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ECOLOGICAL RELATIONSHIPS BETWEEN MULE DEER AND WHITE-TAILED DEER IN SOUTHEASTERN ARIZONA¹

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Abstract. Niche relationships between the desert mule deer (*Odocoileus hemionus crooki*) and Coues white-tailed deer (*Odocoileus virginianus couesi*) were studied in the San Cayetano and Dos Cabezas mountains in southeastern Arizona from September 1969 to March 1972. Walk transects were established on the study areas on which deer were observed. Altitude, slope exposure, and habitat selection were used to describe distributional patterns of the two species. Food habits were studied by analyzing fecal samples microscopically for epidermal fragments of important forage plants. Behavioral interaction between mule deer and white-tailed deer, browse utilization on *Cercocarpus breviflorus*, and recruitment were also investigated.

Spatial distributions according to altitude and slope exposure indicated that a "buffer" zone existed between populations of mule deer and white-tailed deer in the San Cayetano Mountains. Mule deer were associated with fewer vegetational types than white-tailed deer on this study area; *Prosopis juliflora* and *Fouquieria splendens* were indicative of mule deer habitat. White-tailed deer utilized a greater diversity of vegetational types in the San Cayetano and did not appear to be associated with any particular plant species, although *Quercus oblongifolia*, *Dasyllirion wheeleri*, and *Eysenhardtia polystachya* were important. The most important forage plants for white-tailed deer in the San Cayetano Mountains were *E. polystachya*, *Eriogonum wrightii*, *Krameria parvifolia*, and *Fendlera rupicola*. Similarly, the primary food items of mule deer were *E. polystachya*, *Calliandra eriophylla*, and *K. parvifolia*. There was much overlap in food preferences of mule deer and white-tailed deer (55% to 67% seasonally) particularly on *E. polystachya* and *K. parvifolia*.

Populations of mule deer and white-tailed deer were sympatric in the Dos Cabezas Mountains; the coefficients of association were highly positive. There was also a great similarity in habitat selection between the two species. Both species were associated with those habitat types dominated by *Quercus emoryi*, *Juniperus deppeana*, *C. breviflorus*, *Quercus gambelii*, *Nolina microcarpa*, *Symphoricarpos ereophilus*, and/or *Bouteloua* spp. White-tailed deer displayed a greater preference for the *Quercus-Symphoricarpos* and *Quercus-Cercocarpus* habitat types than mule deer, whereas *Juniperus-Cercocarpus* habitats were preferred more by mule deer. Food habits of mule deer and white-tailed deer were very similar; all plant species important to white-tailed deer were also important to mule deer. The most frequent forage plants, in order of importance, were *C. breviflorus*, *E. wrightii*, *J. deppeana*, and *Q. gambelii*. Recruitment to the population was higher for mule deer than for white-tailed deer. Utilization of the annual leader growth on the key browse plant (*C. breviflorus*) was extremely high.

Mule deer were dominant over white-tailed deer in all behavioral interactions observed during the study. In half of these instances, mule deer displayed aggressive threat in asserting their dominance; the rest were of a passive nature.

The low coefficients of distributional overlap and high indices of overlap in food habits for the San Cayetano Mountains lead us to conclude that mule deer and white-tailed deer competitively exclude each other. The high overlap in spatial distributions, habitat selection, and food habits coupled with the high utilization of the key forage plant (*C. breviflorus*) in the Dos Cabezas Mountains during the winter months lead to the conclusion that direct competition between the two species probably was occurring during that time. This direct competition can be explained on the basis that it is a temporary phenomenon. It is hypothesized that the factors that have brought mule deer and white-tailed deer into direct competition in this area have been vegetational changes, livestock overgrazing and/or range fire suppression.

Key words: Arizona; Artiodactyla; behavioral interactions; competitive exclusion; interspecific competition; niche relationships; *Odocoileus*.

INTRODUCTION

The desert mule deer (*Odocoileus hemionus crooki*) is one of the primary herbivores of the desert shrub habitats in southern Arizona. According to Hoffmeister (1962), desert mule deer inhabit those areas south of the Gila River in Arizona and extend 650 to 800 km

south into Mexico and east into New Mexico. This subspecies is associated primarily with the desert shrub and desert grassland life zones, and, in some areas, its range extends into the chaparral vegetation. The Coues white-tailed deer (*Odocoileus virginianus couesi*) has been reported from north of the Mogollon Rim in the upper Verde River and San Francisco Peaks in northern Arizona (McCulloch 1967), from Organ Pipe National Monument east to western New Mexican and south onto Sonora, Mexico (Hoffmeister

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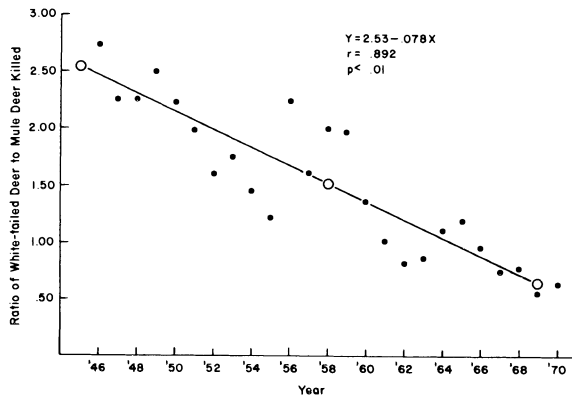


FIG. 1. Ratio of white-tailed deer to mule deer killed (bucks only) in southeastern Arizona (Management Units: 29, 30, 31, 32, 33, 34, 35, and 36) from 1946 to 1970. These data were taken from the Arizona Game Management Data Summary published annually by the Arizona Game and Fish Department.

1962). It is associated with the desert grassland, oak woodland, chaparral, and coniferous forest life zones characteristic of the higher elevations. Coues white-tailed deer are also subjected to the severity of the desert environment in the lower parts of its range.

Local distributions of mule deer and white-tailed deer are closely associated in many areas and overlap considerably in others. The transition between mule deer and white-tailed deer populations may be as low as 900 m or as high as 1,800 m in elevation, depending on the mountain area. The net effect from an aerial viewpoint is islands of white-tailed deer habitat surrounded by a sea of mule deer range. Generally, no gap exists between mule deer and white-tailed deer populations which are often microsympatric in narrow zones between each of their populations.

Reports by biologists, ranchers, hunters, and long-time residents of Arizona suggest that desert mule deer have extended their range substantially in various parts of southeastern Arizona during the past 25 yr or more. Range extension of desert mule deer usually has been to areas previously inhabited by Coues white-tailed deer. During this time, white-tailed deer have disappeared or declined drastically from the Black Hills, Reddington Pass, and the Tucson, Winchester, Tortolita, and Picacho mountains. Documentation of this alleged change in distributions of mule deer and white-tailed deer is very difficult, but the annual kill records published by the Arizona Game and Fish Department appear to substantiate the change. The ratio of white-tailed deer to mule deer killed in southeast Arizona has declined significantly ($r = -.89$, $P < .01$) since 1946 (Fig. 1). Mortality due to hunting has probably not influenced the shift in the ratio because there is considerable evidence that mule deer are more vulnerable to hunting than white-tailed deer (Bailey 1936; Peabody and Hlavachick 1968; Havel and Menzel 1969; Kramer 1971).

In view of the history of mule deer and white-tailed deer distributions, their occasional overlapping populations and their morphological, physiological, and ecological similarities, we hypothesized that interspecific competition could occur between desert mule deer and the Coues white-tailed deer. If so, it acts as a limiting factor to white-tailed deer populations. Martincka (1968) surveyed the habitat relationships of white-tailed deer and mule deer, and Kramer (1973) studied the interspecific behavior and dispersion of these species in the Northwest. To the best of our knowledge, interspecific competition between mule and white-tailed deer has not been studied directly.

Cameron (1971), Grant (1969, 1971), Murie (1971), Morris (1969), Koplin and Hoffman (1968), Sheppe (1967), and Caldwell (1964) have studied the niche relationships of various pairs of small mammals. The niche relationships between large mammalian herbivores have received little attention. Papers by Kramer (1973), Mackie (1970), Martincka (1968), Morris and Schwartz (1957), Cowan (1947), and Cliff (1939) are the only studies on North American species that relate to the topic. Numerous studies have revealed the occurrence of competition between ungulate populations and livestock, but these relationships are unnatural in an evolutionary sense. Interspecific competition in these situations, therefore, is to be expected.

In this paper, we will refer to interspecific competition as the act of 2 species seeking the same space and food (exploitation), which are in short supply, or interacting in such a way that their growth and survival are affected (interference). The purpose of this study was to investigate the niche relationships of 2 large and mobile mammalian species, mule deer and white-tailed deer by: (1) quantifying spatial distributions, habitat selection and food habits of mule deer and white-tailed deer where they coexisted; (2) studying behavioral interactions of the 2 species in these areas; and (3) investigating vegetative characteristics pertinent to niche relationships of the 2 species.

THE STUDY AREAS

Field research for this project was conducted in the San Cayetano and Dos Cabezas mountains. These areas were chosen according to 2 primary criteria: deer densities had to be large enough to facilitate numerous observations, and populations of mule deer and white-tailed deer had to be closely associated.

The San Cayetano Mountains are ≈ 16 km north of Nogales, Arizona, and occupy ≈ 21 km² of mountainous country. The climate is hot and dry with most of the precipitation occurring during August and September. Mean annual temperature at the Tumacacori National Monument (≈ 8 km from the study area) is 18.8°C, and average annual precipitation is 35.9 cm. This relatively small mountain mass rises abruptly from the surrounding, rolling hills at an elevation of 1,200 m to a height of 1,800 m. Most of the preferred

deer habitat was between 1,370 and 1,680 m in elevation, because the areas below 1,370 m were severely overgrazed by livestock. Three vegetational zones did occur in this mountain area: (1) upper desert shrub; (2) desert grassland; and (3) oak woodland. The desert shrub areas appeared to be disclimax communities because most of these habitats were originally desert grassland. Mesquite (*Prosopis juliflora* var. *velutina*) had invaded these areas and was the dominant species. Ocotillo (*Fouquieria splendens*) and many cactus species frequently occurred as codominants with mesquite. *Calliandra eriophylla* and *Krameria parvifolia* were prominent low-growing shrubs and were major sources of food to deer. *Bouteloua curtipendula* and *Bouteloua chondrosiodes* were the dominant grass species.

The desert grassland zone comprised the majority of the mountain area. *Bouteloua curtipendula*, *B. chondrosiodes*, *Lycurus phleoides*, *Andropogon cirratus*, and *Heteropogon contortus* were the most abundant grass species. A variety of other plants were associated with these grasses depending on altitude, slope exposure, and soil type. These species were *Nolina microcarpa*, *Eysenhardtia polystachya*, *Eriogonum wrightii*, *K. parvifolia*, *C. eriophylla*, *Dasyllirion wheeleri*, *Agave schottii*, *F. splendens*, and *Opuntia* spp.

Remnants of the oak woodland were found on the north-facing slopes at the higher elevations with Mexican blue oak (*Quercus oblongifolia*) the dominant species. The following plants were often associated with the oaks: *Fendlera rupicola*, *N. microcarpa*, and *D. wheeleri*. The most frequent grass species are *B. curtipendula* and *L. phleoides*. Many herbs and annuals can be found in this zone after the summer rains.

The Dos Cabezas Mountains are southeast of Willcox, Arizona, and comprise ≈ 129.5 km² of mountainous terrain. This area has a cooler, moister climate than the San Cayetano Mountains, and a higher percentage of the annual precipitation occurs during the winter months. The mean annual temperature at Willcox, ≈ 24 km away, is 15.0°C with an average annual precipitation of 28.9 cm. The elevation of the surrounding flatlands ranges from 1,370 to 1,525 m, and the highest portions of the mountain are around 2,400 m. Livestock use was heavy throughout most of the area. Deer densities were highest between 1,800 and 2,290 m in elevation, and mule deer and white-tailed deer occurred throughout these areas.

Three vegetational zones were recognized in the Dos Cabezas study area: (1) desert grassland; (2) mixed oak-woodland chaparral; and (3) deciduous oak. Many habitat types within these vegetational zones were recognized, but only eight were used extensively by deer. The *Nolina-Bouteloua* association was the major habitat type in the desert grassland. *Nolina microcarpa* and *B. curtipendula* were the dominant species, and *Bouteloua gracilis*, *E. wrightii*, and

A. cirratus were usually associated with these dominants. This habitat type was restricted to south-facing slopes above an elevation of 1,830 m.

