass on use of habitat ($P > 0.10$); therefore, all locations of feral asses were treated as a common group.

There were 13 landscape variables and interactions in the estimated resource-selection functions in winter for mule deer and feral asses (Table 1) that explained observed variation in use of habitat in winter as well as the full model containing 17 terms (likelihood-ratio test = 3.92, $df = 4$, $P = 0.417$). There was no evidence that distances to roads, catchments, and rivers and canals played different roles in use of habitat between the two species of ungulates. For each component, observed use by both species was associated with areas closer to those features than were random locations. However, magnitude of their effects (based on estimated coefficients) was small relative to that of other components in the fitted model (Table 1).

The variable of landscape with the largest effect in winter was slope (Table 1). There was evidence that mule deer and feral asses used slopes differently, with locations of feral asses being associated with areas of steeper slopes than those of mule deer. There also was evidence for species-specific selection for areas based on the normal-

ized-difference-vegetation index, but only weak evidence for a similar effect of normalized-difference-vegetation-index rate (Table 1). Mule deer were associated with areas having lower normalized-difference-vegetation index and lower rates of change in normalized-difference-vegetation index, suggesting they selected areas of lower biomass and rates of growth of plants than did feral asses. There was strong evidence for an effect of distance to wash on observed use by mule deer and feral asses (Table 1); use by feral asses was associated with areas farther from washes than was use by mule deer. Use of habitat by feral asses appeared random with respect to elevation, whereas there was weak evidence for a negative relationship between use and elevation in mule deer (Table 1).

The logistic-regression model for spring contained 10 landscape variables and interactions (comparison to full model: likelihood-ratio test = 7.213, $df = 7$, $P = 0.407$), two of which (normalized-difference-vegetation index and distance to catchment) indicated common use by mule deer and feral asses (Table 1). For both species, observed use was associated with areas of greater normalized-difference-vegetation index than was random use; magnitude of that effect was the largest of landscape variables considered (Table 1). Further, use by mule deer and feral asses was associated with areas closer to catchments than were random locations. Despite strong evidence for this effect, its magnitude was the smallest of landscape variables in the model for spring (Table 1).

Use of different elevations appeared to be species-specific (Table 1). Observed use by feral asses was associated with higher elevations than those used by mule deer. There also was evidence for species-specific use with respect to washes; observed use by feral asses was farther from washes than that by mule deer. By contrast, we observed feral asses in areas farther from roads but closer to rivers and canals than we did mule deer, with magnitude of effect being substantially larger for roads than for rivers (Table 1).

Seven landscape variables and interactions were included in the logistic-regression model for summer (comparison to full model: likelihood-ratio test = 8.321, $df = 10$, $P = 0.598$); only one variable, distance to rivers and canals, indicated common use. There was strong evidence for an effect of distance to river, with feral asses and mule deer being associated with areas farther from the river than random locations, but magnitude of the effect was small (Table 1).

During summer, there was strong evidence that feral asses used areas farther from washes than did mule deer (Table 1). In contrast, there was no association between use by feral asses and distance to roads or to catchments, indicating random distribution with respect to those features. Mule deer appeared to avoid those features. Overall, effect of roads and catchments were small in comparison to that of distance to wash (Table 1).

The logistic-regression model for autumn was the

TABLE 1—Seasonal resource-selection functions: a comparison of use of habitat by mule deer (*Odocoileus hemionus*) and feral asses (*Equus asinus*) in the Sonoran Desert, Imperial County, California.

