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Abstract—In 1975, wildlife managers reintroduced desert bighorn sheep (*Ovis canadensis mexicana*) to Tiburón Island, Mexico, where endemic mule deer (*Odocoileus hemionus sheldoni*) occur. We predicted that these species would use both mountain and plains habitats, but would have different diets, minimizing negative interspecific effects. By censusing pellet groups, we found that both ungulates occurred in both habitats, but bighorn sheep were more abundant in mountains and mule deer were more abundant in plains. Microhistological analyses determined that diets of both species consisted of the same 39 plant species, of which 13 plant species each composed ≥4% of the diet and together composed 70–80% of the total diet. Plants in low abundance represented 26–32% of diets in the mountains and 45–56% of diets in the plains. Overall diet overlap was 68% and overlap did not differ between mountains or plains, but did differ among seasons. Overlap in habitat agreed with predictions, but diet overlap was contrary to our predictions. Our results differ from studies on the mainland, which found overlap in habitat use, but not in diet. Overlap in resource use coupled with the rapid increase in abundance of bighorn sheep since their reintroduction to Tiburón may have an impact on mule deer. Additional research is needed to determine whether abundance of mule deer has changed in response to the reintroduction of bighorn sheep.

Resumen—El borrego cimarrón (*Ovis canadensis mexicana*) fue reintroducido a la isla Tiburón, México, en 1975, donde habita el venado bura (*Odocoileus hemionus sheldoni*), endémico a esta isla. Predijimos que estas especies utilizarían los hábitats de planicies y de montaña, pero que habría una diferencia en las dietas, minimizando así los efectos negativos inter-específicos. Por medio del censo de excretas, se encontró que ambos ungulados utilizaron ambos hábitats, pero que el borrego cimarrón fue más abundante en las montañas y el venado bura más abundante en las planicies. Los análisis micro histológicos determinaron que las dietas de ambas especies consistieron de las mismas 39 especies de plantas, de las cuales cada una de 13 especies comprendió ≥4% de la dieta y en conjunto comprendieron del 70–80% del total de la dieta. Las plantas con abundancia baja representaron del 26–32% de las dietas en el hábitat de montaña y del 45–56% de las dietas en las planicies. En general, el traslape de la dieta fue de 68% y no difirió entre las montañas y las planicies, pero sí difirió entre estaciones. El traslape en el hábitat concurrió con nuestras predicciones, pero el traslape en la dieta fue contrario a nuestras predicciones. Nuestros resultados difirieron de estudios en tierra firme donde se encontró traslape en el uso de hábitat, pero no en la dieta. El traslape en la dieta y el hábitat considerado en conjunto con el rápido incremento en la abundancia de borrego cimarrón desde su reintroducción a la isla Tiburón puede causar impactos negativos en el venado bura. Se necesita investigación adicional para determinar si la abundancia del venado bura ha cambiado en respuesta a la reintroducción del borrego cimarrón.

Numerous studies have investigated interactions among native ungulates, between native and introduced/feral grazers, and between native and domestic ungulates. These studies have evaluated whether overlap in resource use was sufficient to cause negative effects on co-occurring species. For example, dietary shifts during periods of high density of elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*; Stewart et al., 2011), and overlap of diets among mule deer, moose (*Alces alces*), and elk (Hodder et al., 2013) indicated a potential for competition between and among these native herbivores. Similarly, high overlap in space use and summer diet between feral asses and mule deer also suggested potential negative interactions (Marshal et al., 2012).

On the other hand, Smith et al. (1998) found little overlap in diet between pronghorn (*Antilocapra americana*) and feral horses (*Equus caballus*), indicating little potential for negative interactions.

Tiburón Island (hereafter Tiburón), the largest island in Mexico (119,875 ha; 28°59′20″N, 112°22′23″W), is located off the coast of Sonora state, in the Sea of Cortez (Colchero et al., 2009). Until recently, the primary ungulate on this island was the endemic Tiburón Island mule deer (*O. h. sheldoni*, hereafter mule deer; Weber and Gonzalez, 2003). Although it had been considered that desert bighorn sheep (*Ovis canadensis mexicana*, hereafter bighorn sheep) were not native to the island, recent evidence indicated that they were present on the island but were extirpated in the last 1,500–100 years (Wilder et al., 2014).

The reintroduction of bighorn sheep to Tiburón and their consequent population expansion has resulted in their co-occurrence with mule deer. In arid mainland habitats with vegetation similar to that on Tiburón, diets of bighorn sheep and desert mule deer (*O. h. crooki*) differ, limiting potential impacts. For example, Tarango et al. (2002) determined that the diet of bighorn sheep in northwestern Sonora was composed of 46% browse, 32% forbs, 18% succulents, and 5% grass (averaged over seasons), whereas Krausman et al. (1997) reported that the diet of desert mule deer in southwestern Arizona was primarily browse (83% averaged over seasons and years). Similarly, Krausman et al. (1989) concluded that there was no significant dietary overlap between these species in western Arizona. These results suggest that diets of bighorn sheep and mule deer should differ when they occur in the same habitats.