Four of the habitat types in the mixed oak-woodland chaparral zone were dominated by *Quercus emoryi* with *N. microcarpa*, *C. breviflorus*, and/or *Juniperus deppeana* as codominants. Four other species (*E. wrightii*, *B. gracilis*, *B. curtipendula*, and *L. phleoides*) were associated with the dominants with varying importance. *Quercus hypoleucoides* occasionally replaced *Q. emoryi* as a codominant in the above habitat types where microclimatic conditions were slightly cooler and moister. The *Cercocarpus-Nolina* habitat type appeared indicative of areas of shallow soil over limestone bedrock as reported by Whittaker and Niering (1968) for the Santa Catalina Mountains. *Eriogonum wrightii* and *B. gracilis* were usually associated with the two dominants in this habitat type. The *Juniperus-Cercocarpus* habitat type was widely distributed with *Cercocarpus breviflorus* and *Juniperus deppeana* as codominants. *Nolina microcarpa*, *E. wrightii*, *B. gracilis*, and *L. phleoides* were commonly associated with the dominants.

The last habitat type (*Quercus-Symphoricarpos*) was found only at higher elevations on north-facing slopes and was part of the deciduous oak zone. Gambel's oak (*Q. gambelii*) and mountain snowberry (*Symphoricarpos oreophilus*) are the dominant species. *Holodiscus dumosus*, *Ptelea angustifolia*, and/or *Robinia neomexicana* were often associated with the dominant species. This habitat type was indicative of those microclimates having the coolest and moistest conditions on the mountain.

METHODS AND MATERIALS

Field techniques

Fieldwork was conducted on the study areas from August 1969 to March 1972. Surveys on foot were carried out in areas where both white-tailed deer and mule deer could be located simultaneously. Once located, the species was identified and the sex-age classifications were recorded. The dominant vegetation of the immediate area around the deer was also recorded. Altitude of the location of deer was determined with topographic maps and/or an altimeter and slope exposure by a compass. When mule deer and white-tailed deer were located within 45 m of each other, notes were taken on any behavioral interactions observed. Fresh fecal samples were collected for microscopic analysis of food habits and each sample was identified as mule deer or white-tailed deer by observations or by backtracking known species of deer to fresh samples. Some observations were made by vehicle, but these observations were generally unsatisfactory because deer usually fled from vehicles and the rugged terrain precluded vehicular travel in most parts of the study area.

Habitat selection of deer was characterized by not-

ing the dominant plant species in the immediate vicinity of the deer observed. These areas varied in size from a minimum of ≈ 1 hectare to as large as 50 hectares and were designated as "habitat types" or "vegetational types" depending on the nature (i.e., successional status, homogeneity, and repeatability) of the plant community. A habitat type may be thought of as a climax or a disclimax plant community (determined by climatic, edaphic, and/or topographic factors) which is homogeneous as to dominants in all layers, highly discontinuous, and repeated throughout the landscape (Daubenmire 1968). The term vegetational type was used somewhat synonymously with habitat type, but it was applied to those plant communities, which were not climax, homogeneous, or repeated throughout the landscape. A number of habitat types may occur within one vegetational zone. Daubenmire (1968) gave a more detailed discussion of the terminology used in classification of plant communities. Classification of plant communities during this study was carried out by general reconnaissance methods. All plant species mentioned have been identified according to the nomenclature set forth by Kearney and Peebles (1964).

Key forage plants were sampled in the Dos Cabezas Mountains to estimate the percentage of the annual growth that had been utilized by deer and cattle. These surveys were carried out in late winter and early spring and followed the procedure described by Cole (1956). Plants were sampled randomly along a compass or contour line. Utilization of annual growth by herbivores was estimated by recording use in one of seven categories: 0–10, 10–25, 25–50, 50–75, 75–90, and 90–100% use. Form class, age-class, availability, and distance between random step and plant were also recorded on a standard field form. Surveys of *Quercus* spp. were conducted for estimation of age composition, successional status, and vigor. Slope exposure, altitude height, and percentage decadence were recorded for each plant sampled. These plants were selected by Cole's (1956) technique as described above.

Laboratory techniques

The only feasible technique for securing adequate samples for studying food habits of mule deer and white-tailed deer throughout the year was microscopic fecal analysis. Because every plant species has unique cuticular characteristics, and most plant cuticles are not digested in ruminant digestive processes, forage plants can be identified microscopically in fecal samples of grazing or browsing herbivores (Martin 1955; Adams 1957; Hercus 1960; Storr 1961; Stewart 1965, 1967; Stewart and Stewart 1970). Epidermal characters have been used to study herbivorous habits of waterbuck (Kiley 1966), pocket gophers (Myers and Vaughan 1965), African game species (Stewart 1967), deer (Zyznar and Urness 1969, Anthony and Smith 1974), red fox (Scott 1941), and small mammals

(Meserve 1976). The use of this technique requires the preparation of a reference slide collection, and collection, preservation, and preparation of fresh fecal samples.

Reference slides were prepared from fresh leaves of deer forage plants by the method of Storr (1961). Because the abaxial and adaxial surfaces of leaves usually display different cuticular characteristics (Stewart 1965), slides were prepared of both leaf surfaces of each plant species. Fecal samples were collected in the field and preserved in formal acetic acid (85 parts 70% alcohol, 10 parts 40% formaldehyde, and 5 parts glacial acetic acid) until they could be prepared for analysis. Four pellets from each sample were fragmented in a blender and prepared according to procedures described by Stewart (1967).

From each prepared fecal sample, subsamples were spread out on slides under 22-mm² cover slips. These subsamples were acquired by stirring the sample thoroughly and removing several drops of the solution with an eye dropper. A couple of these drops were added to the slide under the cover slip. Five slides (subsamples) were analyzed for each sample by traversing the slide systematically. For each slide analyzed, the presence of each species was tabulated, and the percentage of the total recognizable cuticular fragment that each species contributed was estimated. Estimation of this percentage was carried out by placing each species' contribution into one of six categories: 0–5, 5–25, 25–50, 50–75, 75–95, and 95–100%. The midpoint of each of these ranges was used as the percentage contribution of each species to the total recognizable cuticular fragments in each subsample. An average of the five subsamples for each plant species was used as an estimate of the percentage of the deer diet that a particular plant species contributed. The importance of each plant species to mule deer and white-tailed deer diets was ascertained by averaging percentages of each plant species' contribution for each sample over the total number of samples for a particular season of the year. For further discussions on procedures, advantages, and biases in the use of microscopic fecal analysis to study herbivore diets, see Anthony and Smith (1974) and Stewart (1967).

Statistical techniques

The statistical design used to test for differences in the number of plant species identified in each fecal sample with respect to deer species and season of the year was an analysis of variance with a 2×6 factorial experiment (Steel and Torrie 1960). Because there were unequal sample sizes for each species by season category, the least-squares method of fitting parameters was used for the analysis (Graybill 1961). The model is mixed with species of deer (*A*) fixed, season (*B*) fixed, and subsamples (*e*) or samples within each species by season category, random. The model is

$$Y_{ijk} = u + A_i + B_j + (AB)_{ij} + e_{ijk}.$$

In this study, it was necessary to calculate indices of overlap in spatial distributions, habitat selection, and foot habits of mule deer and white-tailed deer for different seasons of the year. Since data on these parameters were percentages, the calculation of these indices was very simple. For example, if the mule deer diet consisted of 15.5% *Eysenhardtia polystachya* and that of white-tailed deer 7.2% or *vice versa*, then the overlap, Y_i on *Eysenhardtia polystachya* would be 7.2%. The total overlap in food habits for a particular season was calculated as the sum of the overlaps,

$$\sum_{i=1}^n Y_i,$$

for each individual plant species utilized during that time period where n equals the total number of plant species utilized. This same approach was used for the indices of overlap in spatial distributions and habitat selection. These indices should be treated as single measurements rather than as estimates of population parameters, for little is known about the statistical distributions of these measurements, and statistical inferences cannot be made concerning them (Oriens and Horn 1969). Coefficients of species association were calculated on spatial distributions of mule deer and white-tailed deer. The formula used is that of Whitaker and Fairbanks (1958) as modified by Southwood (1966)

$$I_{ai} = 2[J_i/(A + B) - 0.5],$$

where J_i is the number of individuals of species A and B in samples where both species occur, A is the number of individuals of A , and B is the number of individuals of B . This coefficient ranges from -1 (repulsion) to $+1$ (complete association) and takes into account the number of individuals of each species.

CONTIGUOUS ALLOPATRY: SAN CAYETANO MOUNTAINS

Relationships between mule deer and white-tailed deer were studied in the San Cayetano Mountains from August 1969 to January 1972. During that time, 828 deer were observed, of which 584 were white-tailed deer and 244 were mule deer. The 584 white-tailed deer were observed in 252 different groups or 2.3/group. The 244 mule deer were observed in 65 groups or 3.8/group.

Spatial distributions

White-tailed deer were observed primarily at the higher elevations throughout the study; only a few were found in the desert shrub vegetational zone (Fig. 2). The desert grassland and oak-woodland zones both received comparable use by white-tailed deer. Mule deer were found mainly at the lower elevations in the desert shrub and desert grassland zones, but they were occasionally observed in the oak woodland (Fig. 2). Distributions of mule deer were not precisely deter-

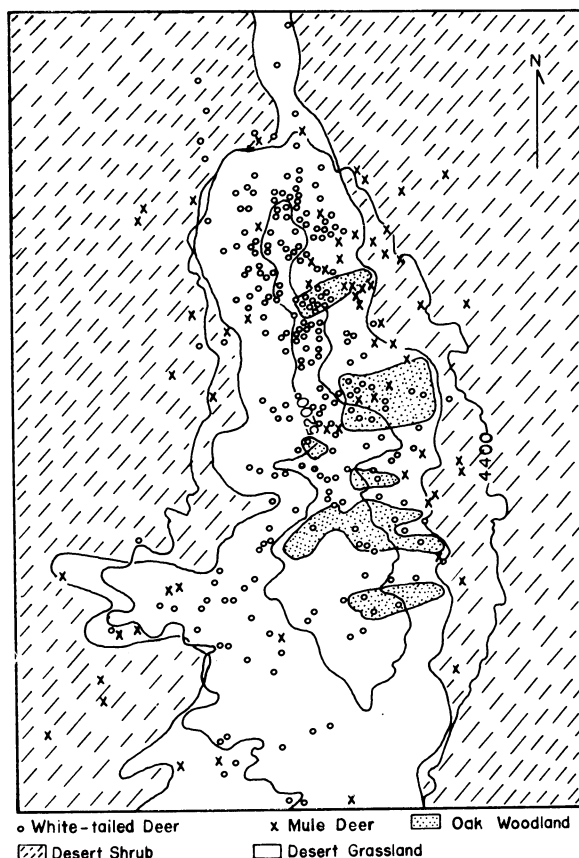


FIG. 2. Distributional patterns of mule deer and white-tailed deer in relation to altitude and vegetational zone in the San Cayetano Mountains. Each circle and cross represent a sighting of a group of white-tailed deer and mule deer, respectively, and not individual deer.

mined by altitude nor vegetation. In some parts of the study area, they were found at higher elevations associated with the more mesic vegetation; in other parts they were observed predominantly at the lower elevations in the xeric vegetation. Overlap in the distributions of mule deer and white-tailed deer occurred primarily in the desert grassland zone, and there was some overlap in specific areas of the oak woodland. The data in Fig. 2 represent a compilation of information over all seasons for the duration of the study, so actual overlap in spatial distributions is misrepresented.

Because there were seasonal changes in use of various slope exposures and altitudes, data were presented on a seasonal basis: the cool, dry period (February to April); the hot, dry period (May to July); the hot, wet period (August to October); and the cool, wet period (November to January). Spatial distributions of mule deer and white-tailed deer for the cool, dry period (February to April) are based on 110 and 56 white-tailed deer and mule deer observations, respectively (Table 1). Both used northerly slopes exten-

TABLE 1. Percentages of mule deer (MD) and white-tailed deer (WT) observed at the various slope exposure-altitude intervals in the San Cayetano Mountains (1969–1971)¹

Altitude interval (m)	Deer species	Slope exposure ²						
		S	SW	SE	Ne	NW	NE	N
February to April								
1,600–1,750	WT					7.3	4.6	13.8
	MD							
1,444–1,599	WT	.9	4.6	11.0	.9	13.8	18.3	8.3
	MD	1.8					1.8	16.1
1,295–1,443	WT	.9		.9	3.7		2.8	8.3
	MD						28.6	44.6
1,143–1,294	WT							
	MD				7.1			
May to July								
1,600–1,750	WT	.6	9.2	3.1	3.1	9.8	8.0	1.2
	MD					5.7		
1,444–1,749	WT	1.8	9.8	4.3	.6	11.7	11.0	4.3
	MD		2.9		2.9		5.7	5.7
1,295–1,443	WT		4.9		3.7	6.1		
	MD		5.7	8.6	17.1			
1,143–1,294	WT		1.2		3.1	1.2		1.2
	MD		17.1	2.9	22.9	2.9		
August to October								
1,600–1,750	WT	1.9	6.5	2.6	3.2	8.4	1.3	5.8
	MD							
1,444–1,799	WT		3.9	10.4	3.9	18.8	8.4	11.0
	MD		1.5	13.6			6.1	16.7
1,295–1,443	WT		2.6	3.9		1.9	1.3	2.6
	MD			4.5	25.8		18.2	4.5
1,143–1,294	WT							1.3
	MD				9.1			
November to January								
1,600–1,750	WT	.6	.6	6.3	1.9	6.3	5.1	
	MD							
1,444–1,749	WT	1.2	20.8	8.2	4.4	13.9	8.2	7.6
	MD		9.2	10.3	16.1		10.3	
1,295–1,443	WT	1.9	5.1	1.2		3.8	.6	
	MD	2.3	3.4	10.2	14.9			
1,143–1,294	WT							
	MD	5.7	2.3	2.3	12.6			

¹ Percentages for each season and species are independent (i.e., percentages for white-tailed deer during February–April add to 100%).