Variable	Coefficient	95% CI	
		Lower	Upper
Winter			
Species (feral ass = 0, mule deer = 1)	21.013	8.000	34.029
Slope	0.110	-0.029	0.249
Slope × species	-0.144	-0.285	-0.003
Normalized-difference-vegetation index	0.077	-0.031	0.184
Normalized-difference-vegetation index × species	-0.148	-0.263	-0.033
Normalized-difference-vegetation index × rate	0.064	-0.074	0.203
Normalized-difference-vegetation index rate × species	-0.150	-0.308	0.008
Distance to wash	0.003	0.001	0.004
Distance to wash × species	-0.004	-0.005	-0.002
Elevation	0.001	-0.006	0.007
Elevation × species	-0.007	-0.014	≤0.001
Distance to roads	≥-0.001	≥-0.001	≤0.001
Distance to catchment	≥-0.001	≥-0.001	≥-0.001
Distance to river or canal	≥-0.001	≥-0.001	≥-0.001
Spring			
Species (feral ass = 0, mule deer = 1)	6.003	1.973	10.034
Normalized-difference-vegetation index	0.058	0.025	0.091
Elevation	0.038	≤0.001	0.075
Elevation × species	-0.057	-0.095	-0.020
Distance to wash	0.003	0.001	0.005
Distance to wash × species	-0.005	-0.008	-0.003
Distance to road	-0.002	-0.003	-0.001
Distance to road × species	-0.002	-0.004	-0.001
Distance to river or canal	-0.001	-0.001	≥-0.001
Distance to river or canal × species	0.001	≤0.001	0.001
Distance to catchment	≥-0.001	≥-0.001	≥-0.001
Summer			
Species (feral ass = 0, mule deer = 1)	-0.056	-0.830	0.715
Distance to wash	0.003	0.002	0.005
Distance to wash × species	-0.004	-0.005	-0.002
Distance to road	≥-0.001	-0.001	≤0.001
Distance to road × species	0.001	≤0.001	0.001
Distance to catchment	≥-0.001	≥-0.001	≤0.001
Distance to catchment × species	≤0.001	≤0.001	≤0.001
Distance to river or canal	≤0.001	≤0.001	≤0.001
Autumn			
Species (feral ass = 0, mule deer = 1)	2.391	1.130	3.647
Slope	-0.083	-0.121	-0.044
Distance to wash	0.003	0.002	0.005
Distance to wash × species	-0.003	-0.005	-0.002
Distance to river or canal	≤0.001	≥-0.001	≤0.001
Distance to river or canal × species	≥-0.001	≥-0.001	≥-0.001

simplest of the seasonal models and included five landscape variables and interactions (comparison to full model: likelihood-ratio test = 14.004, $df = 12$, $P = 0.300$); only slope appeared to be used similarly by feral asses and mule deer. Effect of slope was the largest of landscape variables in the model for autumn (Table 1). Both species were associated with shallower slopes than were random locations during autumn. For the two attributes of

landscape where differences between species were evident, distance to wash had the larger effect; feral asses appeared to use areas farther from washes than did mule deer (Table 1). Similarly, use by feral asses was associated with areas farther from rivers than was use by mule deer, but evidence was weak and effect was small relative to those of slope and distance to wash.

To summarize, common use of habitat components

TABLE 2—Average percentage of taxa in diets of mule deer (*Odocoileus hemionus*) and feral asses (*Equus asinus*) and feral ass based on microhistological analysis of fecal pellets in the Sonoran Desert, Imperial County, California.