Both mule deer and bighorn sheep use similar habitats in the Sonoran Desert. Male mule deer prefer lowland habitats during spring and winter and prefer both lowland and mountain habitats during summer. Females prefer mountains during all seasons. Use of mountain habitats during summer by both sexes reflected availability of water during the hot season. Diets differ, with males including both mountain and nonmountain vegetation and diets of females containing only mountain vegetation. Bighorn sheep in Arizona also occupy similar habitats. Ram groups and male-female groups prefer nonprecipitous woodland and semidesert grassland often at bases of rocky cliffs, whereas ewe-juvenile groups prefer areas of steep terrain, which offer protection from predators. Rams join these groups during May–June and into the July rut season (Gionfriddo and Krausman, 1986; Ordway and Krausman, 1986).

We hypothesized that bighorn sheep and mule deer would use both mountain and plains habitats on Tiburón, but bighorn sheep would use the mountain habitat to a greater extent than mule deer and would use the plains habitat less than mule deer. Because of their use of both habitats, we further hypothesized that their diets would differ between habitats and/or among seasons. Thus, partial habitat separation coupled with dietary separation could minimize any potential negative interspecific effects. Learning whether habitat use or diet of bighorn sheep and mule deer overlap can be important to design a management plan for these ungulates.

MATERIALS AND METHODS—*Study Area*—In 1975, 20 desert bighorn sheep were reintroduced to Tiburón from western Sonora (Hedrick et al., 2001; Medellín et al., 2005). The objective was to allow their population to increase to a level that would serve as a source to repopulate the historic ranges in northern Mexico and the southwestern United States (Fulbright et al., 2001; Medellín et al., 2005; Espinosa-T. et al., 2006; Hedrick and Wehausen, 2014). By the late 1990s the population of bighorn sheep on Tiburón had increased to >800 (Medellín et al., 2005; Hedrick and Wehausen, 2014) and, to date, about 500 bighorn sheep have been translocated to repopulate historic ranges in northern Mexico (Hedrick and Wehausen, 2014).

Two mountain ranges, the Sierra Menor and the Sierra Kun Kaak, cover approximately 60% of the island (Colchero et al., 2009). These mountains are rocky with steep slopes, whereas the terrain between the mountains and from the mountains to the Sea of Cortez is a relatively flat desert plain. Climate of the island is hot and dry with an annual mean temperature of 20.5°C and an mean annual precipitation of 125.2 mm (1974–1993, Kino Bay meteorological station, Servicio Metereológico Nacional, http://smn.cna.gob.mx). Vegetation on the island is typical of the Sonoran Desert with desert scrub (e.g., *Encelia farinosa*), microphyllous shublands (e.g., *Cercidium microphyllum*, *Olneya tesota*, and *Larrea tridentata*), and cacti (e.g., *Carnegiea gigantea*, *Lophocereus schottii*, *Pachycereus pringlei*, *Stenocereus thurberi*, and *Stenocereus gummosus*; Ezcurra et al., 1987; Cody, 1989).

We established 10 transects (250 m long and 5 m wide) on Tiburón to sample pellet groups of bighorn sheep and mule deer and determine abundance of plants. Five transects were situated in the plains habitat adjacent to Sierra Kun Kaak, and five transects were placed in steep, rocky areas of the Sierra Kun Kaak. We placed the transects randomly; they were separated by ≥5 km to account for variation in abundance of pellet groups and plants across the study area.

We used data from the Kino Bay meteorological station to determine seasons on Tiburón as cold-dry (November–February; mean temperature 14.8°C, mean precipitation 11.6 mm), hot-dry (March–June; mean temperature 20.0°C, mean precipitation 1.3 mm), and hot-wet (July–October; mean temperature 26.8°C, mean precipitation 24.4 mm).

Census and Identification of Pellet Groups—We determined habitat use by bighorn sheep and mule deer by counting the number of pellet groups along each transect in the plains and mountain habitats. We sampled once in each of the months December 1996, April–May 1997, August 1997, November 1997, February 1998, and August 2000. We removed pellet groups to allow for the accumulation of new pellet groups for the next census (Wemmer et al., 1996). Distinct physical characteristics allowed us to distinguish pellet groups of bighorn sheep from those of mule deer. Compared with mule deer, pellets of bighorn sheep are shorter, wider, and conical with a blunt proximal end and a rounded or pointed distal end. Conversely, fecal pellets of mule deer are longer and narrower with both ends rounded or with one end somewhat pointed (Fig. 1; Wilder

Fɪɢ. 1—Pellets from desert bighorn sheep (*Ovis canadensis mexicana*; left group) and mule deer (*Odocoileus hemionus sheldoni*; right group) collected from Tiburón Island, Mexico. We describe distinguishing morphological features of pellets in "Materials and Methods."

et al., 2014). Using these physical characteristics, we determined that 95 of 185 pellet groups were from bighorn sheep and 90 were from mule deer.