² S = south, SW = southwest, SE = southeast, Ne = neutral, NW = northwest, NE = northeast, N = north.

sively; 77% of white-tailed deer and 91% of mule deer observations were from these slopes. South-facing slopes were not used much during this period. There was 22% overlap between their distributions only on north- and northeast-facing slopes at elevations between 1,295 and 1,600 m.

Spatial distributions of mule deer and white-tailed deer for the hot, dry season (May to June) are based on 163 white-tailed deer and 35 mule deer observations. The total overlap for this period was 33.3%. Mule deer

were extremely hard to find during May, June, and July; they apparently became predominantly nocturnal in those months and spent the daylight hours bedded in the mesquite thickets. Most deer observations for that period were made on southwest, neutral, and northwest slopes; and overlap between the two species occurred only on those slopes (Table 1). Overlap was again in the 1,295- to 1,600-m range in elevation.

During the hot, moist months (August, September, and October) the overlap between mule deer and white-tailed deer distributions was the greatest, 36.8% (Table 1). For these months, 154 and 66 observations of white-tailed deer and mule deer, respectively, were made. Overlap for this period occurred on the southeast-, northeast-, and north-facing slopes between 1,295 and 1,600 m. Mule deer used these slopes plus neutral exposures, while white-tailed deer used all exposures equally, except the south-facing slopes.

Spatial distributions of mule deer and white-tailed deer for the cool, damp months of November, December, and January are based on 158 observations of white-tailed deer and 87 of mule deer (Table 1). Overlap between mule deer and white-tailed deer was also moderate during this period, 36.5%. White-tailed deer used all slopes approximately equally, but mule deer used the south-facing and neutral slopes more extensively (89.7%).

Coefficients of species association calculated for the above data are as follows: February to April, +.191; May to July, +.121; August to October, −.038, and November to January, +.09. These coefficients indicate that there is little association (no attraction or repulsion) between mule deer and white-tailed deer in the San Cayetano Mountains for all seasons. Populations of these species are contiguously allopatric because they overlapped only slightly (Fig. 2), and indices of association indicate no attraction or repulsion.

Habitat selection

Many types of dominant vegetation were recognized during the study, but only the following were significant to deer distributions in the San Cayetano Mountains: *Quercus-Fendlera*, *Quercus-Nolina-Dasyllirion*, *Quercus-Bouteloua*, *Dasyllirion-Nolina*, *Dasyllirion-Bouteloua*, *Nolina-Bouteloua*, *Dasyllirion-Eysenhardtia*, *Bouteloua-Andropogon*, *Fouquieria-Eysenhardtia*, *Fouquieria-Bouteloua*, *Prosopis-Quercus*, *Prosopis-Agave*, *Prosopis-Eysenhardtia*, *Fouquieria-Dasyllirion*, *Prosopis-Fouquieria*, *Eysenhardtia-Bouteloua*, *Fouquieria-Opuntia*, and *Fouquieria-Calliandra*. These vegetational types were used in excess of 5% for at least 1 season.

Although mule deer were found predominantly (84%) in the *Prosopis* dominated vegetational types from February to April (Fig. 3), they were also observed in the *Quercus-Dasyllirion-Nolina* habitats (16%). White-tailed deer displayed a marked preference for those habitats composed of *Quercus*, *Dasyllirion*,

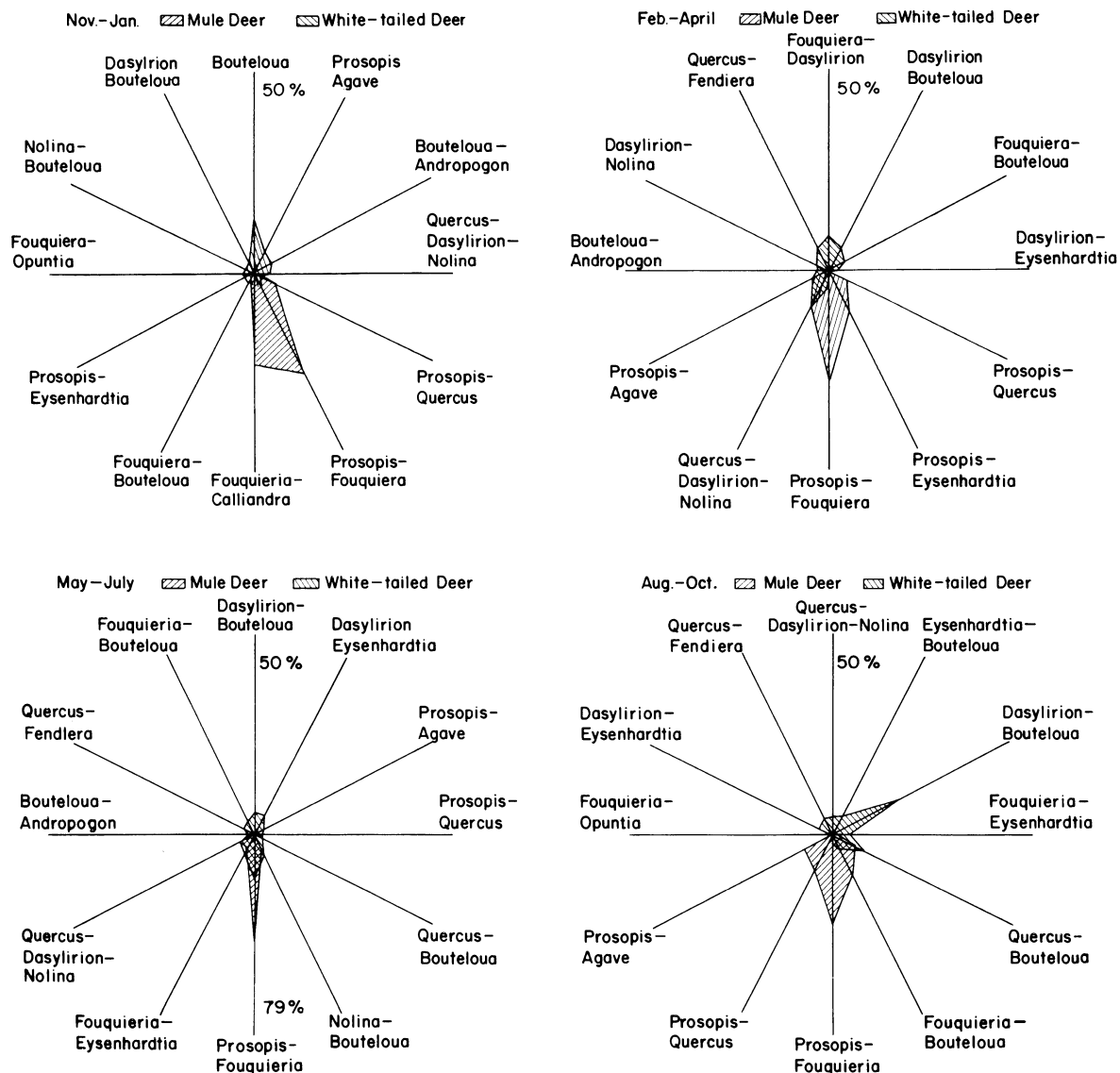


FIG. 3. Habitat selection of mule deer and white-tailed deer according to habitat type in the San Cayetano Mountains. Diagrams indicate the percentage of each species observed in each habitat type.

Nolina, *Bouteloua*, and/or *Fouquieria*. Overlap in habitat selection between the two species of deer occurred in the *Quercus-Dasyliirion-Nolina*, *Prosopis-Agave*, and *Prosopis-Fouquieria* habitat types. The estimated overlap in habitat selection for this season was 31%.

Most mule deer (79%) were observed in the *Prosopis-Fouquieria* habitat type during May, June and July (Fig. 3); some mule deer used the *Quercus-Dasyliirion-Nolina*, *Fouquieria-Eysenhardtia*, and *Nolina-Bouteloua* habitat types. White-tailed deer utilized a greater diversity of vegetation than did mule deer; no vegetational type appeared to be predominantly preferred. *Quercus*, *Dasyliirion*, *Nolina*, *Bouteloua*, *Prosopis*, *Fouquieria*, and/or *Eysenhardtia* were the plant genera with which white-tailed deer

were primarily associated. Areas dominated by *Eysenhardtia* were used as a result of this plant's importance as a food item during the hot, dry months. There was dual use of the *Prosopis-Fouquieria*, *Quercus-Dasyliirion-Nolina*, *Fouquieria-Eysenhardtia*, and *Nolina-Bouteloua* habitat types by mule deer and white-tailed deer. This overlap in habitat selection amounted to 39%, the greatest for any season.

Mule deer were found predominantly (63%) in the habitats dominated by *Prosopis* during the hot rainy season (August to October). Mule deer also made use of the *Quercus-Bouteloua* (11%) and *Fouquieria-Bouteloua* (7%) habitats. White-tailed deer showed greatest preference for the *Dasyliirion-Bouteloua* (33%) and *Quercus-Bouteloua* (14%) habitats, but also

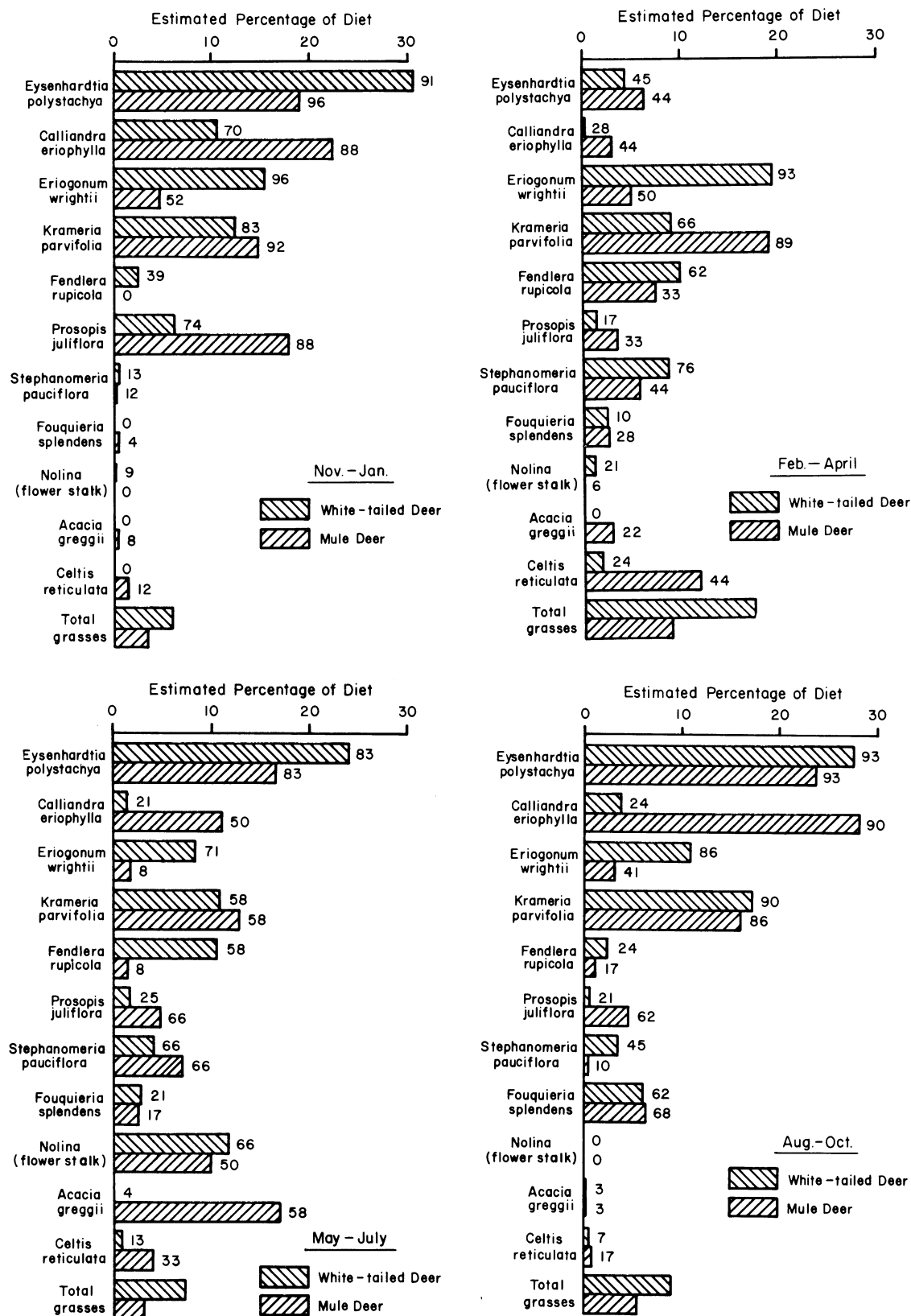


FIG. 4. Food preferences of mule deer and white-tailed deer at the San Cayetano Mountains. The numbers at the end of each bar are the frequency of occurrence of each plant species in the samples for the designated season.

used those habitats associated with *Eysenhardtia*, *Nolina*, *Fouquieria*, and *Prosopis*. Overlap in habitat selection (31%) occurred on the *Quercus-Bouteloua*, *Fouquieria-Bouteloua*, *Prosopis-Fouquieria*, and *Prosopis-Agave* habitat types.