Taxon	January–March		April–June		July–September		October–December	
	Mule deer	Feral ass	Mule deer	Feral ass	Mule deer	Feral ass	Mule deer	Feral ass
Browse								
<i>Acacia greggii</i>	0	13.9	0	13.4	5.8	10.8	0.1	13.0
<i>Ambrosia dumosa</i>	9.1	15.3	9.0	13.5	7.5	10.4	3.8	8.8
<i>Atriplex</i>	18.0	8.0	16.9	10.5	12.2	7.7	15.9	7.0
<i>Calliandra eriophylla</i>	8.1	0	10.0	0	10.1	0	4.7	0
<i>Ephedra californica</i>	12.7	10.2	12.7	11.6	9.1	5.9	11.7	5.0
<i>Fouquieria splendens</i>	1.1	0	0.9	0	0.9	0	0.1	0
<i>Krameria</i>	1.2	14.9	4.1	7.8	4.6	7.0	4.3	4.8
<i>Larrea tridentata</i>	6.4	0	4.5	0	2.8	0	5.5	0
<i>Lycium</i>	1.5	0	0.7	0	0.4	0	0.9	0
<i>Obeya tesota</i>	11.3	5.9	7.4	3.7	5.8	7.7	9.9	5.3
<i>Parkinsonia florida</i>	14.1	0	10.1	0	5.7	0	18.6	0
<i>Pluchea sericea</i>	0.2	0.8	0.3	0.1	0.2	0.3	0	0.4
<i>Prosopis glandulosa</i>	0.1	0.2	0	4.8	11.0	22.6	9.5	21.1
Total browse	83.9	69.2	76.6	65.4	76.1	72.3	84.9	65.4
Forbs								
<i>Amsinckia</i>	0	0	0	0	0	0	0.1	0
<i>Astragalus</i>	0.1	0.2	0.4	0.2	0.4	0.3	0.1	0.2
Boraginaceae	0.2	0.2	0.6	1.2	0.1	0.9	0.1	1.7
Brassicaceae	0	0	0.1	0	0	0	0	0.1
<i>Brassica tournifortii</i>	0	0	0	0.1	0	0	0	0
<i>Eriogonum</i>	2.9	12.1	4.8	13.7	6.6	11.5	4.5	15.8
<i>Erodium cicutarium</i>	0	0	0	0	0	0.2	0	0
<i>Senecio</i>	0.2	0.1	0.2	0.4	0	0.2	0.2	0
<i>Sphaeralcea</i>	0.4	0	0.7	0	0.9	0.2	0.9	1.9
<i>Tidestromia oblongifolia</i>	0.2	0.4	0.1	0.2	0.3	0.3	0.1	0.2
Total forbs	4.1	13.1	7.0	15.9	8.4	13.5	5.9	19.9
Grasses	1.6	15.5	1.7	15.1	1.6	11.8	0.8	13.6
Succulents								
<i>Opuntia</i>	10.4	2.2	14.8	3.6	13.9	2.4	8.7	1.8

occurred with respect to distances to roads, catchments, and rivers and canals in winter, normalized-difference-vegetation index and distance to catchments in spring, distance to rivers and canals in summer, and slope in autumn. Those for which there was strong evidence of a large effect on distribution of mule deer and feral asses were normalized-difference-vegetation index in spring and slope in autumn. Other attributes of landscape considered in this analysis appeared to be used differently by the two species.

We identified 25 taxa of plants in diets of mule deer and feral asses, including 13 taxa of browse, 10 taxa of forbs, grasses, and cacti (*Opuntia*), and we summarized proportions in diets by 3-month quarter (Table 2). Diets of mule deer consisted primarily of browse, ranging from 76% in summer to 85% in autumn; diets of feral asses also consisted primarily of browse, but in somewhat lower proportions (65% in spring and autumn to 72% in summer; Table 2). Forbs and grasses comprised a small proportion of diet of mule deer and were never >10% in

any quarter. Diet of feral asses, however, contained larger proportions of those components; range in quarterly averages was 13–20% for forbs and 12–16% for grasses. Individual taxa of plants having a high occurrence in diets of mule deer and feral asses included ephedra (*Ephedra californica*; 9–13% for mule deer, 5–12% for feral asses), burro-weed (4–9% and 9–15%), salt bush (*Atriplex*; 12–18% and 7–11%), desert-ironwood (6–11% and 4–8%), and wild buckwheat (*Eriogonum*; 3–7% and 12–16%; Table 2).

Although there was some variation among years, there was evidence of substantial overlap in diet for summer only (Fig. 1). For 2001, high-overlap was during July–October. For other years, high-overlap spanned 2 (2000) or 3 (2002) months at the same time of year (Fig. 1). Lowest overlap in diets that occurred consistently in all years was December and March (Fig. 1).

DISCUSSION—Evidence presented here suggests limited overlap in use of habitat and diets of mule deer and feral