We collected approximately 250 g from each of the 185 pellet groups identified to species, and stored each sample in a paper bag labelled with transect number and date for use with the diet analyses described (see below). Microbial decomposition can adversely affect the integrity of fecal samples (Wagner and Peek, 2006), but in the arid environment of Tiburón pellets dried quickly after deposition limiting microbial decomposition.

Vegetation Abundance—In August 2000, we used a line-intercept method to measure vegetation abundance (Mueller-Dombois and Ellenberg, 1974). We randomly placed a 100-m measuring tape in each of the five transects in the plains and mountain habitats. We first identified each plant whose base intersected the tape (taxonomic references: Felger and Moser, 1985; Gómez-Pompa and Dirzo, 1994; Rzedowski, 1994). Then we measured the basal intercept of grasses and the canopy intercept of shrubs, forbs, and succulents along the tape. We computed percent relative abundance of plant species included in the diet by dividing the total cover (i.e., sum of intercepts along all transects in each habitat) of each plant species in the diet by the total cover of all plant species in the diet and multiplying by 100.

Diet Analysis—We determined diets of bighorn sheep and mule deer using microhistological analysis. While differential digestibility may affect the accuracy of this technique, Todd and Hansen (1973) determined that differential digestibility was negligible in assessing diets of bighorn sheep, and Anthony and Smith (1974) obtained similar diet information from rumen and fecal samples of mule deer. In addition, as noted below ("Results, Diet of Bighorn Sheep and Mule Deer"), nearly all plant species in the diet were browse that likely have similar digestibility.

We selected 51 samples of pellet groups from mule deer and 54 samples of pellet groups from bighorn sheep that represented all transects and all sample dates for the diet analysis. Five fecal pellets were randomly selected from the sample of each pellet group and air-dried. After trying several mesh sizes, we ground fecal pellets through a 1-mm screen in a Wiley mill (Thomas Scientific, Swedesboro, New Jersey) because that mesh size gave us the best spread and definition of epidermal cells (Todd and Hansen, 1973). Some studies recommend treating ground samples with sodium hydroxide, bleach, or dilute nitric acid to clear the samples (Stewart, 1967; Holechek, 1982), but these treatments resulted in agglutination of our samples or loss of cell definition making identification of plant cells difficult. We obtained satisfactory results by placing fecal samples in boiling water for 30 min to remove plant pigments (Alipayo et al., 1992), and then removing the remaining water by vacuum filtration and treating the residue with 95% alcohol. We mounted samples from each fecal mixture on five slides with Permount (Fisher Scientific, Inc., Pittsburgh, Pennsylvania).

When we measured abundance of vegetation along transects, we also collected representatives of each plant species encountered. Immediately after collection, we stripped samples of epidermal tissue from plant parts (i.e., stems, leaves, flowers, fruits), mounted them on glass slides with Permount, and air-dried them. Each slide contained sufficient plant material to allow identification of epidermal cells. In the laboratory, we photographed each plant part for each plant species at $100\times$ with an Olympus 35-mm camera mounted on an Olympus compound microscope (Olympus Corporation of the Americas, Center Valley, Pennsylvania). A single observer was trained to use this photographic reference collection to identify plant species (Holechek and Gross, 1982). The trained observer used an Olympus compound microscope to view 50 systematically selected 1-mm^2 fields at $100\times$ for each fecal sample (10 fields on each of five slides; Holechek and Varva, 1981), and determined identity of plant species by comparing characteristics of epidermal cells (e.g., hairs, trichomes, guard cells, size and shape of pavement or petal cells; Glover et al., 2000) of plant species from the reference collection to epidermal cells in the fecal samples.

Data Analysis: Habitat Use by Bighorn Sheep and Mule Deer—We analyzed counts of pellet groups to assess habitat use by bighorn sheep and mule deer. We used a generalized linear mixed model with binomial error accounting for the number of bighorn sheep pellet groups relative to mule deer. We used model comparison techniques to determine whether there was a significant difference in the use of mountain and plains habitats by bighorn sheep or mule deer and also to determine whether habitat use by species differed among seasons. The full model included habitat, season, and the habitat by season interaction. We then sequentially removed this interaction as well as each individual variable, and tested the reduced models against the higher-order model using likelihood ratio tests to determine whether the removed variable was significant and should be included in the final model ($P < 0.05$). In this fashion, we arrived at a final model that contained a reduced set of significant variables. We considered transect to be a random effect for all models. To account for overdispersion in these data, we jointly modelled the mean and dispersion (McCullagh and Nelder, 1989).