Observation of habitat selection by mule deer and white-tailed deer for November to January (Fig. 3) revealed that mule deer utilized the *Prosopis-Fouquieria* (48%) and *Fouquieria-Calliandra* (39%) vegetations almost exclusively during this season; the only other vegetational type that mule deer frequented was *Quercus-Prosopis* (10%). White-tailed deer displayed definite preference for the *Eysenhardtia-Bouteloua* habitat type (26%), which was associated with high use of *Eysenhardtia polystachya* for food (to be presented later). White-tailed deer also used those habitats with which *Quercus*, *Dasyllirion*, *Nolina*, *Bouteloua*, *Fouquieria*, and *Prosopis* were associated. There was dual use by mule deer and white-tailed deer on the *Prosopis-Fouquieria* and *Fouquieria-Bouteloua* habitat types only. This overlap in habitat selection was estimated at 12%, the smallest for any season.

Considering all seasons, mule deer used fewer habitat types than white-tailed deer. Only 10 habitat types were used to any degree by mule deer, and white-tailed deer used all 18 of those mentioned previously. Mule deer were associated primarily with *Prosopis* and/or *Fouquieria* and were observed occasionally in the oak habitats. White-tailed deer did not display any particular preference for a certain habitat type but utilized all habitats. Overlap in habitat selection between mule deer and white-tailed deer ranged from 12 to 39% with an average over all seasons of 28%.

Food habits

A total of 189 fecal samples (84 from mule deer and 105 from white-tailed deer) from the San Cayetano Mountains were analyzed (Fig. 4).³ *Eriogonum wrightii* was the single most important food item for white-tailed deer during the cool, dry months of February to April (Fig. 4) comprising an estimated 19% of the diet. Grasses also were used extensively (18%). Other important foods to white-tailed deer were *Fendlera rupicola* (10%), *Krameria parvifolia* (9%), and *Stephanomeria pauciflora* (9%). The major constituents of the mule deer's diet were *K. parvifolia* (19%) and *Celtis reticulata* (12%). Grasses (9%) were not as abundant in mule deer samples. *Fendlera rupi-*

cola (8%) was also common in mule deer samples. Of the 12 major foods (Fig. 4), there was dual usage by mule deer and white-tailed deer on all but *Acacia greggii*. Considering the entire diets of both species³ there was an estimated 56% overlap in food habitats.

The most important food item for white-tailed deer during May to July was *Eysenhardtia polystachya*, which amounted to almost a quarter (24%) of their diet (Fig. 4). Flower stalks of *Nolina microcarpa* (12%), were also eaten frequently during this season. Other species important in the white-tailed deer diet were *K. parvifolia* (11%), *F. rupicola* (11%), and *E. wrightii* (8%). Five plant species contributed to the major portion of mule deer's diet: *A. greggii* (19%), *E. polystachya* (16%), *K. parvifolia* (13%), *Calliandra eriophylla* (11%), and *Nolina* flower stalks (10%). There was considerable overlap between mule deer and white-tailed deer in use of *E. polystachya*, *K. parvifolia*, and *N. microcarpa* during May to July. The total estimated overlap in food habits was 55%, the smallest for all seasons.

Three species of forage plants were eaten most extensively during the hot rainy season (Fig. 4). *Eysenhardtia polystachya* comprised 28% of the diet, *K. parvifolia*, 17%, and *E. wrightii*, 11%. Grasses were used moderately by white-tailed deer. *Calliandra eriophylla* (28%) and *E. polystachya* (24%) were the most important food for mule deer during August to October. *Krameria parvifolia* (16%) was also eaten frequently during these months. White-tailed deer and mule deer both ate *Fouquieria splendens*, which accounted for 6% of the diet of both species. Dual use by mule deer and white-tailed deer was primarily on *E. polystachya* and *K. parvifolia*. Total overlap in food preferences was estimated at 67%, the highest of all seasons.

Eysenhardtia polystachya contributed the largest portion (31%) to the white-tailed deer diet, and *E. wrightii* (16%), *K. parvifolia* (13%), and *Calliandra eriophylla* (11%) were also important during the moist part of the winter (Fig. 4). Mule deer diets were composed mainly of *C. eriophylla* (22%), *E. polystachya* (19%), *Prosopis juliflora* (18%), and *K. parvifolia* (15%). Overlap in food habits of mule deer and white-tailed deer occurred mostly on three species: *E. polystachya*, *K. parvifolia*, and *C. eriophylla*, in that order. Total overlap was estimated at 60%.

The order of importance of plant species eaten by white-tailed deer in the combined seasons was: (1) *E. polystachya*; (2) *E. wrightii*; (3) *K. parvifolia*; (4) *F. rupicola*; (5) *B. chondrosiodes*; (6) *K. parvifolia*; (7) *C. eriophylla* and *N. microcarpa* (flower stalks). Similarly the primary food items of mule deer in order of importance were: (1) *E. polystachya*; (2) *C. eriophylla*; (3) *K. parvifolia*; (4) *P. juliflora*; (5) *A. greggii*; (6) *C. reticulata* and *N. microcarpa* (flower stalks). Three plant species were, therefore, very important to both species of deer, and these plant species

³ See NAPS document #02965 for 5 pages of supplementary material. Order from ASIS/NAPS, Microfiche Publications, 440 Park Avenue South, New York, NY 10016. Remit in advance \$3.00 for microfiche copy or for photocopy, \$5.00 up to 20 pages plus 25¢ for each additional page. All orders must be prepaid. Foreign orders add \$3.00 for postage and handling.

TABLE 2. Percentage of mule deer (MD) and white-tailed deer (WT) diets from the major growth forms for the San Cayetano Mountains

Growth forms	Season							
	Feb to Apr		May to Jul		Aug to Oct		Nov to Jan	
	WT	MD	WT	MD	WT	MD	WT	MD
Grasses	17.7	9.0	7.2	3.0	9.0	5.5	6.0	3.6
Herbs	12.4	7.4	13.5	7.4	6.9	2.6	2.3	.3
Flower stalks and fruits	2.3	.6	13.3	10.4	1.2	2.3	1.6	6.0
Shrubs	47.6	49.8	65.7	49.8	71.8	82.7	74.8	65.5
Trees	9.2	24.4	4.1	27.3	1.3	5.8	10.1	21.8

contributed to the majority of the dual use. Differences in the major food items between mule deer and white-tailed deer can be explained by distributions of plants and deer. For example, *E. wrightii*, *F. rupicola*, and *S. parvifolia* were very important to white-tailed deer but only moderately so to mule deer. These plant species were distributed primarily at the higher elevations, which were inhabited mainly by white-tailed deer. *P. juliflora*, *A. greggii*, and *C. reticulata*, which were important to mule deer only, were distributed at the lower elevations where mule deer primarily existed.

A comparison of food preferences according to the major growth forms showed that white-tailed deer ate $\approx 2\times$ as much grass and herbs as did mule deer (Table 2). Shrubs were eaten the most and equally by both deer species. Flower stalks and fruits were also consumed similarly by mule deer and white-tailed deer, but mule deer ate $\approx 3\times$ as much food from tree species as did white-tailed deer. Mule deer utilized more browse species than white-tailed deer in this area.

The number of different plant species identified in the analysis of each fecal sample provided a comparison of the diversity between each species' diet. The difference of numbers of plant species per fecal sample for mule deer and white-tailed deer was statistically significant ($F_{(1,177)} = 64.59$). The difference between the seasons is also statistically significant ($F_{(5,177)} = 3.35$) at the .05 level. The number of different plant species in a fecal sample was, therefore, significantly influenced by the season and species of deer from which the sample was acquired. The mean number of plant species per fecal sample for white-tailed deer was consistently higher than those for mule deer (Ta-

ble 3). For all seasons, the difference between the mean number of plant species per fecal sample for white-tailed deer and mule deer was statistically significant at the .05 level. White-tailed deer used a more diverse diet, on the average, than did mule deer.

Niche overlap

The indices of niche overlap between mule deer and white-tailed deer (Table 4) indicate that the overlap in spatial distributions (slope exposure-altitude intervals) ranged from 22 to 37%, with a mean of 32%. Overlap was greatest during the late summer, fall, and winter months and least during the spring months. Overlap in habitat selection was seasonally more variable than overlap in spatial distributions (range, 12 to 39%; mean, 28%). The greatest overlap in habitat selection was during May to July, and the least was during November to January. Because the same slope exposure-altitude intervals may display different vegetation (habitat), we reasoned that it was necessary for white-tailed deer and mule deer to use the same habitat at the same slope exposure-altitude intervals simultaneously. Consequently, a better estimate of the true distributional overlap for these two species is the product of the preceding indices of overlap ($S \times H$, Table 4). These indices are low in comparison with the others, and we believe they present the most accurate picture of where mule deer and white-tailed deer were distributed in the San Cayetano Mountains.

Throughout the study there was much dual use of the forage plants which is affirmed by the high overlap in food habits between the two species. Overlap was greatest during August to October (67%) and smallest during May to July (55%). These data suggest that

TABLE 3. Mean number of plant species per fecal sample for deer in the San Cayetano Mountains from August 1969 to January 1972 (Numbers of samples in parentheses)¹

Deer species	Season					
	Dec to Jan	Feb to Mar	Apr to May	Jun to Jul	Aug to Sep	Oct to Nov
Mule deer	7.71 \pm .68 (17)	8.46 \pm .80 (13)	7.17 \pm 1.33 (6)	7.73 \pm .89 (11)	8.73 \pm .89 (11)	7.50 \pm .54 (26)
White-tailed deer	9.12 \pm .68 (17)	9.86 \pm .61 (21)	10.29 \pm .76 (14)	8.78 \pm .66 (18)	9.95 \pm .64 (19)	9.31 \pm .71 (16)

¹ Values are: $\bar{x} \pm (t_{.05})$ (standard error).

TABLE 4. Indices of overlap in spatial distributions, habitat selection, and food habits between mule deer and white-tailed deer at the San Cayetano Mountains (August 1969 to January 1972)

Season	Spatial distributions (S)	Habitat selection (H)	Coefficient of distributional overlap (S × H)	Food habits (F)	Coefficient of competition	
					(S × H × F) product α	(S + H + F)/3 summation α
Feb–Apr	.22	.31	.07	.56	.04	.36
May–Jul	.33	.39	.13	.55	.08	.42
Aug–Oct	.37	.31	.11	.67	.07	.45
Nov–Jan	.37	.12	.04	.61	.02	.37
Seasonal \bar{x}	.32	.28	.09	.60	.05	.40

mule deer and white-tailed deer partitioned the food resource most during the critical period of the year (May to July) and least when forage was in abundance (August to October).

Interpretation of coefficients of competition is not a simple matter as May (1975) points out, for the proper computation depends on the relationship (dependence or independence) between the various resource dimensions. Where the resource dimensions are independent, the total competition coefficient is the product of the individual one-dimensional coefficients as suggested by Levins (1968). However, if the resource dimensions are dependent, the total competition coefficient is the arithmetic mean of the individual one-dimensional coefficients. With the present situation, resource dimensions (spatial distributions, habitat selection, food habits) are not completely dependent or independent, so summation α , calculated as the arithmetic mean, is an upper bound on the true multidimensional α (May 1975) and product α is conservative. Coefficients of competition are presumably measures of direct competition and convey no information about the phenomena of competitive exclusion.

