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

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

by

Robert Gene Anthony

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF BIOLOGICAL SCIENCES

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN ZOOLOGY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by **Robert Gene Anthony**

entitled **Ecological relationships between mule deer and white-tailed deer in southeastern Arizona**

be accepted as fulfilling the dissertation requirement of the degree of **Doctor of Philosophy**

NS Smith — 5 July 1972
Dissertation Director — Date

After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

R O Kuehl — July 3, 1972
Lyle K. Sowls — July 3, 1972
Charles R. Hungerford — July 5, 1972
Russell Davis — July 5, 1972

*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.

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ABSTRACT

Research on the niche relationships between mule deer and white-tailed deer was conducted from September, 1969, to March, 1972, at the Dos Cabezas and San Cayetano Mountains, southeastern Arizona. The major objective was to ascertain whether these two species compete for food and/or space in areas where they are closely associated. Spatial distributions, habitat selection, and food preferences of mule deer and white-tailed deer were compared. Behavioral interactions, recruitment to populations, and forage utilization were also studied.

Spatial distributions of mule deer and white-tailed deer at the San Cayetano Mountains indicated that their populations were contiguously allopatric. Mule deer were usually associated with the desert shrub vegetation while white-tailed deer were found primarily in the desert grassland and oak woodland habitats. There was more than 50 per cent overlap in the food preferences of mule deer and white-tailed deer; most of this overlap was on *Eysenhardtia polystachya* and *Krameria parvifolia*. It was hypothesized that mule deer and white-tailed deer competitively exclude each other at the San Cayetano Mountains.

Spatial distribution of mule deer and white-tailed deer at the Dos Cabezas Mountains indicated that their populations were sympatric from 6,500 to 8,000 feet in elevation. There was also a great similarity in habitat selection and food preferences between the two species. *Cercocarpus breviflorus*, *Eriogonum wrightii*, *Juniperus deppeana*, and *Quercus gambelii* were the most important forage species for both mule deer and white-tailed deer. Since the key browse species, *Cercocarpus breviflorus*, was highly overutilized by deer and cattle, mule deer and white-tailed deer probably compete directly for food during the critical time of the year (February and March).

White-tailed deer utilized a greater diversity of food items than did mule deer on both study areas. Grasses and herbs appear to be more important in the diets of white-tailed deer than mule deer. Mule deer were dominant over white-tailed deer in all behavioral interactions observed during the study. The influences of vegetative change, overgrazing by livestock, and fire suppression are discussed with respect to the ecological relationships between mule deer and white-tailed deer.

INTRODUCTION

The desert mule deer (Odocoileus hemionius crooki) is the primary herbivore 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 400 to 500 miles south into Mexico and east into New Mexico. This subspecies of mule deer is primarily associated with the desert shrub and desert grassland life zones, and in some areas its range extends into the chaparral vegetation. Desert mule deer appear to have adapted to the desert environment primarily by behavioral mechanisms.

The Coues white-tailed deer (O. virginianus couesi), the desert mule deer's counterpart, occupies the mountain ranges of the Southwest. It 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 Mexico and south into Sonora, Mexico (Hoffmeister, 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 extensively in others. The transition between mule deer and white-tailed deer populations may be as low as 3,000 feet in elevation or as high as 6,000 feet depending on the mountain area. The net effect from an aerial viewpoint is islands of white-tailed deer populations emerging from a sea of desert mule deer range. There is generally no gap between populations of mule deer and white-tailed deer, and they 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 years or more. Range extension of desert mule deer has usually been to areas previously inhabited by the Coues white-tailed deer. During this time white-tailed deer have disappeared or declined drastically from the following areas: Tucson Mountains, Winchester Mountains, Tortolita Mountains, Reddington Pass, Picacho Mountains, and Black Hills. Desert mule deer now occupy these areas. Documentation of this alleged change in mule deer and white-tailed deer distributions is very difficult, but the annual kill records published by the Arizona Game and Fish Department appear to substantiate this concept. The ratio of white-tailed deer to mule deer killed in southeast Arizona (Game Management Units 29-36) has declined steadily from 1946 to present (see Appendix A).

In view of the history of mule deer and white-tailed deer distributions, their occasional overlapping populations, and their morphological, physiological, and ecological similarities the following questions arose: Does interspecific competition between desert mule deer and the Coues white-tailed deer exist, and if so, does it act as a limiting factor to white-tailed deer populations? Martincka (1968) published on the habitat relationships of white-tailed deer and mule deer in Montana, but to the best of my knowledge competition between these two species has never been directly studied.

In this work I will refer to interspecies competition as the act of two species seeking the same space and food, which are in short supply, or interacting in such a way that it affects their growth and survival. From this definition four objectives were proposed for the study: (1) to study and quantify the spatial distributions of mule deer and white-tailed deer where their ranges overlap, (2) to study habitat selection of mule deer and white-tailed deer where they coexist, (3) to study food habits of mule deer and white-tailed deer in these areas, and (4) to determine if the forage plants common to the diet of both species are overutilized.

Hutchinson (1957) laid the groundwork for studies of ecological niches of animals, both vertebrate and invertebrate. Review articles on competition and niche theory have been published recently by Miller, 1967; Levins, 1968; and MacArthur, 1967. It was Darwin (1859) who first noted that similar species should not occupy the same niche, and Gause (1935) expanded his ideas. In more recent years the concepts of interspecific competition, niche theory, and competitive exclusion have stimulated the theoretical biologist as well as the field biologist. Passerines and rodents have been the object of study for most field biologists, for the former are easy to observe and the latter easy to trap and not extremely mobile. 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 mammal species. The list of studies on avian species is more extensive, and laboratory populations of invertebrates (*Drosophilia spp*. and *Tribolium spp*.) have probably been researched most extensively.