Data Analysis: Diet of Bighorn Sheep and Mule Deer—We determined the number of species of browse, grass, succulents, and forbs and the percent occurrence of each plant species in diets of bighorn sheep and mule deer in mountain and plains habitats from fecal pellets collected from December 1996 through August 2000. We computed overlap between bighorn sheep and mule deer for overall diet, for diet in each habitat, and for diet in each season using Schoener's index ($O = 100[1.0 - 0.5 \sum |p_{x,i} - p_{y,i}|]$, where $p_{x,i}$ and $p_{y,i}$ represent the proportional use of diet item i by species x and species y, respectively [Schoener, 1970; Abrams, 1980]). We determined whether diet overlap between bighorn sheep and mule deer differed among seasons and habitat using a general linear mixed model with transect considered as a random effect. We began with the full model considering both terms and their interaction and then used likelihood ratio tests to identify factors that could be removed from the model. Once we arrived at a final model, we tested its significance vs. a null model containing the mean effect and the random effect, transect. We conducted post hoc tests using predicted marginal means and Tukey's HSD and based degrees of freedom on a Satterthwaite approximation. Because Schoener's index is a percentage but does not have corresponding counts, we applied an arcsine–square root transformation to the corresponding proportion to meet distributional assumptions for the analysis (Sokal and Rohlf, 2012), rather than using a binomial distribution.

We conducted all analyses in R (version 3.0.2; R Core Team 2013, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS—*Habitat Use by Bighorn Sheep and Mule Deer*—The total number of pellet groups was similar between bighorn sheep and mule deer (Table 1). The ratio of pellet groups of bighorn sheep to mule deer was greater in the mountain habitat, indicating greater use of mountain habitat by bighorn sheep (Tables 1 and 2). In addition, the ratio of pellet groups of bighorn sheep to mule deer was higher in the cold-dry season compared with the hot-dry or hot-wet season, but the ratio did not differ between the hot-wet and hot-dry seasons (Tables 1

TABLE 1—Total number of pellet groups (mean $\pm$ *SE*) of desert bighorn sheep (*Ovis canadensis mexicana*) and mule deer (*Odocoileus hemionus sheldoni*) counted on Tiburón Island, Mexico, along five transects in mountain and five transects in plains habitats. Number of pellet groups were censused in each habitat and during each season (November–February, cold-dry; March–June, hot-dry; July–October, hot-wet) between 1996 and 2000. NPG = number of pellet groups; NT = number of transects sampled.

	Deer	NPG	Sheep	NPG	NT
Total	3.00 ± 0.75	90	3.17 ± 0.87	95	60
Habitats					
Mountain	2.53 ± 0.97	53	5.53 ± 1.47	83	30
Plains	2.47 ± 1.16	37	0.80 ± 0.38	12	30
Seasons					
Cold-dry	1.10 ± 0.46	11	2.90 ± 4.38	29	30
Hot dry	1.50 ± 0.54	15	1.00 ± 0.39	10	10
Hot-wet	6.40 ± 1.72	64	5.60 ± 1.99	56	20

and 2). Mule deer and bighorn sheep did not differ in their use of habitats among seasons, i.e., the season by habitat interaction was not significant and was not included in the final model ($\chi^2 = 3.80$, $df = 2$, $P = 0.15$). The random effects variance due to transect was low ($SD = 5.243 \times 10^{-1} \pm 7.241 \times 10^{-1}$) and that attributable to jointly modelling the mean and dispersion to control for overdispersion was quite low ($1.317 \times 10^{-9} \pm 3.629 \times 10^{-5}$).

Diet of Bighorn Sheep and Mule Deer—We identified 39 species of plants in the diets of bighorn sheep and mule deer (Table 3). These plant species included 27 browse, 1 grass, 4 succulents, and 4 forbs (we could not categorize 3 diet items to type because they were keyed only to family; Table 3). The diet of bighorn sheep and mule deer contained the same number of species of browse (26), grass (1), succulents (4), and forbs (4) in the mountain habitat and in the plains (27), grass (1), succulents (3), and forbs (3) habitat. Thirteen plant species each

TABLE 2—Results of the generalized linear mixed model used to determine whether the proportion of pellet groups by species (desert bighorn sheep [*Ovis canadensis mexicana*], mule deer [*Odocoileus hemionus sheldoni*]) differed by habitat (plains, mountains) or season (November–February, cold-dry; March–June, hot-dry; July–October, hot-wet). The season by habitat interaction was not significant and was not included in the final model (see "Results"). $Z = Z$ statistic.

	Estimate	*SE*	Z	P
(Intercept)	1.310	0.523	2.509	0.01
Habitat (plains)	−1.640	0.456	−3.597	<0.01
Season effects				
Cold-dry vs. hot-dry	−1.305	0.621	−2.102	0.036
Cold-dry vs. hot-wet	−1.148	0.447	−2.567	<0.01
Hot-wet vs. hot-dry	0.640	0.514	0.304	0.761

TABLE 3—Percent relative abundance of plant species in mountain (Mt) and plains (Pt) habitats and percent occurrence of plant species in the diet of desert bighorn sheep (*Ovis canadensis mexicana*) and mule deer (*Odocoileus hemionus sheldoni*) in Mt and Pt habitats. Type: B = browse (perennial shrubs); F = forbs (annual herbaceous vegetation); G = grasses; S = succulents (cacti).