Both product α and summation α were calculated for niche relationships between mule deer and white-tailed deer in the San Cayetano Mountains (Table 4). Since there was little to no overlap in distributions of the two species, product α is more appropriate. Seasonal values of product α indicate a low potential for direct competition. The similarity in food preferences of the two species and the contiguously allopatric nature of their distributions lead us to speculate that mule deer and white-tailed deer competitively excluded each other in the San Cayetano Mountains during the study.

Recruitment

White-tailed deer showed higher recruitment to their populations than mule deer from 1969 to 1971 (Table 5). The magnitude of this difference was 9.3 fawns per 100 does in 1969–1970 and 13.2 fawns per 100 does in 1970–1971. Populations of both species declined drastically during the drought of late 1970 and early 1971 (Anthony 1976), so the number of deer classified was low. Mule deer appeared to have much higher recruitment after the drought. During the winter of 1971–1972

the mule deer population had a doe:fawn ratio of 100:56 and white-tailed deer, 100:06. Total recruitment for the entire study was higher for white-tailed deer than mule deer.

COEXISTENCE: DOS CABEZAS MOUNTAINS

Data from the Dos Cabezas Mountains were divided into three seasons: April to mid-July, mid-July through October, and November through March. This division was based in part upon plant phenologies. From November through March, all deciduous plants were dormant, so deer were restricted primarily to evergreen browse for food. During that time there was no evidence in either fecal analysis or direct observations that deer were eating twigs of deciduous plants. By the first of April, the deciduous plants began to sprout and were available to feeding deer. The summer rains begin around the middle part of July, so from this time until the end of September grasses were green, and many herbaceous plants were available for deer to feed upon.

Spatial distributions

Spatial distributions of deer in the Dos Cabezas Mountains were analyzed from 1,762 deer observations. A total of 389 white-tailed deer were observed in 173 groups or 2.2 white-tailed deer/group. Similarly, 1,373 mule deer were observed in 284 groups or 4.8 mule deer/group. Mule deer were, therefore, more gregarious and numerous than white-tailed deer in the Dos Cabezas Mountains.

Distributions of mule deer and white-tailed deer were related to altitude and vegetational zone (Fig. 5). Distributions of white-tailed deer were more restricted

TABLE 5. Doe-fawn counts of deer in the San Cayetano Mountains, November through February 1969–1972

Year	White-tailed deer			Mule deer		
	Does	Fawns	Fawns/100 does	Does	Fawns	Fawns/100 does
1969–1970	60	18	30.0	34	7	20.7
1970–1971	66	20	30.3	41	7	17.1
1971–1972	18	1	5.5	9	5	55.6
Totals	144	39	27.0	84	19	22.6

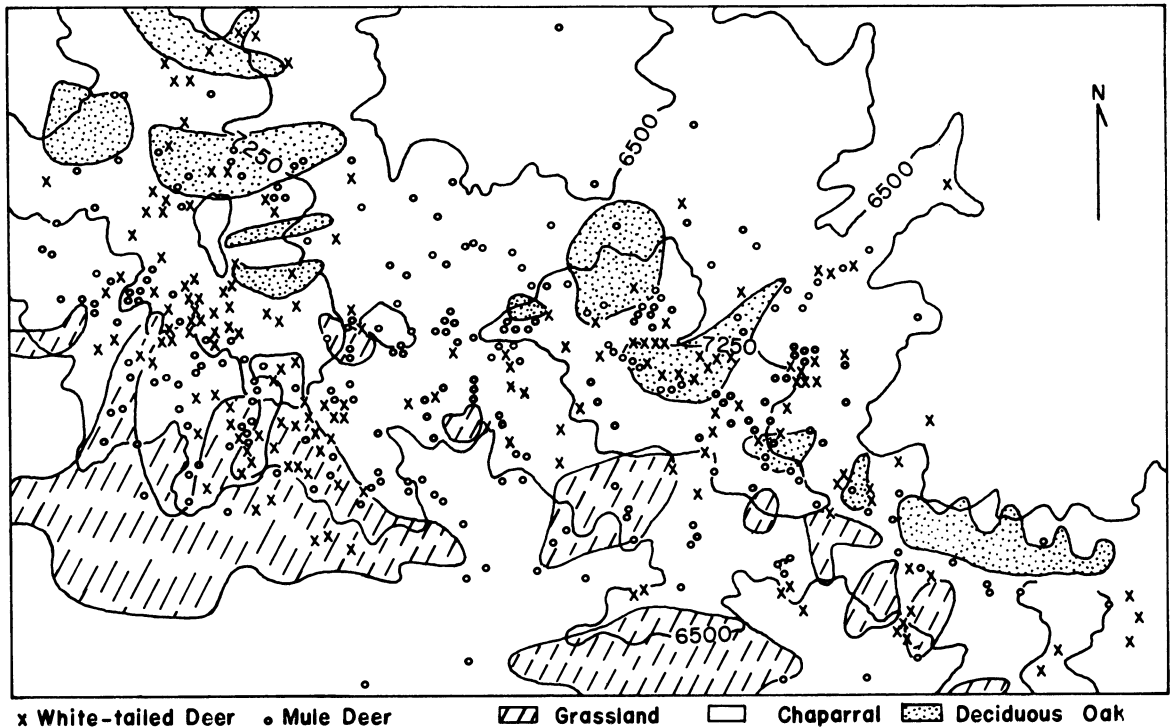


FIG. 5. Distributional patterns of mule deer and white-tailed deer in relation to altitude and vegetational zone at the Dos Cabezas Mountains. Each circle and cross represents a sighting of a group of white-tailed deer and mule deer, respectively, and not individual deer.

than mule deer because observations of this species tended to be clumped. This restriction was not associated with any particular vegetational zone; however white-tailed deer were almost always found above 1,980 m. Distributions of mule deer were more scattered than white-tailed deer, and they were much less restricted. Mule deer used all 3 vegetational zones during some part of the study. They were also found at lower elevations than white-tailed deer. Both species were observed at the highest elevations on the study area, and the nature of their distributions (Fig. 5) shows that their populations were sympatric in the Dos Cabezas Mountains. Overlap between mule deer and white-tailed deer populations occurred on the 3 major vegetational zones.

From April to mid-July, we made 125 observations of white-tailed deer and 481 observations of mule deer. During that period both species used all slopes to some extent (Table 6). The southeast and neutral slopes appeared to be used the most as were the elevations from 1,980 to 2,290 m. Overlap between mule deer and white-tailed deer, according to the various slope exposure-altitude intervals, was 66%.

From mid-July to the end of October, 106 white-tailed deer and 320 mule deer were observed. Spatial distributions of the 2 species according to the various slope exposure-altitude intervals show no real preferences for any particular slope exposure (Table 6). However, mule deer observations were more frequent

on north-facing slopes between 1,980 and 2,290 m. Overlap was considerable between the 2 species from 1,980 to 2,440 m. Total overlap for this time period was estimated to be 64%.

During the winter, 158 white-tailed deer and 572 mule deer were observed. These observations indicate that both species sought out the south-facing slopes more than the north-facing slopes (Table 6). Most deer were observed between 1,980 and 2,290 m. White-tailed deer were more often found on south- and southwest-facing slopes than mule deer, and mule deer were more common on southeast and neutral slopes. As in other seasons, overlap (57%) between mule deer and white-tailed deer populations was considerable.

The sympatric nature of mule deer and white-tailed deer is also reflected in the coefficients of association. Coefficients for the various seasons are as follows: April to mid-July, +.858; mid-July through October, +.878; and November through March, +.872. These coefficients are extremely high and reflect the positive association between mule deer and white-tailed deer in the Dos Cabezas Mountains. There is sufficient evidence, therefore, that they were sympatric in their distributions.

Habitat selection

Habitat selection by mule deer and white-tailed deer in the Dos Cabezas Mountains was ascertained on the basis of 1,784 deer observations in 19 habitat types.

TABLE 6. Percentages of mule deer (MD) and white-tailed deer (WT), observed on the various slope exposure-altitude intervals in the Dos Cabezas Mountains from August 1969 to March 1972¹

Altitude interval (m)	Deer species	Slope exposure ²						
		S	SW	SE	Ne	NW	NE	N
April to mid-July								
2,286–2,438	WT	3.2	2.4	5.6	2.4	4.0	4.8	5.6
	MD	.8			.6	.8	4.8	3.7
2,134–2,285	WT	3.2	2.4	19.2	.8	2.4	4.0	3.2
	MD	4.0	4.8	12.9	9.6	1.2	5.4	4.2
1,981–2,133	WT	3.2	8.8	8.8	4.0		2.4	
	MD	9.1	8.5	3.3	6.0	2.1	2.5	
1,229–1,980	WT			3.2	2.4		1.6	
	MD	2.1		3.3	.8	1.2	2.1	
1,676–1,228	WT			1.6	.8			
	MD	.2			5.0	.8		
Mid-July to October								
2,286–2,438	WT	6.6	2.8	3.8	3.8	.9	8.5	9.4
	MD	.9	3.1	2.5	3.1	3.1	4.1	5.0
2,134–2,285	WT	6.6	4.7	6.6	2.8	.9	13.2	6.6
	MD	2.8	3.8	7.5	5.6	5.0	3.4	8.8
1,981–2,133	WT	1.9	6.6	3.8	.9	.9	.9	1.9
	MD	5.9	6.6	5.0	4.1	5.6	3.4	.6
1,229–1,980	WT	1.9	3.8					
	MD	.6	1.3	3.4	.3		1.6	
1,676–1,228	WT							
	MD				2.8			
November to March								
2,286–2,438	WT	6.3	3.8	7.0	4.4	.6	1.9	
	MD	1.4	.9	.9	1.7	5.8	1.7	1.4
2,134–2,285	WT	10.1	8.9	6.3	8.2	2.5	2.5	1.9
	MD	3.0	4.9	12.1	16.1	4.4	4.2	5.8
1,981–2,133	WT	4.4	9.5	9.5	3.8	.6	1.9	1.9
	MD	4.9	5.6	3.0	6.5	5.9	2.3	
1,229–1,980	WT	1.9			1.9			
	MD		3.7	.9	1.2			
1,676–1,228	WT							
	MD				.9			.3

¹ Percentages for each season and species are independent (i.e., percentages for white-tailed deer during November to March add to 100%).

² S = south, SE = southeast, SW = southwest, Ne = neutral, NW = northwest, NE = northeast, N = north.

Both species usually frequented eight types of habitat: *Quercus-Cercocarpus*; *Cercocarpus-Nolina*; *Juniperus-Cercocarpus*; *Quercus-Juniperus*; *Quercus-Nolina*; *Quercus-Juniperus-Cercocarpus*; *Nolina-Bouteloua*, and *Quercus-Symphoricarpos*.

Habitat selection of mule deer and white-tailed deer

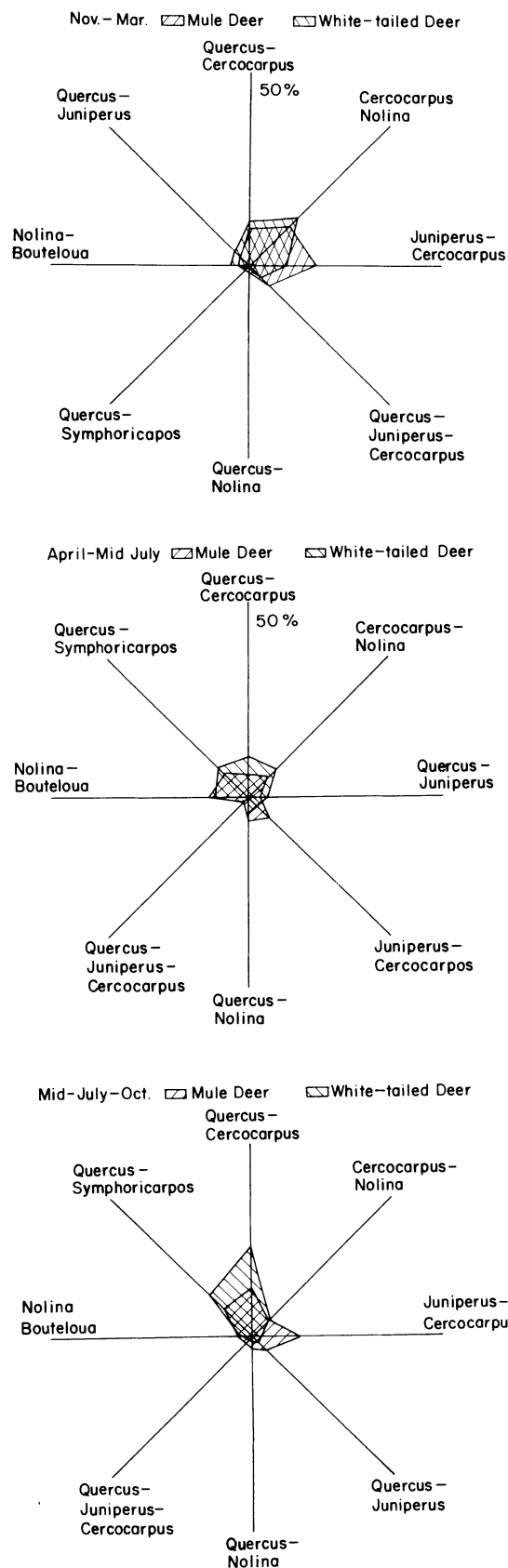


FIG. 6. Habitat selection of mule deer and white-tailed deer according to habitat type in the Dos Cabezas Mountains. Diagrams indicate the percentage of each species observed in each habitat type.