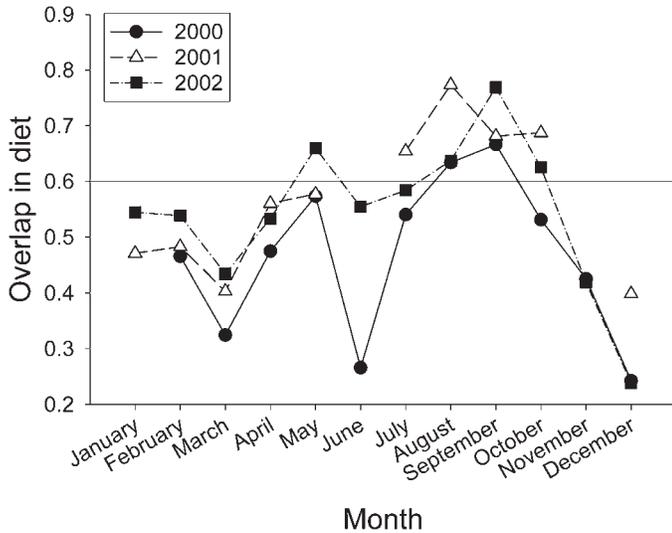


FIG. 1—Monthly overlap in diets (estimated with the simplified Morisita index) between mule deer (*Odocoileus hemionus*) and feral asses (*Equus asinus*) based on plants identified in feces. The horizontal line indicates the lower limit at which substantial overlap in diets occurred. Observations are missing for June and November 2001.

asses. For most features of landscape in most seasons, we observed mule deer to use habitat differently from feral asses. Some effects were consistent through the year; mule deer were associated with areas closer to washes in all seasons. Some effects changed by season, at times suggesting similar and at times suggesting different distributions with respect to a feature of landscape (e.g., distance to catchments or to roads). Among the seven instances indicating common use of a feature in the landscape, in only two (normalized-difference-vegetation index in spring and slope in autumn) was effect large relative to influence of other variables, and in those instances, their effect was the largest of variables considered in their respective seasons. For diet, overlap appeared minimal in three seasons, with biologically significant overlap occurring only in summer. Species of browse were far most common in diets of mule deer. Feral asses frequently used browse, but their diet contained a greater proportion of grasses and forbs. Use of browse by mule deer and feral asses varied across species of plants. Degree of similarity in use ranged from those species that showed substantially similar use in most seasons (e.g., ephedra) to those that showed heavy use by one herbivore but no evidence of use by the other (e.g., palo verde).

What conclusions about competition can come from studies of overlap in diet or habitat? Interspecific competition between sympatric herbivores presumably leads to separation of niches, which can occur via differential use of habitat, species of plants, or parts of plants (Sinclair, 1985). Thus, mechanisms that arise from interspecific competition should lead to decreases in overlap of habitat or diet (Sinclair, 1985). Low overlap

between herbivores suggests a response to past competition. However, high overlap is not necessarily evidence of competition for forage (Schoener, 1974) if, for example, the two foraging herbivores use the same species in different patches (high overlap in diet) or different species in the same patches (high overlap in habitat). Further, substantial separation in diet or use of habitat might not indicate absence of competition (Hansson, 1995). If separation is the consequence of competition, rather than a strategy to avoid it, two species with different diets or differences in use of habitat could still compete for resources.

For most factors that strongly influenced distribution of animals (i.e., had coefficients with the largest magnitude, positive or negative), there also was evidence of an interaction, also indicating that mule deer and feral asses were distributed differently with respect to the most important features of landscape. One exception was the variable slope, which had the largest coefficient in the resource-selection function for autumn, but indicated no evidence of differing use by feral asses and mule deer. Once effect of slope was accounted for in the resource-selection function, however, remaining variables suggested differing distributions with respect to distances to washes and to rivers and canals, and, thus, minimal overlap with respect to use of those resources.

Research comparing use of habitat by mule deer and feral asses is scarce in the literature. Overall patterns of use of habitat, however, support our discovery of low overlap between these species, based on separate studies of feral asses and bighorn sheep and of bighorn sheep and mule deer. Overlap in use of habitat between bighorn sheep and feral asses has been well documented (Seegmiller and Ohmart, 1981; Douglas and Leslie, 1996). Feral asses and bighorn sheep demonstrate substantial overlap in use of vegetational associations (Dunn, 1984) and characteristics of terrain, although bighorn sheep are capable of using terrain that is steeper and more rugged (Seegmiller and Ohmart, 1981).

Overlap between mule deer and bighorn sheep tends to be somewhat lower, and by extension, overlap with feral asses also should be lower. Mule deer and bighorn sheep show differing use of vegetational associations and attributes of terrain, and on average, mule deer are closer to catchments and canals (Krausman and Etchberger, 1995). Although not designed to be a comparison of use of habitat by mule deer and bighorn sheep, results of these studies suggest distinct use of landscape that reduce overlap in use of resources between bighorn sheep and mule deer. By extension, similar use of habitat between feral asses and bighorn sheep, and dissimilar use of habitat between mule deer and bighorn sheep, suggest that differing preferences for various elements of the landscape might be operating to limit overlap in use of habitat and resources between feral asses and mule deer.