The niche relationships between large mammalian herbivores have been practically unstudied. Papers by Mackie (1970), Martincka (1968), Morris and Schwartz (1957), Cowan (1947), and Cliff (1939) are the only studies on North American species that even relate to the topic. Numerous studies have pointed out the occurrence of competition between ungulate populations and livestock, but these unnatural relationships have been brought about by man and are artificial in an evolutionary sense. Interspecific competition in these situations therefore, is to be expected.

The purpose of this study aside from the specific objectives outlined above was to study the niche relationships of two larger and more mobile mammalian species, mule deer and white-tailed deer. And, since these two primary consumers were microsympatric on one of the study areas, I wanted to test the validity of Gause's Hypothesis under natural field conditions. Gause's Hypothesis, as stated in the British Ecological Society's 1944 Symposium on the ecology of closely related species (Anonymous, 1944), reads "two species with similar ecology cannot live together in the same place." The usefulness of this hypothesis has already been questioned on a theoretical basis by Cole (1960), Hardin (1960), and Gilbert, Reynoldson, and Hobart (1952).

METHODS AND MATERIALS

Field Techniques

Field work was conducted on the study areas from September, 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 deer were located the species was identified and the sex-age classifications were recorded. The dominant vegetation of the immediate area around the deer was recorded as was altitude and slope exposure. Altitude of the location of deer was determined by use of topographic maps and/or an altimeter and slope exposure by use of a compass. Feeding observations were tabulated by recording each time an individual deer was observed to feed on any particular plant species. This information provided qualitative data on food habits of mule deer and white-tailed deer and was used as a guideline for the preparation of reference slides of the epidermal characters of forage plants. When mule deer and white-taled deer were located within approximately 50 yards of each other, notes were taken on any behavioral interactions that were observed. If deer were observed defecating, their fecal samples were collected for microscopic analysis of food habits. Only fresh fecal samples were collected for these analyses, and each sample was identified as mule deer or white-tailed deer by observations or by tracking known species of deer to fresh fecal samples. Some observations were made by vehicle, but these observations were generally unsatisfactory. Deer usually fled from vehicles and the rugged terrain prohibited vehicular travel in most parts of the study areas.

The study of food habits and habitat selection of deer necessitates a knowledge of plant taxonomy and the classification of plant communities, respectively. All plants mentioned in this work have been identified according to the nomenclature set forth by Kearney and Peebles (1964). Habitat selection of deer was noted according to the two dominant plant species in the immediate vicinity of the deer being observed. These areas were designated as "habitat types" or "vegetative 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 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 vegetative type was used somewhat synonymous to habitat type, but it was applied to those plant communities, which were not climax, homogeneous, or repeated throughout the landscape. All the area over which one plant association is climatic climax represents a "vegetative zone" of essentially uniform macroclimate insofar as vegetation is concerned. Within one vegetative zone there occurs a number of habitat types. Daubenmire (1968) gives 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.

Key forage plants were sampled at 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). A compass or contour direction was selected in the desired area. Each plant that was sampled was selected by use of a random number table, the random number indicating the number of forward steps to take. The closest individual of the desired species within a 180 degree radius was sampled. 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 <u>Quercus</u> <u>spp</u>. were conducted for estimation of age composition, successional status, and vigor. Slope exposure, altitude, height, and per cent decadence were recorded for each plant sampled. Selection of these plants was done by Cole's (1956) technique as described above.

Hunter check stations were operated during the hunting season. Rumen samples, kidneys with fat, fecal samples, and lower mandibles were collected when possible. Information from these stations was used to supplement other data collected during the study.

Laboratory Techniques

The major obstacle of the project was securing adequate samples for food habits of mule deer and white-tailed deer throughout the year. Rumen analysis was deemed impractical because of limited samples, and the feeding minutes technique because of the time requirement. The only technique that was feasible to meet the objectives of the project was that of studying food habits by fecal analysis. Since every plant species has unique cuticle 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 (Stewart, 1965, 1967; Stewart and Stewart, 1970; Adams, 1957; Hercus, 1960; Martin, 1955; Storr, 1961). Epidermal characters have been used to study herbivore food habits by Dusi (1949) on cottontail rabbits, Kiley (1966) on waterbuck, Myers and Vaughn (1965) on pocket gophers, Stewart (1967) on Africa game species, Zyznar and Urness (1969) on deer, Scott (1941) on red fox, and others. 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 Storr (1961) method. Leaf fragments were boiled in 5 ml each of 5 per cent nitric and chromic acids for three minutes under an acid fume hood until the mesophyll disintegrated and the epidermis separated. The contents were poured into a 250 ml beaker and topped with water. These leaf fragments were stained in methylene blue for 10-30 minutes, washed in water, and dehydrated in an alcohol-xylene series (50, 75, and 95% alcohol and xylene). The stained leaf fragments were mounted to slides with Permount mounting media. Since the abaxial and adaxial surfaces of leaves usually have different cuticular characteristics (Stewart, 1965), slides were prepared of both leaf surfaces of each plant species.

Fecal samples, which were collected in the field, were 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. The fragments were boiled in 4 ml of concentrated nitric acid over a water bath for 2-3 minutes and then placed in 200 ml of water, which was boiled and stirred to complete clearing of cuticular fragments. The cuticular fragments were allowed to settle to the bottom, and the supernate was poured off. The fragments were stored in 1 part formal acetic acid and 1 part 30% glycerin until they could be analyzed microscopically.