| | | % Relative abundance | | % Occurrence of plants in the diet of: | | | |
| | | | | Sheep | | Deer | |
Plant species	Type	Mt	Pt	Mt	Pt	Mt	Pt
Acacia willardina	B	10.3	2.5	1.0	2.4	2.5	1.2
Bursera hindsiana	B	0.3	0.4	1.1	0.2	0.7	0.6
Bursera laxiflora	B	0.3	0.2	0.2	0.3	0.1	0.1
Bursera microphylla[a]	B	16.1	3.7	3.8	5.1	4.8	6.7
Cardiospermum corindum	F	0.3	0.2	0.3	0.5	0.1	0.2
Carnegiea gigantea	S	0.3	0.2	0.2	1.0	0.4	0.8
Celtis ehrenbergiana[a]	B	0.3	0.2	5.3	5.3	4.5	7.7
Cercidium microphyllum	B	1.7	0.2	0.6	0.4	1.2	2.3
Colubrina viridis	B	1.8	3.9	1.0	0.8	1.8	1.2
Croton ciliatoglandulifer	B	0.3	0.2	2.0	1.4	0.5	0.1
Encelia farinosa[a]	B	0.3	2.1	3.9	2.8	3.6	5.5
Euphorbia sp. a	F	0.3	0.2	2.8	3.1	3.7	2.4
Fabaceae sp. a[a]		0.3	0.2	4.7	3.6	3.0	4.8
Ferocactus cylindraceus	S	0.3	0.2	0.3	0.7	0.2	0.2
Fouquieria splendens	B	7.6	0.2	0.3	0.6	0.4	0.1
Hyptis emoryi	B	3.5	0.7	2.0	1.6	2.1	1.5
Jacquinia pungens	B	0.3	0.2	0.1	0.1	0.2	0.1
Janusia gracilis	F	1.2	0.2	0.5	0.4	0.7	0.5
Jatropha cuneata[a]	B	2.0	0.2	10.1	7.5	12.2	7.5
Krameria grayi	B	6.6	3.0	0.7	1.8	1.2	0.8
Larrea tridentata	B	0.3	0.2	0.9	1.7	3.9	2.1
Lippia palmeri	B	4.6	1.7	0.4	1.4	1.0	0.4
Lycium californicum[a]	B	0.3	0.2	7.0	8.8	6.7	9.6
Lysiloma divaricata	B	0.3	0.2	0	0.2	0.2	0.1
Malpighiaceae sp. a		1.0	8.7	2.3	3.9	1.0	1.1
Malvaceae sp. a[a]		0.1	0.2	6.0	6.1	4.2	0.6
Melochia tomentosa[a]	B	3.7	0.2	10.0	11.0	5.6	1.9
Mimosa distachya[a]	B	3.2	0.2	10.8	10.0	6.7	9.6
Olneya tesota[a]	B	2.9	10.2	4.7	1.9	5.8	5.1
Pachycereus pringlei	S	0.3	0.2	0.1	0.3	0.3	0.1
Poaceae sp. a	G	2	17.6	1.1	1.7	1.0	1.5
Prosopis glandulosa	B	0.3	0.2	1.1	0.9	1.5	1.9
Ruellia californica[a]	B	22.3	37.3	2.2	1.7	3.4	5.6
Sebastiania bilocularis	B	0.3	0.2	0.4	0.9	0.8	0.8
Simmondsia chinenisis[a]	B	1.8	2.4	5.8	2.5	7.8	12.8
Stenocereus thurberi	S	1.2	0.2	0.1	0	0.1	0
Tabebuia impetiginosa	B	0.3	0.2	0.2	0.9	0.1	0.1
Tephrosia palmeri[a]	F	0.3	0.2	5.4	4.8	4.7	3.3
Viscainoa geniculata	B	0.3	0.2	0.7	1.1	1.4	1.5

[a] Plants that composed ≥4% of diet of bighorn sheep or mule deer in at least one habitat.

composed ≥4% of the diet of bighorn sheep and mule deer in at least one habitat (identified with a superscript "a" in Table 3). These plant species composed 79.7 and 70.3% of the diet of bighorn sheep and 73.0 and 80.7% of the diet of mule deer in the mountain and plains habitats, respectively. All of these species were browse except the forb *T. palmeri* (Table 3). Occurrence of each of the remaining 26 plant species in the diet was <4%.

In the mountain habitat, the diet of bighorn sheep contained a higher proportion of 8 of the 13 plant species composing ≥4% of the diet (*Celtis ehrenbergiana*, *Encelia farinosa*, Fabaceae sp., *Lycium californicum*, Malvaceae sp., *Melochia tomentosa*, *Mimosa distachya*, and *Tephrosia palmeri*) than were in the diet of mule deer (Table 3; Fig. 2). The remaining five species (*Bursera microphylla*, *Jatropha cuneata*, *Olneya tesota*, *Ruellia californica*, and *Simmondsia chinensis*) occurred at a higher frequency in the diet of the mule deer in the mountain habitat. In the plains habitat, the diet of mule deer included a higher proportion of 8 of the 13 plant species composing ≥4%

of the diet (*B. microphylla, C. ehrenbergiana, E. farinosa,* Fabaceae sp., *L. californicum, O. tesota, R. californica,* and *S. chinensis*) than were in the diet of bighorn sheep (Table 3; Fig. 2): Four plant species (Malvaceae sp., *Melochia tomentosa, Mimosa distachya,* and *T. palmeri*) occurred at a higher frequency in the diet of bighorn sheep in the plains habitat. Occurrence of *J. cuneata* was the same in the diet of bighorn sheep and mule deer in the plains habitat.