In our study, high overlap in diet coincided with season

of abundant forage. As generalist herbivores, feral asses might be expected to expand diet to take advantage of both higher-quality and lower-quality forages when they become abundant in the environment (Westoby, 1974). The implication, however, is that feral asses have the capacity to vary selection of quality of forage and rate of intake according to what is available in the environment (Douglas and Leslie, 1996). Mule deer, as ruminants, are constrained to use higher-quality forage, even when it is scarce, because of metabolic requirements relative to their size (Demment and Van Soest, 1985). In contrast, however, overlap in diets appeared to be reduced when forage was less abundant (i.e., winter, spring, and autumn), suggesting that as forage becomes scarce, mule deer and feral asses focus more on resources that each is better adapted to exploit (Rosenzweig, 1981; Schoener, 1982).

In contrast to our determination of reduced overlap during periods of scarcity, an increase in overlap of diet between herbivores has been documented for other arid and semiarid regions. Guanacos (*Lama guanicoe*) and domestic sheep in Argentine Patagonia increased overlap in diet during summer, when forage was scarce (Baldi et al., 2004). Dietary overlap between Przewalski's gazelles (*Procapra przewalskii*) and domestic sheep near Qinghai Lake, China, was greatest during the annual die-back of plants in winter (Liu and Jiang, 2004). Red kangaroos (*Macropus rufus*) and domestic sheep in semiarid Australia demonstrated high dietary overlap during drought, when diets were composed largely of grasses (Dawson and Ellis, 1994). High overlap occurred between pronghorns (*Antilocapra americana*) and cattle in Colorado during seasonal scarcity of forage in winter when pronghorns foraged largely on grasses (Schwartz and Ellis, 1981).

That forbs also were more abundant in diet of feral asses could reflect either greater searching effort for forbs or incidental intake while foraging on grasses, differences between digestive efficiency of feral asses and mule deer, or differential digestibility of types of forage. Indeed, description of diets of herbivores via fecal analysis is affected by differential digestibility of parts and species of plants (Gill et al., 1983). Nonetheless, fecal analysis of diet is less invasive and more convenient than other methods (Litvaitis et al., 1996), and it is useful for providing approximate comparisons of use of classes of forage. For these reasons, this method is common in studies of diets of ungulates (Bleich et al., 1997; Krausman et al., 1997; Tarango et al., 2002) but likely is more problematic when making interspecific comparisons. Differences in differential digestibility between fore-gut and hind-gut fermenters might be a factor influencing results of analysis of overlap in diet. One might expect low-fiber forage to be under-represented in the diet of mule deer (Gill et al., 1983). Because digestion of low-fiber forage is less efficient for feral asses, effect of differential digestibility might not be as large for that species. Thus, given the

same proportion of high-quality forage in the diet, there would be a larger representation in fecal pellets of feral asses than in those of mule deer, and as a consequence, overlap in diet could be greater than our calculations indicate.

Analysis presented here suggests that mule deer usually used resources differently than feral asses. Those differences could be due to pre-existing preferences in use of habitat; they could represent outcome of recent competition (Schoener, 1974), or they could be consequences of current competition (Hansson, 1995). To evaluate which possibility is most likely, manipulations of populations of feral asses will be required to distinguish current from potential habitat of mule deer in absence of feral asses (i.e., realized and fundamental niche; Hutchinson, 1957). Fortunately, such experiments might be possible as part of existing management strategies, i.e., reductions of populations of feral asses regularly occur on some public lands in the western USA. Conducting reductions of populations of feral asses as controlled manipulations in the context of adaptive management, while monitoring responses of native ungulates, would provide experimental evidence about competitive interactions between exotic and native ungulates and inform management strategies necessary to conserve native species.