From each prepared fecal sample, sub-samples were spread out on slides under 22 mm^2 cover slips. These sub-samples 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 22 mm^2 cover slip. Five slides (sub-samples) were analyzed for each sample by transversing the slide systematically. For each slide analyzed 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 mid-point of each of these ranges was used as the percentage contribution of each species to the total recognizable cuticular fragments in each sub-sample. An average over the five sub-samples for each plant species was used as an estimate of the per cent 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.

The biases involved with the use of fecal analysis for studying food preferences of herbivores has been discussed by Stewart (1967). Differences in digestibility of the various plant species cause over- and underestimates of the proportion that each species contributes to the total diet. Stewart (1967) found that the cuticles of perennial grasses were more resistant to digestive processes than those of annual grasses. Storr (1961) in his work with quokkas (Setonix brachyurus), marsupials with ruminant-like digestive systems, concluded that perennial dicots showed no differential breakdown, but succulent annuals survived digestion very poorly. Because deer are primarily browsers, these biases are probably insignificant for this study. An exception to this may occur during the rainy season when many succulent annuals are available to deer. The same type of biases have been documented for rumen analysis in studying food habits of deer.

The major advantages in using fecal analysis for studying food habits of herbivores is that it allows practically unlimited sampling, and the disturbance to the animal population is minimal. The major disadvantage, however, is that it is very time-consuming and therefore, not very feasible for short-term studies. To use this technique for studying food habits of deer, I believe, it is necessary (1) to tally or take notes on feeding observations of deer in the field, and (2) to also take notes on plant phenologies, so one will know when a particular species is available or most desirable to deer. This way a list of "possibles" for a particular season can be used to increase accuracy of identification and reduce the time required for identifying epidermal fragments in the feces.

Statistical Techniques

A secondary objective of studying food habits of mule and white-tailed deer was to analyze for statistical differences in the number of plant species identified in each fecal sample with respect to deer species and season of the year. I wanted to know, in particular (1) if there was any statistical difference in the diversity of plant species used by mule deer as compared to white-tailed deer and (2) if there was any statistical difference in the number of plant species per fecal sample from season to season.

The statistical design used to answer the above questions was an analysis of variance with a 2 x 6 factorial experiment with an interaction (Steel and Torrie, 1960). Since there was unequal sample sizes in 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:

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

The model states that the number of plant species in each fecal sample (Y_{ijk}) in the j^{th} season ($j = 1, \ldots, 6$) for the i^{th} species ($i = 1,2$) is a linear function of the grand mean u, the fixed species effect (A_i), the fixed season effect (B_j), and the random individual effect (e_{ijk}). The errors (e_{ijk}) are assumed to be normally and independently distributed with mean zero and homogeneous variance. This statistical model was used to compare the number of plant species per fecal sample according to species and season for data collected at both the San Cayetano and Dos Cabezas Mountains.

In this study it became necessary to calculate indices of overlap in spatial distributions, habitat selection, and food habits of mule deer and white-tailed deer for various seasons of the year. Since data on these parameters was of the frequency type, the calculation of these indices was very simple. For example, if the mule deer diet consisted of 15.5 per cent _Eysenhardtia polystachya_ and that of white-tailed deer 7.2 per cent, then the overlap, Y_i, for _Eysenhardtia polystachya_ would be 7.2 per cent. 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. 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. According to Orians and Horn (1969) little is known about the statistical distributions of these measurements, so that statistical inferences can not be made concerning them.

THE STUDY AREAS

Field research for this project was conducted on two study areas, the San Cayetano and Dos Cabezas Mountains. These two areas were chosen according to two primary criteria: (1) deer densities were great enough to facilitate numerous observations and (2) populations of mule deer and white-tailed deer were closely associated.

The San Cayetano Mountains are located approximately ten miles north of Nogales, Arizona, and total around eight square miles of mountainous country. The climate is hot and dry with the majority of the precipitation coming during the months of August and September. The mean annual temperature at the Tumacacori National Monument about five miles away is 64.1°F with an average annual precipitation of 14.15 inches. This relatively small mountain mass rises abruptly from the surrounding, rolling hills at 4,000 foot in elevation to 6,000 foot at its highest point. Most of the good deer habitat is between 4,500 and 5,500 foot in elevation, since the areas below 4,500 foot are marginal and severely overgrazed by livestock. Three vegetative zones occur on or around this mountain area: (1) upper desert shrub, (2) desert grassland, and (3) oak woodland. The desert shrub areas appeared to be disclimax communities, since most of these habitats were originally desert grassland. Mesquite (*Prosopis juliflora* var. velutina) has invaded into these areas and is now the dominant species. Ocotillo (*Fouquieria splendens*) and many cactus species frequently occur as co-dominants with mesquite. *Calliandra eriophylla* and *Krameria parvifolia* are prominent low-growing shrubs and are major sources of food to deer. *Bouteloua curtipendula* and *B. chondrosiodes* are the dominant grass species. The desert grassland zone comprises the majority of the mountain area. *Bouteloua curtipendula*, *B. chondrosiodes*, *Lycurus phleoides*, *Andropogon ciratus*, and *Heteropogon contortus* were the most prominent grass species. A variety of other plants were associated with these grasses depending on altitude, slope exposure, and soil type. These species are: *Nolina microcarpa*, *Eysenhardtia polystachya*, *Eriogonum wrightii*, *Krameria parvifolia*, *Calliandra eriophylla*, *Dasylirion wheeleri*, *Agave schottii*, *Fouquieria splendens*, and *Opuntia spp*. Remnants of the oak woodland occur on the north-facing slopes at the higher elevations. Mexican blue oak (*Quercus oblongifolia*) is the dominant plant species. Any or all of the following plants may be associated with the oaks: *Fendlera rupicola*, *Nolina microcarpa*, and *Dasylirion wheeleri*. The most frequent grass species are *B. curtipendula* and *Lycurus phleoides*. Many herbs and annuals can be found in this zone after the summer rains.