FIG. 7. Food habits of mule deer and white-tailed deer for all seasons in the Dos Cabezas Mountains. The numbers at the end of each bar are the frequency of occurrence of each plant species in the samples for the designated season.

for April to mid-July represents 118 white-tailed deer and 482 mule deer observations (Fig. 6). Overlap in habitat selection for this season was estimated at 76%. White-tailed deer used a higher percentage of the *Quercus-Cercocarpus*, *Cercocarpus-Nolina*, *Quercus-Juniperus*, and *Quercus-Symphoricarpos* habitat types but these habitats were also very important to mule deer. Mule deer selected the *Juniperus-Cercocarpus* habitat type much more than did white-tailed deer. The *Quercus-Juniperus-Cercocarpus* habitat type was not used much by either species.

From mid-July through October, 102 white-tailed deer and 314 mule deer were observed. White-tailed deer were observed much more in the *Quercus-Cercocarpus* and *Quercus-Symphoricarpos* habitat types than in the previous season (Fig. 6). Mule deer were associated with the *Juniperus-Cercocarpus* and *Quercus-Juniperus* types with more frequency than white-tailed deer. Neither species used the *Nolina-Bouteloua*, *Quercus-Nolina*, or *Quercus-Juniperus-Cercocarpus* vegetations with any great frequency. Overlap between mule deer and white-tailed deer for this season was high but lowest (66%) of all seasons.

There were 152 observations of white-tailed deer and 616 observations of mule deer for the winter

months (November–March). Mule deer again used the *Juniperus-Cercocarpus* habitat much more than white-tailed deer (Fig. 6). Extensive use of this habitat type by mule deer was correlated with their use of *Juniperus deppeana* as an important food item (to be discussed later). The other habitat types were used similarly by both species. There was considerably high overlap in habitat selection, which was estimated to be 82%, the greatest of all seasons. Both species displayed a change in habitat selection during the winter months compared with other months. Contrary to other periods the *Quercus-Symphoricarpos* habitat type was rarely used during winter. Both *Q. gambelii* and *Symphoricarpos ereophilus* are deciduous, so this habitat is quite undesirable in winter when these dominant plants were leafless and dormant. During spring and summer, deer found these areas most desirable because the 2 dominants of this habitat type provide good food and cover. The *Quercus-Nolina* habitat type was not used much by either species during winter, but the *Quercus-Juniperus-Cercocarpus* type was. This was the only season during which it was of any importance to either mule deer or white-tailed deer.

Food habits

Diets of mule deer and white-tailed deer in the Dos Cabezas Mountains were determined from 263 pellet group samples, 153 from mule deer and 110 from white-tailed deer.⁴ Seven food items were the most important and comprised the bulk of the diets of both mule deer and white-tailed deer (Fig. 7). These items, in the order of importance, are *Cercocarpus breviflorus*, *J. deppeana*, *Eriogonum wrightii*, *Quercus gambelii*, *Q. emoryi*, seeds of *J. deppeana*, and flower stalks of *N. microcarpa*.

For April through mid-July, 35 fecal samples from white-tailed deer and 47 from mule deer were analyzed. *Cercocarpus breviflorus*, *J. deppeana*, *E. wrightii*, *Q. gambelii*, grasses, and *N. microcarpa* (flower stalks) were the most important foods for both mule deer and white-tailed deer (Fig. 7). The primary difference in use of these plants was that mule deer ate about 2× as much *J. deppeana* as did white-tailed deer, and *E. wrightii* was more important to white-tailed deer than to mule deer. Use of all other major plant foods was very similar. The flower stalks of *N. microcarpa* were important food items only during these months. There was even intra- and inter-specific conflict observed in acquiring this choice food item (to be discussed later). Grasses were of greatest importance during this season. Overlap in food habits for this season was estimated to be 74%, the lowest for all seasons.

For the rainy season (mid-July to October), 30 fecal samples from white-tailed deer and 35 from mule deer

⁴ See NAPS document #02965 for 5 pages of supplementary material. Complete information appears in footnote on p. 263.

TABLE 7. Percentage of diets of mule deer (MD) and white-tailed deer (WT) from the major growth forms

Growth forms	Season					
	April to mid-July		Mid-July to October		November to March	
	WT	MD	WT	MD	WT	MD
Grasses	7.9	6.5	5.5	4.4	.4	.8
Herbs	2.8	3.0	10.2	7.9	2.3	2.4
Flower stalks and fruits	6.5	4.3	.8	.3	0.0	0.0
Shrubs	37.0	40.6	49.9	51.7	58.4	51.2
Trees	36.8	43.1	33.4	28.5	34.7	44.3

were analyzed. After the summer rains started, *C. breviflorus* was the single most important food item for both mule deer and white-tailed deer from mid-July through October. *Quercus gambelii*, *J. deppeana*, and *E. wrightii* were also important sources of food. However, *J. deppeana* was again more important to mule deer and *Q. gambelii* was used to a greater extent by white-tailed deer. *Quercus emoryi* and the flower stalks of *N. microcarpa* were only meagerly exploited as food. The overlap in food habits (Fig. 7) was estimated to be 77%. Food of both species was most diverse during this season with the emphasis on herbs and grasses.⁵

From November through March, fecal samples from 45 white-tailed deer and 71 mule deer were obtained. *Cercocarpus breviflorus* was the primary food source for both species. *Juniperus deppeana* and its seeds, *Q. emoryi*, and *E. wrightii* were all of secondary importance. As in the other seasons, *J. deppeana* was much more important to mule deer than to white-tailed deer. *Quercus gambelii* and the flower stalks of *N. microcarpa* were not utilized during the winter. *Quercus gambelii* is dormant in the winter and occupies habitats infrequently used by deer during that season. Use on most plant species was very similar. Overlap in food habits was estimated to be 84%, the highest for all seasons. Because deer were restricted to evergreen browse during November through March, their diet was less variable than in other months. February and

March were considered the most critical for deer in the Dos Cabezas Mountains because of this restriction.

A comparison of food of mule deer and white-tailed deer according to the major growth forms failed to show any outstanding differences (Table 7). Deer did not partition the food source in any obvious way. Food availability, especially grasses and herbs, was greatly influenced by overgrazing by livestock.

Species of deer and season both have statistically significant influences on the number of plant species per fecal sample ($F_{[1,251]} = 57.67$ and $F_{[5,251]} = 21.0$, respectively). The interaction between these 2 effects was also statistically significant ($F_{[1,251]} = 6.47$). A review of the species by season means (Table 8) shows that white-tailed deer utilized significantly ($P < .05$) greater number of plant species than mule deer in all months except February and March, the most critical time of the year for deer with respect to the food supply. The significant interaction between the species and season effects was due to the differing results for these months.

Niche overlap

Indices of overlap in spatial distributions, habitat selection, and food habits reflect the sympatric nature of deer populations in the Dos Cabezas Mountains (Table 9). Overlap in spatial distributions according to altitude and slope exposure averaged 62% and ranged from 57 to 66%. Overlap for this parameter was lowest for those studied. Overlap in habitat selection ranged from 66 to 82% and averaged 75%. Because deer must use the same habitats at the same slope exposure-altitude intervals simultaneously, examination of the product of the indices of spatial distributions and habitat selection is informative. Again these indices are high (about 40 to 50%). Overlap in diet ranged from 74 to 84% and averaged 78%, the highest for the 3 parameters studied. These indices are most likely underestimates because they do not consider overlap in use from one season to the next. In view of the magnitude of these indices, it appears that the two species are quite similar in their use of space and food in the Dos Cabezas Mountains.

Coefficients of competition between mule deer and white-tailed deer at the Dos Cabezas Mountains indicate considerable potential for direct competition (Ta-

TABLE 8. Mean number of plant species per fecal sample for deer in the Dos Cabezas Mountains from August 1969 to January 1972 (Numbers of samples in parentheses)¹

Deer species	Season					
	Dec to Jan	Feb to Mar	Apr to May	Jun to Jul	Aug to Sep	Oct to Nov
White-tailed deer	7.19 ± .51 (27)	6.50 ± .69 (16)	9.79 ± .61 (19)	8.20 ± .61 (20)	9.75 ± .61 (20)	8.75 ± 1.08 (8)
Mule deer	6.49 ± .43 (37)	6.77 ± .52 (26)	7.79 ± .46 (33)	6.89 ± .62 (19)	7.71 ± .55 (24)	7.12 ± .76 (14)

¹ Values are: $\bar{x} \pm (t_{.05})$ (standard error).

TABLE 9. Indices of overlap in spatial distributions, habitat selection, and food habits between mule deer and white-tailed deer at the Dos Cabezas Mountains (August 1969 to January 1972)

Season	Spatial distributions (S)	Habitat selection (H)	(S × H)	Food habits (F)	Coefficient of competition	
					(S × H × F) product α	(S + H + F)/3 summation α
Apr to mid-Jul	.66	.76	.51	.74	.37	.72
Mid-Jul to Oct	.64	.66	.42	.77	.28	.69
Nov to Mar	.57	.82	.47	.84	.39	.74
Seasonal \bar{x}	.62	.75	.46	.78	.35	.72

ble 9). We believe the product α values are slightly conservative and the summation α values are overestimates, so that the true multidimensional α are probably in the range of 0.40 to 0.50. Interestingly, the coefficients for the critical time of the year (November–March) are highest and for the optimal time (mid-July to October) is the lowest.

Recruitment

Mule deer had a higher recruitment to their population than did white-tailed deer during the study (Table 10). The magnitude of this difference was not significant until 1971–1972 when recruitment for mule deer was nearly 2× that for white-tailed deer. Because a drought period preceded the 1971–1972 figures (Anthony 1976), this difference is quite informative. Overall recruitment for mule deer was 7% higher than that for white-tailed deer.

BEHAVIORAL INTERACTIONS

Behavioral interactions between mule deer and white-tailed deer were evaluated in only those encounters in which individuals or groups of individuals of the two species came close enough for antagonism or avoidance to be displayed by either species. Usually, the maximum distance at which any behavioral interactions between individuals became apparent was ≈ 45 m depending on the density of shrubs and trees; this distance agrees with the results presented by Kramer (1973:297). Encounters between the 2 species were more frequent in the Dos Cabezas area (11%) than in the San Cayetano area (3%) (Table 11). The difference in these frequencies reflects the sym-

patric nature of the 2 populations in the Dos Cabezas Mountains and the almost mutually exclusive nature in the San Cayetano Mountains.

Most encounters (48%) between mule deer and white-tailed deer occurred during the hot, dry months of the year (April–July) when the availability of succulent food was restricted. In 59% of these encounters, species dominance could not be determined. When dominance could be ascertained (41% of the encounters), mule deer were always dominant. Dominance of mule deer over white-tailed deer did not appear to depend upon the sex or group composition of either species (Table 11). Mule deer of either sex were always dominant over white-tailed deer. The dominance of mule deer over white-tailed deer was displayed equally by active or passive mechanisms. The term passive was used in reference to those situations in which no overt aggression was observed, and usually occurred when both species were feeding close together. In these situations, if their paths crossed, white-tailed deer would avoid mule deer. Mule deer would continue their feeding without any apparent disturbance or aggression toward white-tailed deer. The term active refers to those situations in which mule deer were dominant by way of aggressive threat. This aggression by mule deer was displayed by the “crouch” and/or “snort” behavior as described by Cowan and Geist (1961) and Dorrance (1966). Mule deer never attacked white-tailed deer. When mule deer displayed dominance over white-tailed deer, they often did so in seeking a choice food item (i.e., flower stalks of *N. microcarpa* during May or June) or bedding site. On 4 occasions, mule deer threatened and displaced white-tailed deer that were feeding on flower stalks of *N. microcarpa*. On another occasion a white-tailed deer tried to displace a mule deer feeding on one of these choice food items but was unsuccessful.