Overlap of plant species in the diet between bighorn sheep and mule deer was relatively high ($O = 68.25 \pm 2.87\%$), and did not differ between the mountain ($O = 68.23 \pm 4.73\%$) and plains ($O = 63.26 \pm 3.83\%$; $\chi^2 = 0.40$, $df = 1$, $P = 0.53$) habitats. Overlap was higher during the hot-wet season ($63.32 \pm 2.99\%$) than during the hot-dry season ($52.76 \pm 1.57\%$; $t = 3.41$, $df = 25$, $P = 0.01$) or the cold-dry season ($51.47 \pm 1.20\%$; $t = 3.81$, $df = 25$, $P < 0.01$). Overlap during the hot-dry season did not differ from overlap during the cold-dry season ($t = 0.40$, $df = 25$, $P = 0.92$). The habitat by season interaction was not significant ($\chi^2 = 0.59$, $df = 2$, $P = 0.75$).

Plant Abundance—Browse that each composed $\geq 4\%$ of the diet of bighorn sheep and mule deer in the mountain habitat was abundant to very abundant ($>3\%$; *B. microphylla, Melochia tomentosa, Mimosa distachya, R. californica*) or moderately abundant (1–3%; *J. cuneata, O. tesota, S. chinensis*). These plants composed 47.4% of the diet of bighorn sheep and 46.3% of the diet of mule deer (Table 3). Similarly, browse that each composed $\geq 4\%$ of the diet of bighorn sheep and mule deer in the plains habitat was abundant to very abundant (*B. microphylla, O. tesota, R. californica*) or moderately abundant (*E. farinosa, S. chinensis*). These plants composed 14.0% of the diet of bighorn sheep and 35.7% of the diet of mule deer (Table 3). Five species (three browse) plus the forb *T. palmeri* that each composed $\geq 4\%$ of the diet were low in abundance ($<1\%$) in the mountain habitat (*C. ehrenbergiana, E. farinosa,* Fabaceae sp., *L. californicum,* Malvaceae sp., and *T. palmeri*), but composed 32.3% of the diet of bighorn sheep and 26.7% of the diet of mule deer (Table 3). Seven species (five browse) plus the forb *T. palmeri* that each composed $\geq 4\%$ of the diet were low in abundance in the plains habitat (*C. ehrenbergiana,* Fabaceae sp., *J. cuneata, L. californicum,* Malvaceae sp., *Mimosa distachya, Melochia tomentosa,* and *T. palmeri*), but composed 56.3% of the diet of bighorn sheep and 45.0% of the diet of mule deer (Table 3).

DISCUSSION—We found that both bighorn sheep and mule deer occupied the mountain and plains habitats (Tables 1 and 2). However, the proportional abundance of bighorn sheep pellet groups relative to mule deer pellet groups was higher in the mountain habitat than in the plains habitat. In addition, the proportional abundance of bighorn sheep pellet groups to mule deer pellet groups was greater during the cold-dry season than during the hot-dry or hot-wet seasons, and the proportional abundance of pellet groups did not differ between the hot-dry and the hot-wet seasons (Tables 1 and 2).

Differential habitat occupancy by these ungulates could reflect responses to predators. Coyotes (*Canis latrans*) are common on Tiburón, but are ineffective predators on these ungulates (R.A.M., pers. observ.). Pregnant bighorn sheep and females with young select rugged terrain in mountain habitats where they aggressively stand their ground against coyotes and protect their young (Berger, 1991; Bleich, 1999; Mooring et al., 2003). As a result, successful predation by coyotes on young bighorn sheep is rare (Bleich et al., 1997). By contrast, mule deer in plains habitats stand their ground rather than fleeing and they confront coyotes by increasing group size with females actively protecting young (Bowyer, 1987; Bleich, 1999). Such differential responses to coyotes by female bighorn sheep and mule deer could explain the higher use of mountains by bighorn sheep, particularly during the latter portions of the cold-dry season and into the hot-dry season when females are pregnant and lambing occurs (Turner and Hansen, 1980; Goldstein and Rominger, 2011).

Availability of vernal pools also may contribute to the greater occupancy in mountain habitats by bighorn sheep. Good physical condition of pregnant and lactating bighorn sheep is attributed to access to water and high-quality browse that enables them to defend their young from predators (Bleich, 1999; Mooring et al., 2003). Because of the requirements of lactation, lactating female bighorn sheep drink water more frequently than nonreproductive females and occur closer to sources of free water (Bleich et al., 1997). Rainfall is highest on Tiburón during the hot-wet season, but vernal pools remain in crevices and under cliffs and rock formations in the mountain habitat during a portion of the cold-dry season when use by bighorn sheep is greatest.