The Dos Cabezas Mountains are located southeast of Willcox, Arizona, and comprise approximately fifty square miles 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, which is approximately 15 miles away, is 58.9°F with an average annual precipitation of 11.39 inches. The surrounding flatlands range from 4,500 to 5,000 foot in elevation, and the highest portions of the mountain are around 8,000 foot. Livestock use is heavy throughout most of the area. The highest deer densities are between 6,000 and 7,500 foot in elevation, and mule deer and white-tailed deer occur throughout these areas. Three vegetative zones were recognized in the areas where the study was carried out: (1) desert grassland, (2) mixed oak-woodland chaparral, and (3) deciduous oak. Many habitat types within these vegetative zones were recognized, but only eight were used extensively by deer. The *Nolina*-*Bouteloua* habitat type was the major type used in the desert grassland. *Nolina microcarpa* and *Bouteloua curtipendula* are the dominant species, and *B. gracilis*, *Eriogonum wrightii*, and *Andropogon cirratus* are usually associated with these dominants. This habitat type is restricted to south-facing slopes above an elevation of 6,000 foot. Four of the habitat types in the mixed oak-woodland chaparral zone are dominated by *Quercus emoryi*.

The difference in these habitat types is based upon the plant(s) that are co-dominant with *Quercus emoryi*. The four habitat types are: (1) *Quercus*-*Cercocarpus*, (2) *Quercus*-*Juniperus*, (3) *Quercus*-*Cercocarpus*-*Juniperus*, and (4) *Quercus*-*Nolina*. So *Cercocarpus breviflorus*, *Juniperus deppeana*, and/or *Nolina microcarpa* are co-dominants with *Q. emoryi* in these habitat types. Four other species (*Eriogonum wrightii*, *Bouteloua gracilis*, *Bouteloua curtipendula*, and *Lycurus phleoides*) were associated with the dominants with varying importance depending on the habitat type. *Quercus hypoleucoides* occasionally replaces *Q. emoryi* as a co-dominant in the above habitat types when microclimatic conditions are slightly cooler and moister. The *Cercocarpus*-*Nolina* habitat type appears to be indicative of areas of shallow soil over limestone bedrock as reported by Whittaker and Niering (1968) for the Santa Catalina Mountains. *Eriogonum wrightii* and *Bouteloua gracilis* are usually associated with the two dominants in this habitat type. The *Juniperus*-*Cercocarpus* habitat type is quite widely distributed with *Cercocarpus breviflorus* and *Juniperus deppeana* as co-dominants. *Nolina microcarpa*, *Eriogonum wrightii*, *Bouteloua gracilis*, and *Lycurus phleoides* are commonly associated with the dominants. The last habitat type (*Quercus*-*Symphoricarpos*) is found only on northerly-facing slopes at the higher elevations; it is part of the deciduous oak zone. Gambel's oaks (*Quercus* *gambelii*) and mountain snowberry (*Symphoricarpos oreophilus*) are the dominant species. *Holodiscus dumosus*, *Ptelea angustifolia*, and/or *Robinia neomexicana* are often associated with the dominant species. This habitat type is indicative of those microclimates having the coolest and moistest conditions on the mountain.

CONTIGUOUS ALLOPATRY: SAN CAYETANO MOUNTAINS

Relationships between mule deer and white-tailed deer were studied at the San Cayetano Mountains from August, 1969, to January, 1972. During this time 828 deer were observed; white-tailed deer comprised 584 and mule deer 244 of these observations. The 584 white-tailed deer were observed in 252 different groups or 2.3 white-tails per group. Likewise, the 244 mule deer were observed in 65 groups or 3.8 mule deer per group. This displays the more gregarious nature of mule deer.

Spatial Distributions

Permanent records of the sightings of each group of deer were kept on duplicate topographic maps of the study area. Figure 1 represents a compilation of all of these records, where distributions of mule deer and white-tailed deer are related to altitude and vegetative zone. Each circle and cross represents a sighting of a group of white-tailed deer and mule deer, respectively, and not a sighting of individual deer. White-tailed deer were found predominately at the higher elevations throughout the study, and only a few were observed in the desert shrub vegetative zone. The desert grassland and oak woodland zones both received comparable use by white-tailed deer.