A good example of mule deer's passive dominance over white-tailed deer is given in the following excerpt of field notes made by one of us (Anthony) in the Dos Cabezas Mountains on 8 September 1970: “I located a heterospecific group of 5 white-tailed bucks and 2 mule deer bucks. Antler points for the 5 white-tailed deer were: 4×4 , 3×3 , 2×2 , 2×2 , and 1×1 ; and for the mule deer 3×3 and 2×2 . This whole group of deer was feeding together early in the morning.

TABLE 10. Herd composition counts of deer in the Dos Cabezas Mountains during November through February 1969 to 1972

Year	White-tailed deer			Mule deer		
	Does	Fawns	Fawns/100 does	Does	Fawns	Fawns/100 does
1969–1970	41	17	41.5	205	89	43.4
1970–1971	30	8	26.7	123	34	27.6
1971–1972	31	6	19.4	103	38	36.9
Totals	102	31	30.4	431	161	37.4

TABLE 11. Summary of behavioral interactions between mule deer and white-tailed deer, Dos Cabezas and San Cayetano mountains (B = bucks, D = does, F = fawns)

Date	Herd composition		Dominant species	Type of dominance ¹
	Mule deer	White-tailed deer		
Dos Cabezas Mountains				
19 Aug 1969	2B, 2D	1D	Not determined	
6 Dec 1969	1B, 5D, 1F	1D, 1F	Not determined	
21 Dec 1969	3D, 1F	2D, 1F	Not determined	
21 Dec 1969	1D, 2F	1B, 1D, 1F	Not determined	
7 Feb 1970	8D, 5F	2D, 1F	Not determined	
27 Feb 1970	2D	2D	Mule deer	Active
25 Jul 1970	2D	2D	Not determined	
8 Sep 1970	2B	5B	Mule deer	Passive
13 Dec 1970	2D, 2F	1D	Not determined	
16 Jan 1971	4D, 2F	1B, 1D, 1F	Not determined	
5 Apr 1971	11D, 3F	1B, 3D	Mule deer	Active
22 Apr 1971	4D, 2F	4D, 1F	Mule deer	Active
23 Apr 1971	3D	1D	Not determined	
8 May 1971	6D	4D	Not determined	
8 May 1971	12D, 2F	2D	Mule deer	Passive
18 May 1971	1B, 12D, 2F	1D	Mule deer	Active
19 May 1971	5B, 15D, 3F	1B, 4D	Not determined	
6 Jun 1971	8D	3B	Mule deer	Passive
6 Jun 1971	12D, 1F	3D, 1F	Mule deer	Active
30 Jun 1971	1D	2B	Not determined	
30 Jun 1971	9D, 3F	1D, 1F	Mule deer	Passive
San Cayetano Mountains				
22 Mar 1970	2D	2B, 4D, 1F	Not determined	
13 Sep 1970	5D	2B	Not determined	
10 Jan 1971	1B	1B, 1D, 1F	Not determined	
26 May 1971	2D	1D	Mule deer	Passive
11 Jun 1971	1D	1D	Mule deer	Active
24 Nov 1971	3D	2B	Not determined	

¹ "Passive" refers to those situations in which mule deer were dominant but no overt aggression was observed. "Active" refers to those situations in which mule deer were dominant by way of overt aggression. Overt aggression was displayed by the crouch or snort as described by Cowan and Geist (1961).

There was much intraspecific aggression among the white-tails, especially the 4×4 white-tailed deer toward the others. The mule deer were obviously dominant; they moved about as they pleased, while the white-tailed deer made room for them to feed upon various mountain mahogany (*C. breviflorus*) plants. The smaller white-tailed deer often ran to get out of the way of the mule deer, even though no aggressive threats were observed from mule deer. The 4×4 white-tailed deer was very aggressive and dominant over the other white-tails, but he was subordinate to the mule deer. From these observations I was able to detect a "peck-order" from the largest (3×3) mule deer down to the smallest (1×1) white-tailed deer. The last I saw of the group, they were feeding together."

The dominance of mule deer over white-tailed deer witnessed throughout this study is not surprising, because the subspecies of mule deer in southern Arizona is nearly $2 \times$ the size of the subspecies of white-tailed deer. This size difference may account for the mule deer's dominance in all circumstances observed during the study, but other factors such as age, period of the

sexual cycle, and antler development may influence dominance in interspecific interactions.

Some of the results of this study differ from those presented by Kramer (1973); he indicated that neither species of *Odocoileus* dominated the other socially in southern Alberta. This discrepancy is not surprising in view of the different vegetational types and size differences of the mule and white-tailed deer of southern Alberta as compared with those of southern Arizona. Kramer suggested that white-tailed deer may be less tolerant of cattle than mule deer. Although we did not collect data related to this question, our general impressions agree with those of Kramer.

VEGETATIONAL SURVEYS

Utilization surveys on *Cercocarpus breviflorus* were conducted on the same plots for 2 years, since it was the key browse plant for deer in the Dos Cabezas Mountains (Fig. 7). Use of the annual growth of this species was high. For all plots sampled, the use on *C. breviflorus*, which was used more extensively in 1971 than in 1972, averaged 75% of the annual leader growth (Table 12). This difference in the yearly use

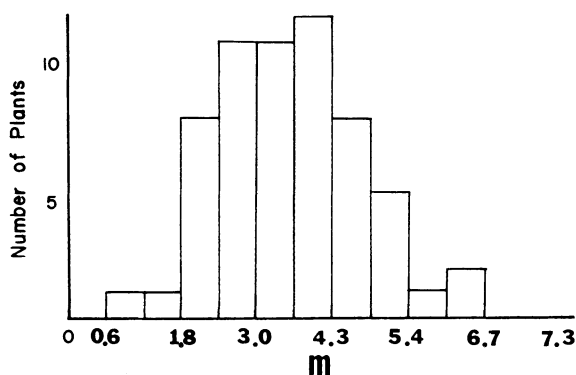


FIG. 8. Height (in metres) distribution of *Quercus emoryi* sampled in the Dos Cabezas Mountains.

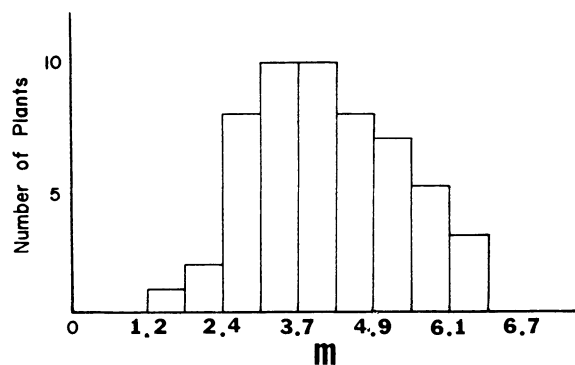


FIG. 9. Height (in metres) distribution of *Quercus oblongifolia* sampled in the San Cayetano Mountains.

was statistically significant ($F_{1,8} = 29.55$). The difference in percentage use for the 2 yr probably is the result of differences in productivity of *C. breviflorus* and/or deer densities. Surveys for 1971 were carried out during a drought period, but good summer rains following these surveys initiated high productivity of plants. This high productivity coupled with a suspected decrease in deer numbers during the drought probably account for the lower percentage use for the following winter.

Deer use of *C. breviflorus* on the various slope exposures was quite variable and the differences were statistically significant ($F_{4,8} = 7.50$). Ranking the slope exposures in order of highest to lowest use (neutral, southeast, northeast, northwest, and south), reveals no explainable reason for these differences. We believe these differences were related to the specific areas where the surveys were made and their associated deer densities rather than any real influence of slope exposure.

Cercocarpus breviflorus was a highly preferred forage plant for deer in the Dos Cabezas Mountains. The high percentage use (up to 85% in some areas) of the annual growth of this species indicates that food derived from this species was limiting during the late months of winter. The extensive use of *Q. emoryi* by

deer during the winter months (Fig. 7) also suggests a food shortage, since its forage value is quite low.

Surveys on *Q. emoryi* and *Q. oblongifolia* were conducted in the Dos Cabezas and San Cayetano mountains, respectively. These surveys were designed to determine the successional status of oak communities and to detect any possible vegetational changes in past years. Individuals were categorized as to height (indication of age) and percentage decadence (indication of condition).

The height distribution of *Q. emoryi* sampled in the Dos Cabezas Mountains (Fig. 8) reveals that the majority (83%) of these plants were >2.4 m tall, and none of the plants sampled were seedlings (0–0.6 m). Several individuals of *Q. emoryi* examined were dead (17%). These data indicate that most of the oaks were in the older age classes and that reproduction was poor to nonexistent.

The data on height distribution of *Q. oblongifolia* sampled at the San Cayetano Mountains (Fig. 9) indicates that practically all (94%) of the individuals of this species were 2.4 m tall or taller, and none of the plants sampled were in the seedling class of 0–0.6 m. Many of the plants examined were dead (20%), and others were in poor condition. As with *Q. emoryi* in the Dos Cabezas Mountains, most oaks in the San Cayetano

TABLE 12. Estimates of the utilization (percentage) of the annual growth of *Cercocarpus breviflorus* by deer and cattle in the Dos Cabezas Mountains¹

Year	Slope exposure					Year means
	South	Southeast	Neutral	Northwest	Northeast	
1971	75.4 \pm 3.9 (2–100)	83.4 \pm 2.7 (1–50)	84.7 \pm 2.5 (2–100)	81.5 \pm 2.5 (3–115)	80.1 \pm 3.7 (1–50)	80.9 (9–415)
1972	61.9 \pm 5.0 (2–75)	71.3 \pm 5.3 (1–40)	82.7 \pm 3.7 (2–70)	67.4 \pm 3.5 (3–115)	71.2 \pm 4.2 (1–50)	70.4 (9–350)
Slope exposure means	68.6 (4–175)	77.3 (2–90)	83.7 (4–170)	74.5 (6–230)	75.6 (2–100)	75.7 (18–765)

¹ Values are: $\bar{x} \pm t_{.05} S_{\bar{x}}$. (Number plots sampled-total number of plants sampled.) The means represent an estimate of the percentage of the annual leader growth of *Cercocarpus breviflorus* that was used by herbivores.

Mountains belonged to the older age classes, and reproduction was poor.

The above results suggest that *Q. emoryi* and *Q. oblongifolia* in the Dos Cabezas and San Cayetano mountains, respectively, are declining and probably will not maintain their dominance in the present plant communities. According to Daubenmire (1968:105) these plants would be classified as "disappearing relics" of an earlier stage of succession. Because the oak communities were climax at one time, these data most likely display the vegetational changes that Hastings and Turner (1965) have documented in connection with a climatic change to hotter and drier conditions. Apparently the elevation of the lower oak zone on our study areas is shifting upward, the trend for many areas in the southwestern part of the United States.

DISCUSSION

Populations of mule deer and white-tailed deer are generally mutually exclusive in the Sonoran Desert of southern Arizona (Powell et al. 1961). Mule deer are usually replaced by white-tailed deer as one travels from the desert habitats up into the mountainous areas. The degree of association between their populations appears quite variable, and the altitude and vegetational type where this association occurs is often different from one mountain area to another. This fact is well supported by the present study in that populations of these 2 species were sympatric at the study area with higher altitudes and more mesic vegetation and climate (Dos Cabezas Mountains), but mutually exclusive in the area with lower altitudes and more xeric vegetation and climate (San Cayetano Mountains). This phenomenon makes it difficult to ascertain what factor or combination of factors determine where mule deer populations dwindle and white-tailed deer populations appear along this environmental gradient from hot-dry to cool-moist conditions. A closer look at their niche relationships documented during this study may provide some hypothetical answers to this question.

Results from the San Cayetano Mountains show that the 2 populations were closely associated between 1,295 and 1,600 m. The coefficients of association (Southwood 1966) were somewhat neutral in that they indicated that there was no attraction or repulsion between the 2 species. Indices of overlap according to altitude and slope exposure (spatial distributions) were moderate; but they probably were an overestimation of any actual overlap, since the data were pooled for the entire mountain area. Throughout the study, mule deer were primarily associated with habitat types dominated by *Prosopis juliflora* and *Fouquieria splendens*, and they were occasionally observed in the habitats dominated by *Q. oblongifolia*. White-tailed deer utilized a greater diversity of habitat types than mule deer and appeared not to be associated directly with any plant species, although *Q. oblongifolia*, *Dasyliroton wheeleri*, and *Eysenhardtia polystachya* received con-

siderable use. Overlap in habitat selection between the two species was variable from season to season. The relationship in distributional patterns (i.e., spatial distributions and habitat selection) of mule deer and white-tailed deer was most accurately quantified as a product of the indices of overlap in spatial distributions and habitat selection (called coefficients of distributional overlap). Because these coefficients were $\approx 10\%$ or lower for the data from the San Cayetano Mountains, the 2 species were contiguously allopatric, a term discussed by Miller (1967).