Habitat selection by both male and female bighorn sheep also may reflect availability of high-quality food, especially browse, which has a high concentration of protein and is highly digestible (Schwartz and Hobbs, 1985; Seegmiller et al., 1990). Bighorn sheep in the Sonoran Desert select forage with a high nitrogen and moisture content, and mule deer also select habitats based upon quality and availability of forage (Marshal et al., 2006; Cain et al., 2017). Similarly, browse constitutes nearly the entire diet of bighorn sheep and mule deer on Tiburón (Table 3). Both bighorn sheep and mule deer ingest higher amounts of browse that compose $\geq 4\%$ in the diet in the habitats where their occupancy is higher—mountains for bighorn sheep and plains for mule deer (Fig. 2). Browse of low abundance composed 32.3 and 56.3% of the diet of sheep and 26.7 and 45% of the diet of deer in mountain and plains habitats, respectively. In spite of low abundance, inclusion of this browse in the
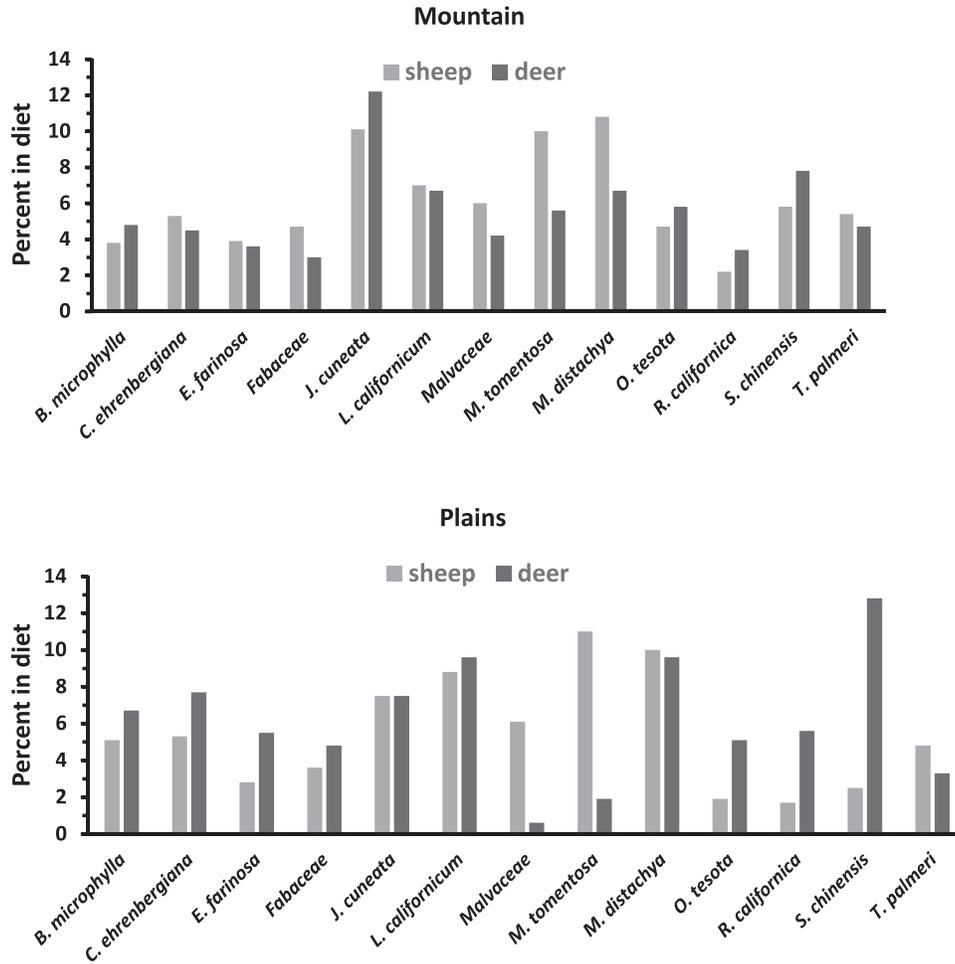
Mountain

Plains

Fig. 2—Percent occurrence in diet of 13 species of plants, each of which composed ≥4% of diet of bighorn sheep and mule deer in at least one habitat (see Table 3).

diet may reflect higher digestibility, nutrient content, or water compared with more abundant browse.

Our results agree with other studies, which also found that desert bighorn sheep concentrated their activities in higher elevations of mountains that contained rugged, steep areas (Singer et al., 2001; McKinney et al., 2003; Bangs et al., 2005; Sappington et al., 2007). The reasons given by these studies for bighorn sheep using these terrains largely agree with those we suggest: protection from predation primarily during pregnancy and rearing of offspring, increased availability of nutritious diet items (see description below), and/or seeking pools of water or shelter from high temperatures, with protection from predators being the primary reason (Smith et al., 1991; Singer et al., 2000; Bangs et al., 2005).