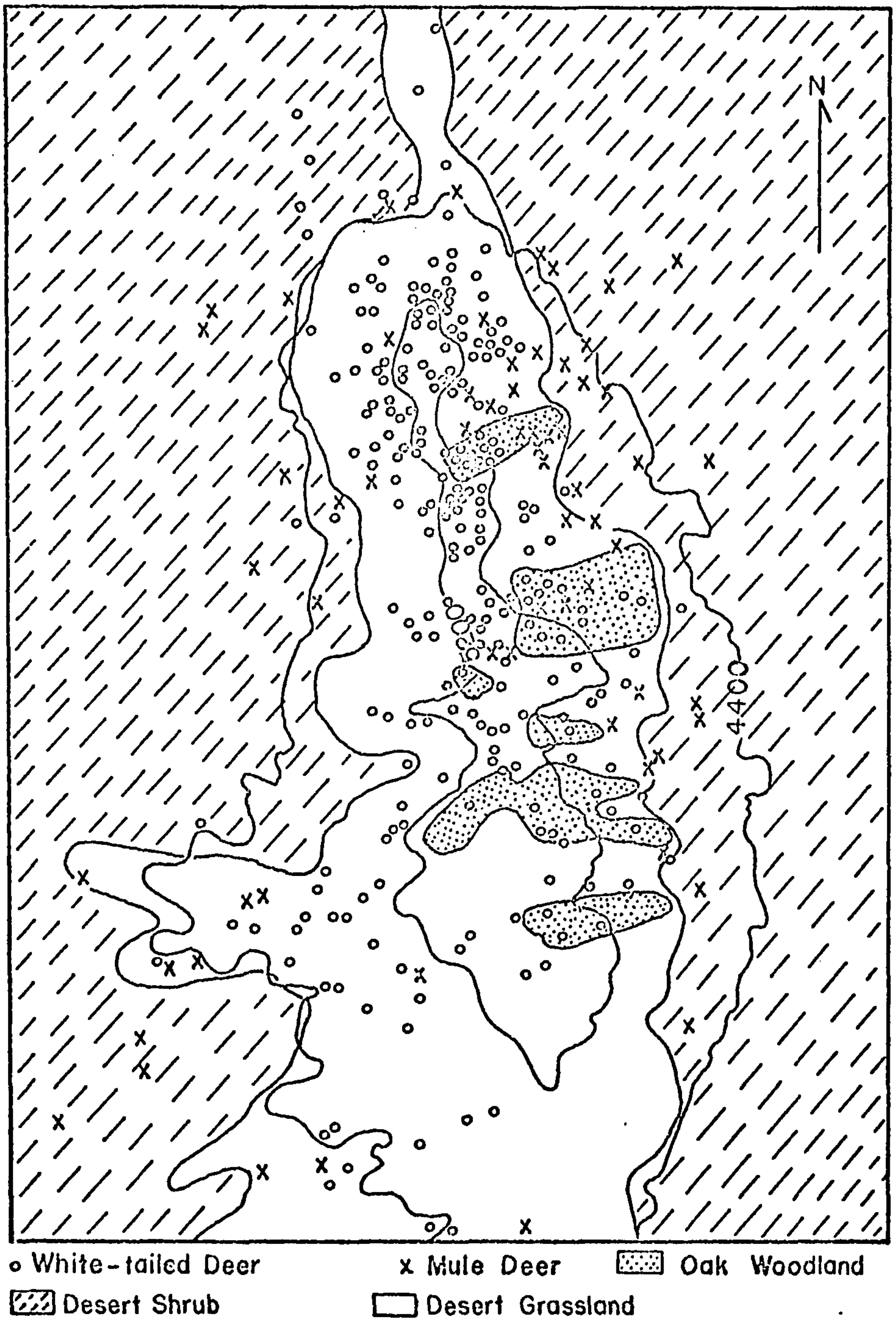


Figure 1. Distributional patterns of mule deer and white-tailed deer in relation to altitude and vegetative zone at the San Cayetano Mountains -- Each circle and cross represent a sighting of a group of white-tailed deer and mule deer, respectively, and not individual deer.

Mule deer were found mainly at the lower elevations in the desert shrub and desert grassland zones, but they were occasionally found in the oak woodland. From Figure 1 it is not exactly clear how mule deer were restricted in distribution. In some parts of the study area they were found at higher elevations and were associated with the more mesic vegetation. In other parts they were observed predominately at the lower elevations in the zeric 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. Because Figure 1 is a compilation of the data over all seasons for the duration of the study, it is obviously an over-estimate of any actual overlap that occurs between the two species.

Spatial distribution of mule deer and white-tailed deer according to slope exposure and altitude are presented in Table 1. Because there were seasonal changes in use of various slope exposures, these data were presented on a seasonal basis: the cool, dry period (February-April); the hot, dry period (May-July); the hot, wet period (August-October); and the cool, wet period (November-January). Table 1a presents the spatial distributions of mule deer and white-tailed deer for the cool, dry period (February-April). These data represent 110 and 56 white-tailed and mule deer observations, respectively. Both mule deer and

Table 1. Percentages of mule deer and white-tailed deer observed at the various slope exposure-altitude intervals at the San Cayetano Mountains (1969-1971).[a]

Altitude Interval	Deer Species[b]	Slope Exposure[c] S	SW	SE	Ne	NW	NE	N
					a: February-April			
5,250- 5,750	WT					7.3	4.6	13.8
	MD							
4,740- 5,249	WT	.9	4.6	11.0	.9	13.8	18.3	8.3
	MD	1.8					1.8	16.1
4,250- 4,749	WT	.9		.9	3.7		2.8	8.3
	MD						28.6	44.6
3,750- 4,249	WT							
	MD				7.1			
					b: May-July			
5,250- 5,750	WT	.6	9.2	3.1	3.1	9.8	8.0	1.2
	MD					5.7		
4,750- 5,249	WT	1.8	9.8	4.3	.6	11.7	11.0	4.3
	MD		2.9		2.9		5.7	5.7
4,250- 4,749	WT		4.9		3.7	6.1		
	MD		5.7	8.6	17.1			
3,750- 4,249	WT		1.2		3.1	1.2		1.2
	MD		17.1	2.9	22.9	2.9		

Table 1.--Continued

Altitude Interval	Deer Species	Slope Exposure						
		S	SW	SE	Ne	NW	NE	N
				c: August-October				
5,250-	WT	1.9	6.5	2.6	3.2	8.4	1.3	5.8
5,750	MD							
4,750-	WT		3.9	10.4	3.9	18.8	8.4	11.0
5,249	MD		1.5	13.6			6.1	16.7
4,250-	WT		2.6	3.9		1.9	1.3	2.6
4,749	MD			4.5	25.8		18.2	4.5
3,750-	WT							1.3
4,249	MD				9.1			
				d: November-January				
5,250-	WT	.6	.6	6.3	1.9	6.3	5.1	
5,750	MD							
4,740-	WT	1.2	20.8	8.2	4.4	13.9	8.2	7.6
5,249	MD		9.2	10.3	16.1		10.3	
4,250-	WT	1.9	5.1	1.2		3.8	.6	
4,749	MD	2.3	3.4	10.2	14.9			
3,750-	WT							
4,249	MD	5.7	2.3	2.3	12.6			

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

[b] WT = white-tailed deer, MD = mule deer.