This research followed protocols approved by the California Department of Fish and Game (Jessup et al., 1986) and American Society of Mammalogists (Animal Care and Use Committee, 1998). We are grateful to two anonymous reviewers for comments on an early draft of the manuscript. This research was a cooperative effort funded by the Bureau of Land Management, California Department of Fish and Game, Desert Wildlife Unlimited, Imperial County Fish and Game Commission, and University of Arizona School of Natural Resources. We thank B. Adams, D. Anderson, J. Brana, J. Davis, D. DeJesus, S. DeJesus, T. Glenner, B. Gonzales, A. Hunter, K. Jones, J. McKeever, J. Olsen, J. J. Olsen, L. Paul, A. Pauli, B. Pierce, D. Sjastaad, T. Stephenson, F. Sutherland, P. Swift, R. Teagle, and G. Verbrugge for help in capturing animals. T. Evans provided aerial telemetry. Telemetry observers were T. Allen, L. Lesicka, R. Owen, R. Presley, and J. Van Diver; N. Andrew, G. Mulcahy, and R. Oyler provided logistical support; C. Wissler, P. Guertin, A. Honaman, and L. Konde provided computing and GIS support; S. Marsh assisted with remote-sensing data; and D. Smith conducted analyses of diets. A fellowship from the Rob and Bessie Welder Wildlife Foundation supported collection of data by JPM. This is a contribution from the California Department of Fish and Game Deer Herd Management Plan Implementation Program and is professional paper 059 from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

- ANDREW, N. G. 1994. Demography and habitat use by desert-dwelling mountain sheep in the East Chocolate Mountains, Imperial County, California. M.S. thesis, University of Rhode Island, Kingston.
- ANDREW, N. G., V. C. BLEICH, AND P. V. AUGUST. 1999. Habitat selection by mountain sheep in the Sonoran Desert:

- implications for conservation in the United States and Mexico. *California Wildlife Conservation Bulletin* 12:1–30.
- ANDREW, N. G., L. M. LESICKA, AND V. C. BLEICH. 1997. An improved fence design to protect water sources for native ungulates. *Wildlife Society Bulletin* 25:823–825.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BALDI, R., A. PELLIZA-SBRILLER, D. ELSTON, AND S. ALBON. 2004. High potential for competition between guanacos and sheep in Patagonia. *Journal of Wildlife Management* 68:924–938.
- BERGER, J. 1985. Interspecific interactions and dominance among wild Great Basin ungulates. *Journal of Mammalogy* 66:571–573.
- BLEICH, V. C., AND N. G. ANDREW. 2000. Mountain sheep, mule deer, and burros in the brush: flourishing wild burros impact habitat and native big game. *Tracks* 17:10–12.
- BLEICH, V. C., R. T. BOWYER, AND J. D. WEHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134:1–50.
- BLEICH, V. C., C. S. Y. CHUN, R. W. ANTHES, T. E. EVANS, AND J. K. FISCHER. 2001. Visibility bias and development of a sightability model for Tule elk. *Alces* 37:315–327.
- DAWSON, T. J., AND B. A. ELLIS. 1994. Diets of mammalian herbivores in Australian arid shrublands: seasonal effects of overlap between red kangaroos, sheep and rabbits and on dietary niche breadths and selectivities. *Journal of Arid Environments* 26:257–271.
- DEMMENT, M. W., AND P. J. VAN SOEST. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641–672.
- DOUGLAS, C. L., AND D. M. LESLIE, JR. 1996. Feral animals on rangelands. Pages 281–292 in *Rangeland wildlife* (P. R. Krausman, editor). Society for Range Management, Denver, Colorado.
- DUNN, W. C. 1984. Ecological relationships between desert bighorn and feral burros in Death Valley National Monument, California. M.S. thesis, University of Nevada, Las Vegas.
- DUNN, W. C., AND C. L. DOUGLAS. 1982. Interactions between desert bighorn sheep and feral burros at spring areas in Death Valley. *Desert Bighorn Council Transactions* 26:87–96.
- FRACKER, S. B., AND H. A. BRISCHLE. 1944. Measuring the local distribution of *Ribes*. *Ecology* 25:283–303.
- GILL, R. B., L. H. CARPENTER, R. M. BARTMANN, D. L. BAKER, AND G. G. SCHOONVELD. 1983. Fecal analysis to estimate mule deer diets. *Journal of Wildlife Management* 47:902–915.
- GILLIES, C. S., M. HEBBLEWHITE, S. E. NIELSEN, M. A. KRAWCHUK, C. L. ALDRIDGE, J. L. FRIAR, D. J. SAHER, C. E. STEVENS, AND C. L. JERDE. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- GINNETT, T. F., AND C. L. DOUGLAS. 1982. Food habits of feral burros and desert bighorn sheep in Death Valley National Monument. *Desert Bighorn Council Transactions* 26:81–87.
- GROSS, J. E., M. C. KNEELAND, D. F. REED, AND R. M. REICH. 2002. GIS-based habitat models for mountain goats. *Journal of Mammalogy* 83:218–228.
- HANSSON, S. 1995. Effects of exploitative food competition on food niche dynamics: a simulation analysis. *Ecological Modelling* 77:167–187.
- HORN, H. S. 1966. Measurement of “overlap” in comparative ecological studies. *American Naturalist* 100:419–424.
- HUTCHINSON, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22:415–427.
- ILSE, L. M., AND E. C. HELLGREN. 1995. Resource partitioning in sympatric populations of collared peccaries and feral hogs in southern Texas. *Journal of Mammalogy* 76:784–799.
- JANIS, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* 30:757–774.
- JESSUP, D. A., W. E. CLARK, AND M. A. FOWLER. 1986. *Wildlife restraint handbook*. Third edition. California Department of Fish and Game, Rancho Cordova.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- KIE, J. G., AND B. CZECH. 2000. Mule and black-tailed deer. Pages 629–657 in *Ecology and management of large mammals in North America* (S. Demarais and P. R. Krausman, editors). Prentice Hall, Upper Saddle River, New Jersey.
- KRAUSMAN, P. R., AND R. C. ETCHBERGER. 1995. Response of desert ungulates to a water project in Arizona. *Journal of Wildlife Management* 59:292–300.
- KRAUSMAN, P. R., AND D. M. SHACKLETON. 2000. Bighorn sheep. Pages 517–545 in *Ecology and management of large mammals in North America* (S. Demarais and P. R. Krausman, editors). Prentice Hall, Upper Saddle River, New Jersey.
- KRAUSMAN, P. R., J. J. HERVERT, AND L. L. ORDWAY. 1984. Radio tracking desert mule deer and bighorn sheep with light aircraft. Pages 115–118 in *Deer in the Southwest: a workshop* (P. R. Krausman and N. S. Smith, editors). School of Renewable Natural Resources, University of Arizona, Tucson.
- KRAUSMAN, P. R., J. J. HERVERT, AND L. L. ORDWAY. 1985. Capturing deer and mountain sheep with a net-gun. *Wildlife Society Bulletin* 13:71–73.
- KRAUSMAN, P. R., A. J. KUENZI, R. C. ETCHBERGER, K. R. RAUTENSTRAUCH, L. L. ORDWAY, AND J. J. HERVERT. 1997. Diets of desert mule deer. *Journal of Range Management* 50:513–522.
- KREBS, C. J. 1989. *Ecological methodology*. HarperCollins Publishers, New York.
- LITVAITIS, J. A., K. TITUS, AND E. M. ANDERSON. 1996. Measuring vertebrate use of terrestrial habitats and foods. Pages 254–274 in *Research and management techniques for wildlife and habitats* (T. A. Bookhout, editor). Wildlife Society, Bethesda, Maryland.
- LIU, B., AND Z. JIANG. 2004. Dietary overlap between Przewalski’s gazelle and domestic sheep in the Qinghai Lake region and implications for rangeland management. *Journal of Wildlife Management* 68:241–246.
- MANLY, B. F. J., L. L. McDONALD, D. L. THOMAS, T. L. McDONALD, AND W. P. ERICKSON. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Second edition. Kluwer Academic, Dordrecht, Netherlands.
- MARSHAL, J. P., V. C. BLEICH, AND N. G. ANDREW. 2008. Evidence for interspecific competition between feral ass and mountain sheep in a desert environment. *Wildlife Biology* 14:228–236.
- MARSHAL, J. P., P. R. KRAUSMAN, AND V. C. BLEICH. 2005a. Dynamics of mule deer forage in the Sonoran Desert. *Journal of Arid Environments* 60:593–609.
- MARSHAL, J. P., P. R. KRAUSMAN, AND V. C. BLEICH. 2005b. Rainfall, temperature, and forage dynamics affect nutritional quality