Our finding that bighorn sheep and mule deer coutilized the mountain and plains habitats agree with mainland studies. Mule deer and bighorn sheep in the Sonoran Desert of Arizona occur in both steep mountain terrain and lower-elevation lowlands. However, female mule deer prefer steep terrains, males prefer lowlands, and both sexes occur in mountains during summer. Male

and female bighorn sheep prefer nonprecipitous habitat and ewe-juvenile groups prefer steep terrains. Males join ewe-juvenile groups prior to the July rut (Gionfriddo and Krausman, 1986; Ordway and Krausman, 1986).

In addition to an overlap in habitat use, plant species in the diet of bighorn sheep and mule deer overlapped by 68% with no difference between habitats. In spite of this overlap, there were differences in the proportion of specific plants in the diet in different habitats suggestive of resource partitioning (Table 3; Fig. 2). Overlap in the diet also was higher during the hot-wet season, which is the rut season for bighorn sheep. Female bighorn sheep may increase ingestion of plants that also are in the diet of mule deer during this season because they contain higher concentrations of nutrients necessary for reproduction.

Our finding of a substantial overlap in diet between bighorn sheep and mule deer differs from mainland studies. For example, Tarango et al. (2002) reported that the diet of bighorn sheep (*O. c. mexicana*) in northwestern Sonora state was composed of 44% browse, 37% forbs, 14% succulents, and 6% grass, whereas Krausman et al. (1997) found that the bulk of the diet (83%) of desert

mule deer in southwestern Arizona was browse. Such a divergence in diets between these ungulates suggests limited diet overlap and supports the conclusion of Krausman et al. (1989) that there was no significant overlap in diet between desert bighorn sheep and desert mule deer in western Arizona.

These studies were conducted in arid environments similar to Tiburón, and the study of diets of bighorn sheep by Tarango et al. (2002) was located about 140 km from Tiburón in an area with a rugged, steep, rocky topography similar to the mountain habitat on Tiburón. One possibility for a higher diet overlap on Tiburón is that abundance of diet plants may differ between study sites on Tiburón and on the mainland, which in turn, could affect diet composition. Another difference between our study and those on the mainland may be that there are fewer succulents on Tiburón, and consequently, succulents may represent a smaller amount of the diet of bighorn sheep and mule deer than on the mainland.

Presence of predators may also affect behavior, habitat use, and diet composition of ungulates. For example, guanacos (*Lama guanicoe*) form groups and move to areas of high vegetative cover to modulate risk of predation (i.e., poaching; Cappa et al., 2017). The Mongolian saiga antelope (*Saiga tatarica*) moves to areas with sufficient forage for lactating females and with sufficient dense cover to decrease exposure to predators (Buuveibaatar et al., 2014). Bighorn sheep also minimize exposure to predators by using steeper mountainous terrain (Gionfriddo and Krausman, 1986; Berger, 1991). When wolves moved back into the Greater Yellowstone ecosystem in 1995 after a 50-year absence, elk shifted their habitat use, avoiding open areas where wolves often hunt (Creel et al., 2005; Mao et al., 2005).

One major difference between mainland study sites and our study site is the absence of mountain lions on Tiburón which prey on bighorn sheep and mule deer on the mainland (Krausman et al., 1989; Cashman et al., 1992; Cunningham et al., 1999; McKinney et al., 2006). An unresolved question is whether mountain lions occupied Tiburón along with bighorn sheep and both were extirpated ~1,500–100 years ago (Wilder et al., 2014). If so, the overlap in habitat use and diet between bighorn sheep and mule deer on Tiburón that we detected may reflect predator release. Hence, bighorn sheep and mule deer on Tiburón face a similar predator environment (i.e., lack of mountain lions) as the Yellowstone elk herd faced from 1926 to 1995. In the absence of mountain lions on Tiburón, abundance of mule deer likely increased in the mountain habitat and abundance of bighorn sheep likely increased in the plains habitat. As a result, we found substantial overlap in diet and habitat between these ungulates. If mountain lions were present on Tiburón, overall density of mule deer and bighorn sheep likely would decline. Then, bighorn sheep would primarily occupy the mountain habitat and mule deer would primarily occupy the plains habitat, habitats to which they are adapted. In these habitats, they would stand a better chance of warding off mountain lions and overlap in habitat and diet would decrease.

Our hypothesis of habitat overlap between bighorn sheep and mule deer was confirmed especially in the mountain habitat. However, contrary to our hypothesis of dietary separation we found significant overlap in diet composition between mule deer and bighorn sheep on Tiburón. This result is especially noteworthy because abundance of bighorn sheep has increased on Tiburón (latest estimates >800; Hedrick and Wehausen, 2014) since their introduction in 1975. Depending on abundance of plants that comprise the diet of mule deer and bighorn sheep, especially those plants that comprise the bulk of their diet, a continued increase in abundance of bighorn sheep could negatively affect endemic mule deer, especially when proportional abundance of bighorn sheep is high during the cold-dry season and when diet overlap is high during the hot-wet season. To fully understand the impact of coutilization of resources on Tiburón, it will be important to ascertain whether abundance of mule deer has declined as a result of the introduction of bighorn sheep. Future studies should monitor the abundance of both ungulates and continue to assess their habitat use and diet. These would be important elements of a plan to conserve the endemic mule deer.

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