[c] S = South, SW = Southwest, SE = Southeast, Ne = Neutral, NW = Northwest, NE = Northeast, N = North.

white-tailed deer used northerly slopes extensively; 77 per cent of white-tailed deer and 91 per cent of mule deer observations were from these slopes. South-facing slopes were not used much during this period. There was overlap between their distributions only on north and northeast-facing slopes between 4,250 and 5,250 feet in elevation. When mule deer and white-tailed distributions occurred in the same slope exposure-altitude interval, this constituted an "overlap" in spatial distributions. There was 22 per cent overlap during this season.

Spatial distributions of mule deer and white-tailed deer for the hot, dry season (May-June) are presented in Table 1b and represent 163 white-tailed deer and 35 mule deer observations. The total overlap for this period was 33.3 per cent. Mule deer were extremely hard to find during the months of May, June, and July; they apparently became predominantly nocturnal in these months and spent the daylight hours bedded in the mesquite (*Prosopis juliflora*) thickets. Most deer observations for this period were made on southwest, neutral, and northwest slopes; and overlap between the two species occurred only on these slopes. Overlap was again in the 4,250 to 5,250 foot range in elevation. Since mule deer observations were scanty from May through July, the data on mule deer for this season should be viewed with caution.

During the hot, moist months (August, September, and October) the overlap between mule deer and white-tailed deer was the greatest, 36.8 per cent. For these months 154 and 66 observations of white-tailed deer and mule deer were made, respectively. Overlap (37 per cent) for this period occurred on the southeast, northeast, and north-facing slopes between 4,250 and 5,250 feet in elevation. 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 given in Table 1d, and represent 158 observations of white-tailed deer and 87 of mule deer. Overlap between mule deer and white-tailed deer was moderate during these months also, 36.5 per cent. White-tailed deer used all slopes approximately equally, but mule deer used the south-facing and neutral slopes more extensively (89.7 per cent).

Association between two species has been discussed by Southwood (1966). One of his formulas, modified from Whittaker and Fairbanks (1958) for coefficients of species association, is applicable to the data collected during this study on spatial distributions of mule deer and white-tailed deer. The formula is:

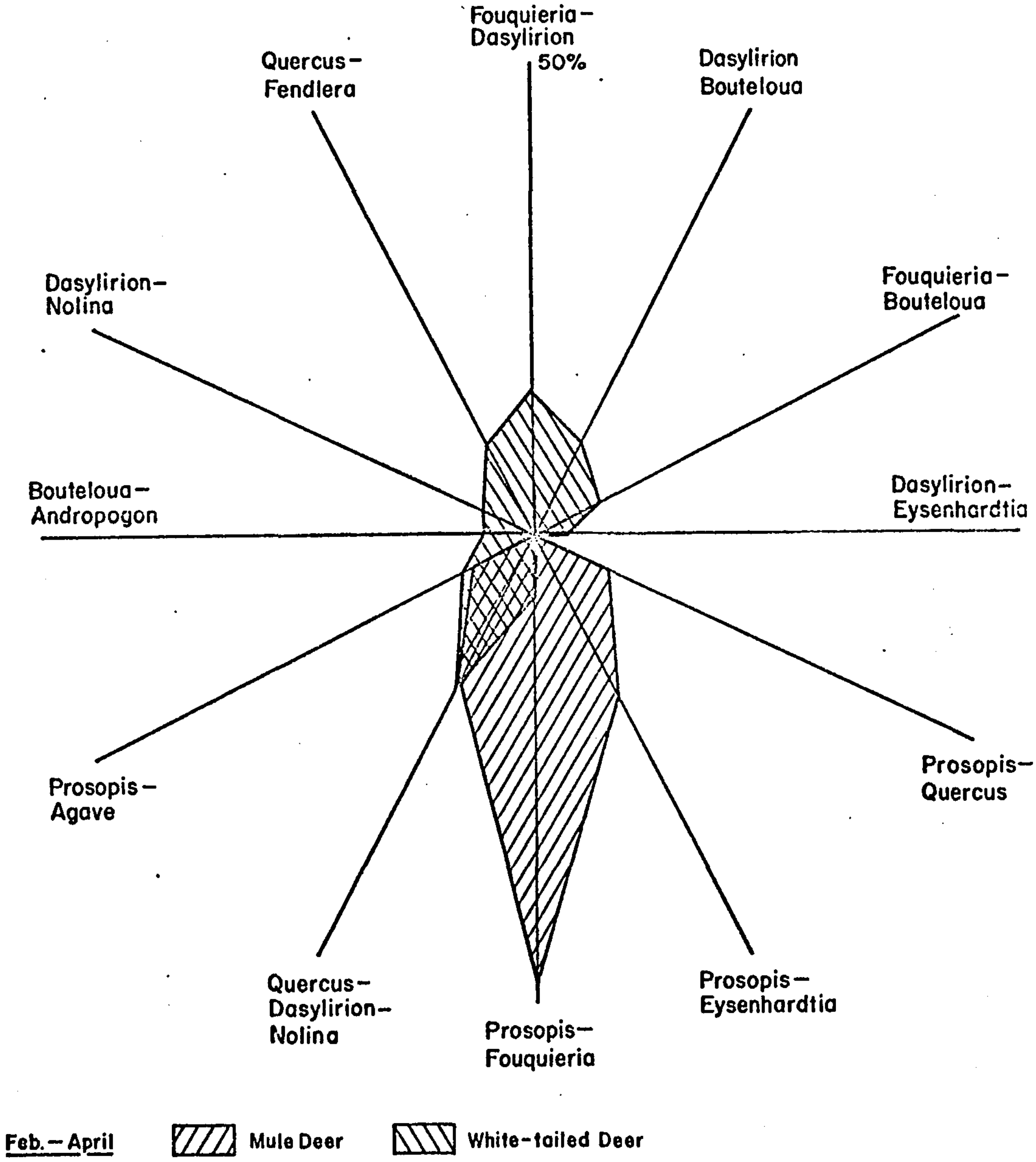
$$I_{ai} = 2\left[\frac{J_i}{A+B} - 0.5\right]$$