Although the populations of mule deer and white-tailed deer were allopatric at the San Cayetano Mountains, there were several key forage plants common to both of their distributions. These plants (*E. polystachya*, *K. parvifolia*, and *C. eriophylla*) were important to the diets of both deer species. Since *E. wrightii* was found primarily within the range of white-tailed deer, it was utilized mostly by that species. The same analogy was applied to *P. juliflora* and distributions of mule deer. The indices of overlap in food habits were high, ranging from 55 to 67%. The low coefficients in distributional overlap and high indices of overlap in food habits led us to speculate that mule deer and white-tailed deer were competitively excluding each other in the San Cayetano Mountains. The concepts of the competitive exclusion principle as outlined by Cole (1960), Hardin (1960), and Miller (1967) support this speculation. The principles of competitive exclusion imply that the removal of one species would allow the other species to disperse and occupy the entire region (i.e., if white-tailed deer were artificially removed from the San Cayetano Mountains, mule deer would soon inhabit the entire mountain). This principle also suggests that 2 similar species mutually avoid each other and select habitats in which each is competitively superior over the other because of certain adaptations. Other pairs of related mammalian species have been found to competitively exclude each other. Koplin and Hoffman (1968) documented this phenomenon for populations of *Microtus montanus* and *Microtus pennsylvanicus* in Montana. *Microtus pennsylvanicus* and *Clethrionomys gapperi* competitively exclude each other (Morris 1969; Grant 1969) as do *Peromyscus* and *Mus* (Sheppe 1967).

Coefficients of competition (product \propto) substantiate the conclusion of competitive exclusion between mule deer and white-tailed deer in the San Cayetano Mountains. These coefficients indicate that they avoid direct competition by the allopatric nature of their distributions.

Contrary to the situation in the San Cayetano Mountains, mule deer and white-tailed deer populations in the Dos Cabezas Mountains were sympatric from 1,980 to 2,440 m. The coefficients of association indicate that there was a high positive association between their populations. The indices of overlap in spatial distributions of their populations were high, ranging from

57 to 66%. Both species were associated with those habitat types dominated by *Q. emoryi*, *J. deppeana*, *C. breviflorus*, *Q. gambelii*, *N. microcarpa*, *S. ereophilus*, and/or *Bouteloua* spp. White-tailed deer displayed a greater preference for *Quercus-Cercocarpus* and *Quercus-Symphoricarpos* habitat types than mule deer, whereas the *Juniperus-Cercocarpus* habitats were preferred by the mule deer. These differences in habitat preference were slight, however, and overlap in habitat selection was also high, ranging from 66 to 81%. The product of the indices of overlap in spatial distributions and habitat selection (coefficients of distributional overlap) indicate the sympatric nature of mule deer and white-tailed deer populations at the Dos Cabezas Mountains.

Several key forage plants in the Dos Cabezas Mountains were important to diets of both deer species; the most prominent were *C. breviflorus*, *J. deppeana*, *E. wrightii*, and *Q. gambelii*. The high overlap in spatial distributions, habitat selection, and food habits coupled with the high utilization of the key forage plant, *C. breviflorus*, during the winter months led us to speculate that competition between the two species was occurring during that critical season. At the higher elevations, February and March are probably the most critical months of the year with respect to the food supply, so direct competition would be most extreme during these months.

The coefficients of competition substantiate the potential for direct competition between mule deer and white-tailed deer in the Dos Cabezas Mountains. These coefficients were highest for the winter months, which indicates that this time was the most critical. At the lower elevations, where the deciduous oak vegetation did not occur, May and June probably are the most critical months, since there would not be an abundance of deciduous forage plants to sustain deer through the hot, dry months.

Because they convey no information about food availability or abundance, the coefficients of competition indicate only if there is a potential for competition. There obviously would not be any direct competition during and shortly after the rainy season because the food supply was not critical. The same conclusion could be made about other seasons or entire years depending on the availability and quality of food present. The degree of direct competition depends upon the level of use of the major forage plants. Since winter utilization of *C. breviflorus* was greater during 1970–1971 than during 1971–1972, there was probably a higher degree of interspecific competition for food between mule deer and white-tailed deer. The density of deer populations (density dependent factor) determines the degree of direct competition in most cases, but at least 1 density-independent factor was probably influential in the present situation. Plant productivity in desert areas is greatly influenced by annual precipitation, so annual precipitation could conceivably in-

fluence the degree of direct competition between these two species.

Data from both study areas indicate that mule deer and white-tailed deer utilize similar forage plants. This similarity in food habitats undoubtedly reflects similar nutritional requirements for mule deer and white-tailed deer. Extensive work on deer nutrition in Arizona chaparral and desert habitats by McCulloch and Urness (1973) has shown similar forage preferences and nutritional characteristics for mule deer and white-tailed deer. However, some differences in their general food habits do exist. First, white-tailed deer appear to choose a greater diversity of plant species in their diet, as indicated by a significantly greater number of plant species in fecal samples in the present study. We interpret these results to mean that mule deer are more opportunistic or selective in their feeding habits and are able to sustain themselves on only a few desirable species. In contrast, white-tailed deer are more adapted to climax or undisturbed plant communities, since they tend to utilize a greater number of plant species. According to Odum (1969), species diversity in plant communities is higher for mature stages of succession than for developmental stages. The above conclusion is at least true for the Dos Cabezas Mountains because plant availability was essentially equal for both species because of the sympatric nature of their populations.

Secondly, white-tailed deer ate a greater percentage of grasses and herbs than mule deer in the San Cayetano Mountains. This difference has two possible explanations; it was either characteristic of their food preferences, or was a function of plant availability, which results from a greater livestock use in the mule deer habitats of the San Cayetano Mountains. No such difference in the use of grasses and herbs was documented for the Dos Cabezas Mountains, but we believe this was because of extreme overuse of this area by livestock. Consequently, differences in food preferences appears to be the primary explanation (i.e., white-tailed deer graze more than mule deer). In any competitive interactions between these 2 species, mule deer would be favored when livestock grazing is heavy or when some other disturbance to the environment occurs. Range fires would be an exception to this conclusion, because this type of disturbance tends to increase grass and herb abundance (McCulloch 1969; Hungerford 1970) and would favor white-tailed deer. Kramer's (1973) observations on deer-cattle interactions suggest that white-tailed deer are less tolerant of cattle than mule deer. The presence of cattle may interfere with white-tailed deer behaviorally.

The previous discussion concerns competition for a common resource; Miller (1967) and Crombie (1947) have termed this component of competition as "exploitation"; this usually involves use of space and food and is believed to be the most primitive and unstable form of interaction between species. The sec-

TABLE 13. Life table for mule deer ♂♂ from the Dos Cabezas Mountains.¹ x = age group, $l'x$ = number living, lx = number of survivors per 1,000, dx = number of deaths per 1,000, qx = mortality rate, Lx = mean number of individuals alive between the stated age class, ex = mean expectation life

x	$l'x$	lx	dx	qx	Lx	ex
½	190	1,000	279	.279	860.5	1.63
1½	137	721	542	.752	450.0	1.06
2½	34	179	58	.324	150.0	1.00
3½	23	121	74	.612	84.0	1.37
4½	9	47	31	.660	31.5	1.76
5½	3	16	5	.313	13.5	3.19
6½	2	11	0	.000	11.0	3.41
7½	2	11	0	.000	16.0	2.41
8½+	4	21	21	1.000	10.5	0.50

¹ Estimates for the ½ and 1½ age groups were taken from the percentages of spike bucks and percentages of fawns (divided by 2) observed in the population. Numbers in the other age groups were estimated from the age distribution of 77 deer killed during the hunting seasons of 1969, 1970, and 1971.

and component of interspecies competition is "interference" (Crombie 1947; Miller 1967), which results from any activity of a species which either directly or indirectly limits a competitor's access to a necessary resource or requirement. In a spatial context this may be territoriality, display, and/or scent communication. From the behavioral interactions observed between mule deer and white-tailed deer in the present study, it was difficult to determine how important interference was in their interactions. However, the infrequent occurrence of behavioral interactions and the usual nonaggressive nature of these encounters suggests that interference was not an extremely important factor in the relationship between these two species. Behavioral interactions (i.e., dominance-subordination relationships) appear to be of considerable importance between similar pairs of small rodents (Koplin and Hoffman 1968; Grant 1969; Cameron 1971; Murie 1971).

Few papers concerned with interspecies relationships conclude that direct competition has occurred. Cameron (1971) reported interspecific competition between *Neotoma lepida* and *Neotoma fuscipes*; similar results have been presented for *Baiomys taylori* and *Sigmodon hispidus* by Raun and Wilks (1964). Many researchers appear reluctant to make such a conclusion, because niche theory and the concepts of the evolution of similar species would be contradicted. Data for part of the present study directly contradict Gause's hypothesis (1935), but we believe this contradiction can be easily explained. First, Gause's hypothesis (1935) is an oversimplification, which considers the environment to be in a stable steady state (i.e., evolution is not occurring). It also fails to adequately consider or recognize that interspecific competition can occur as a temporary and transient phenomenon in response to a changing environment or catastrophic

TABLE 14. Age classification of hunting and natural mortalities of white-tailed deer in the Dos Cabezas Mountains

Parameter	Age group								
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8+
Number	1	3	1	1	4	5	4	3	3
Percentage	4	12	4	4	16	20	16	12	12

disturbance. Interspecific competition between mule deer and white-tailed deer was undoubtedly a transient phenomenon in the Dos Cabezas Mountains. Recruitment to the populations of mule deer and white-tailed deer favored mule deer; the doe:fawn ratio for mule deer was 100:37 and that for white-tailed deer was 100:30. Spike bucks made up 64% of the population of antlered deer for mule deer and only 24% for white-tailed deer. These data indicate that the average recruitment to mule deer populations was higher than that for white-tailed deer, so that the ratio of mule deer to white-tailed deer in the total deer population is probably increasing slowly. This change would be a slow process, when the low turnover rate for deer populations is considered. There are many examples that show selective elimination of species through exploitation of food may require an extremely long time, even in simple environments where food and space are limited. In laboratory populations of *Tribolium* spp., at least 8 generations (270 days) were required for one species to replace another (Park 1948). Consider the difference in turnover rates between *Odocoileus* spp. and *Tribolium* spp. and the corresponding replacement time becomes quite long.

Because we could not conduct a detailed study of the population dynamics of mule deer or white-tailed deer, the status of their populations cannot be determined conclusively. However, the age distribution of mule deer (Table 13) takes the shape of a pyramid and, therefore, suggests that their populations are increasing. Samples for white-tailed deer from the Dos Cabezas Mountains were inadequate but it appears that their populations are declining because deer older than 3.5 yr comprised 76% of known mortalities (Table 14). Consequently, all evidence suggests that the mule deer population is increasing, while the white-tailed population is declining. White-tailed deer may never completely disappear from this mountain area, but we believe their numbers will become so low that interspecific competition will no longer be of significance. Also, there may be microhabitats in which white-tailed deer are still competitively superior to mule deer.

If one accepts the conclusion that competition between mule deer and white-tailed deer has been (or is) occurring, the question is: What factor or combination of factors has brought these species into direct competition? We believe the major factor has been a vegetational change coupled with overgrazing by livestock. Hastings and Turner (1965) gave evidence that there

has been an upward shift in the vegetational zones in southern Arizona during the last 100 yr. Their work shows that there has been a decline in desert grasslands because of the encroachment of desert shrubs (*P. juliflora*, *F. splendens*, *A. greggii*, and *A. constricta*) into grassland communities. They also provided evidence that the lower oak zone is retreating upward in altitude. According to Hastings and Turner (1965), hotter and drier conditions coupled with overgrazing by livestock and fire suppression appear to be the causes of these vegetational changes. Other articles also provide evidence for these vegetational changes in recent (Humphrey 1958) and prehistoric years (Van Devender and King 1971). Surveys conducted on *Quercus* spp. during this study suggest that the lower oak zone is retreating upward in the San Cayetano and Dos Cabezas mountains. Analysis of size classes indicated that the oaks (*Q. oblongifolia* or *Q. emoryi*) are remnant populations with little or no reproduction occurring. Both the documented vegetational changes and overgrazing by livestock would tend to favor mule deer in competitive interactions with white-tailed deer.

With respect to the past historical changes in mule deer and white-tailed deer distributions, 3 factors have probably been influential: (1) a climatic change to hotter and drier conditions that has resulted in an upward shift in the vegetational zones; (2) overgrazing by livestock; and (3) fire suppression. All of these factors create or allow vegetational changes that would favor mule deer encroachment into white-tailed deer range.

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