- of desert mule deer forage. *Rangeland Ecology and Management* 58:360–365.
- MARSHAL, J. P., V. C. BLEICH, N. G. ANDREW, AND P. R. KRAUSMAN. 2004. Seasonal forage use by desert mule deer in southeastern California. *Southwestern Naturalist* 49:501–505.
- MARSHAL, J. P., V. C. BLEICH, P. R. KRAUSMAN, M. L. REED, AND N. G. ANDREW. 2006*a*. Factors affecting habitat use and distribution of desert mule deer in an arid environment. *Wildlife Society Bulletin* 34:609–619.
- MARSHAL, J. P., L. M. LESICKA, V. C. BLEICH, P. R. KRAUSMAN, G. P. MULCAHY, AND N. G. ANDREW. 2006*b*. Demography of desert mule deer in southeastern California. *California Fish and Game* 92:55–66.
- MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223–449.
- PARKER, K. L. 2003. Advances in the nutritional ecology of cervids at different scales. *Ecoscience* 10:395–411.
- PIANKA, E. R. 1981. Competition and niche theory. Pages 167–196 in *Theoretical ecology: principles and applications* (R. M. May, editor). Second edition. Blackwell Scientific Publications, Oxford, United Kingdom.
- PUTMAN, R. J. 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London, United Kingdom.
- RAMSEY, F. L., AND D. W. SCHAFER. 2002. *The statistical sleuth: a course in methods of data analysis*. Second edition. Duxbury, Pacific Grove, California.
- ROSENZWEIG, M. L. 1981. A theory of habitat selection. *Ecology* 62:327–335.
- SCHOENER, T. W. 1974. Competition and the form of habitat shift. *Theoretical Population Biology* 6:265–307.
- SCHOENER, T. W. 1982. The controversy over interspecific competition. *American Scientist* 70:586–595.
- SCHWARTZ, C. C., AND J. E. ELLIS. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *Journal of Applied Ecology* 18:343–353.
- SEEGMILLER, R. F., AND R. D. OHMART. 1981. Ecological relationships of feral burros and desert bighorn sheep. *Wildlife Monographs* 78:1–58.
- SINCLAIR, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology* 54:899–918.
- SPALINGER, D. E. 2000. Nutritional ecology. Pages 108–139 in *Ecology and management of large mammals in North America* (S. Demarais and P. R. Krausman, editors). Prentice Hall, Upper Saddle River, New Jersey.
- SPARKS, D. R., AND J. C. MALECHEK. 1968. Estimating percentage dry weight in diets using a technique. *Journal of Range Management* 21:264–265.
- TARANGO, L. A., P. R. KRAUSMAN, R. VALDEZ, AND R. M. KATTNIG. 2002. Research observation: desert bighorn sheep diets in northwestern Sonora, Mexico. *Journal of Range Management* 55:530–534.
- THOMPSON, J. R., AND V. C. BLEICH. 1993. A comparison of mule deer survey techniques in the Sonoran Desert of California. *California Fish and Game* 79:70–75.
- TUCKER, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of the Environment* 8:127–150.
- VAVRA, M., AND J. L. HOLECHEK. 1980. Factors influencing microhistological analysis of herbivore diets. *Journal of Range Management* 33:371–374.
- VOETEN, M. M., AND H. H. T. PRINS. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia (Berlin)* 120:287–294.
- WALLACE, C. S. A. 2002. Extracting temporal and spatial information from remotely sensed data for mapping wildlife habitat. Ph.D. dissertation, University of Arizona, Tucson.
- WESTOBY, M. 1974. An analysis of diet selection by large generalist herbivores. *American Naturalist* 108:290–304.
- WIENS, J. A. 1989. *The ecology of bird communities*. Volume 2. Processes and variations. Cambridge University Press, Cambridge, United Kingdom.
- ZARET, T. M., AND A. S. RAND. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52:336–342.

Submitted 27 June 2010. Accepted 12 June 2011.

Associate Editor was Floyd W. Weckerly.