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. The desirable quality of this formula is that it takes into account the number of individuals (population densities) of each species involved. This coefficient ranges from -1 (no association) to +1 (complete association). This coefficient calculated for the above data is as follows: (1) February-April, +.192; (2) May-July, +.122; (3) August-October, -.028; and (4) November-January, +.086. These coefficients indicate that there is some association between mule deer and white-tailed deer at the San Cayetano Mountains for all seasons, but that this association is not complete (positive). There is no attraction between mule deer and white-tailed deer at the San Cayetano Mountains, but at the same time there is no repulsion.

Habitat Selection

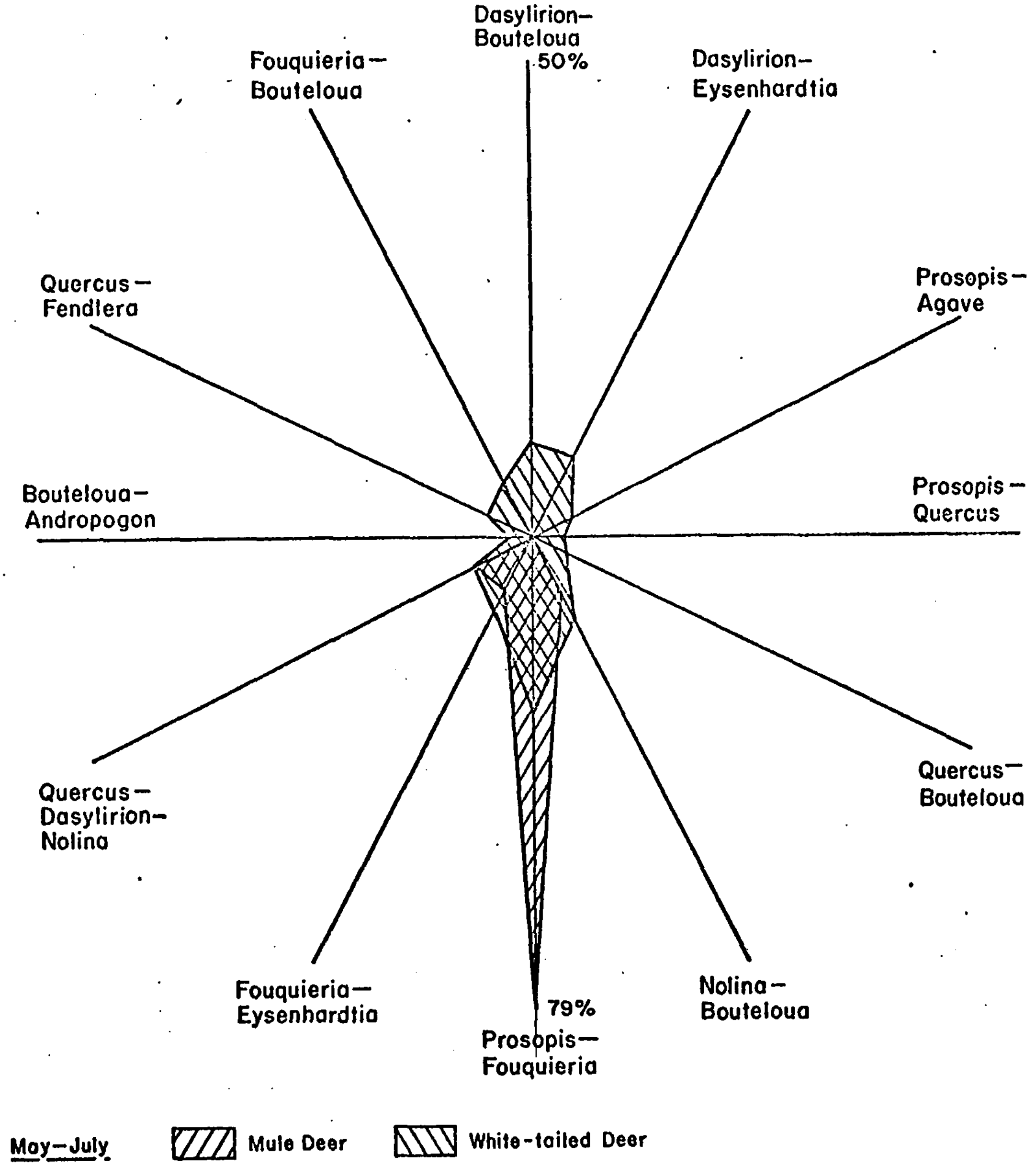
Habitat selection of mule deer and white-tailed deer was studied by noting the dominant vegetation surrounding each individual or group of deer observed. Usually two plant species that were largest in size and/or most dense were designated as the dominant vegetation. Many types of "dominant vegetation" were recognized during the study, but only the following were significant to deer distributions at the San Cayetano Mountains: (1) *Quercus*-*Fendlera*, (2) *Quercus*-*Nolina*-*Dasylirion*, (3) *Quercus*-*Bouteloua*, (4) *Dasylirion*-*Nolina*, (5) *Dasylirion*-*Bouteloua*, (6) *Nolina*-*Bouteloua*, (7) *Dasylirion*-*Eysenhardtia*, (8) *Bouteloua*-*Andropogon*, (9) *Fouquieria*-*Eysenhardtia*, (10) *Fouquieria*-*Bouteloua*, (11) *Prosopis*-*Quercus*, (12) *Prosopis*-*Agave*, (13) *Prosopis*-*Eysenhardtia*, (14) *Fouquieria*-*Dasylirion*, (15) *Prosopis*-*Fouquieria*, (16) *Eysenhardtia*-*Bouteloua*, (17) *Fouquieria*-*Opuntia*, and (18) *Fouqieria*-*Calliandra*. Use of these vegetative types depended on the season of the year.

Figure 2a illustrates habitat selection of mule deer and white-tailed deer during the months of February, March, and April. Mule deer were found predominantly in the *Prosopis*-dominated vegetative types; 84 per cent of all mule deer were observed in this habitat during this season. Mule deer were also observed in the *Quercus*-*Dasylirion*-*Nolina* habitats (16 per cent). White-tailed deer displayed a marked preference for those habitats composed of *Quercus*, *Dasylirion*, *Nolina*, *Bouteloua*, and/or *Fouquieria*. Overlap in habitat selection between mule deer and white-tailed deer occurred on the *Quercus*-*Dasylirion*-*Nolina*, *Prosopis*-*Agave*, and *Prosopis*-*Fouquieria* habitat types. The estimated overlap in habitat selection for this season (February-April) was 31 per cent.



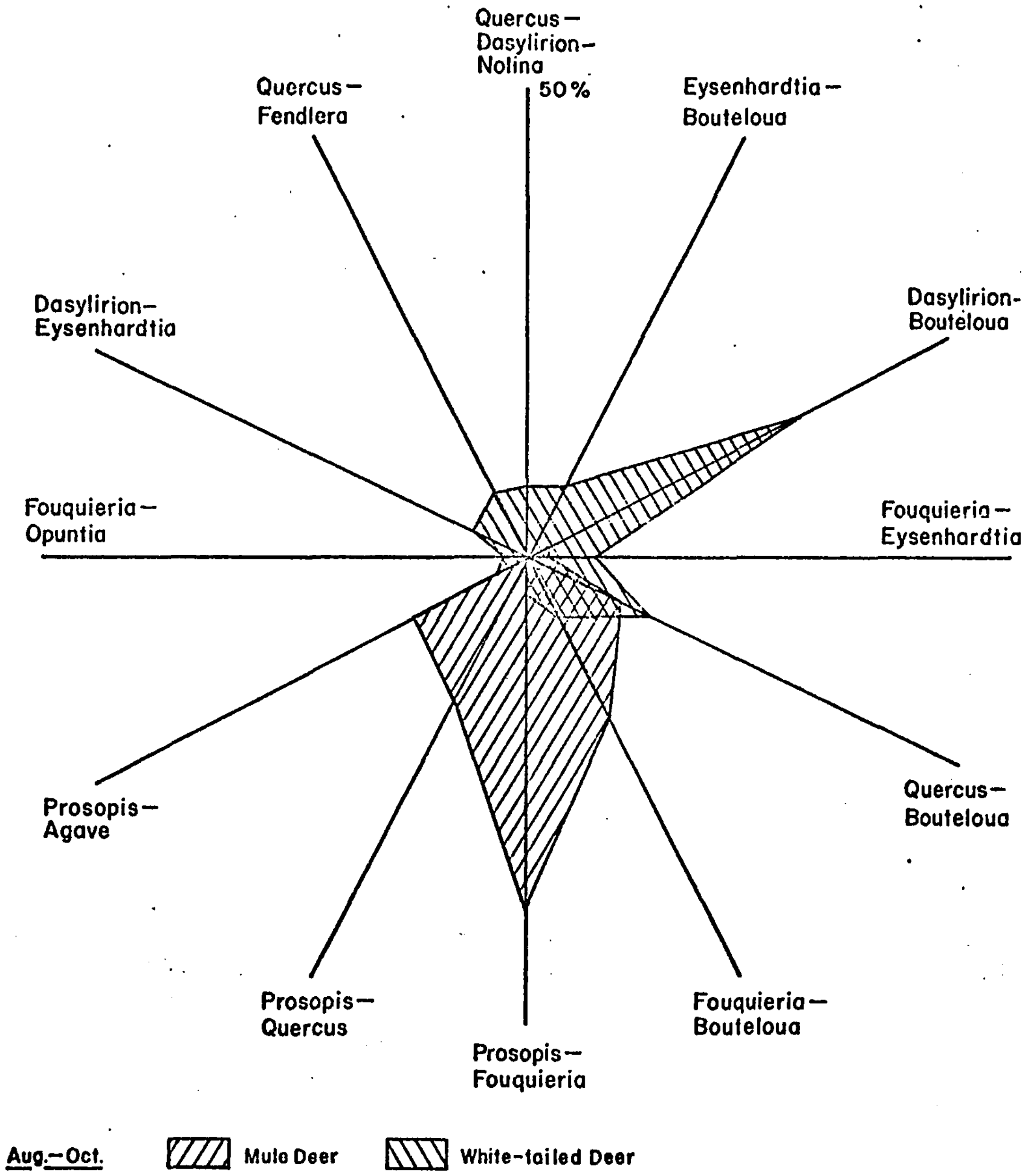
a: February-April

Figure 2. Habitat selection of mule deer and white-tailed deer according to habitat type at the San Cayetano Mountains, southeast Arizona.



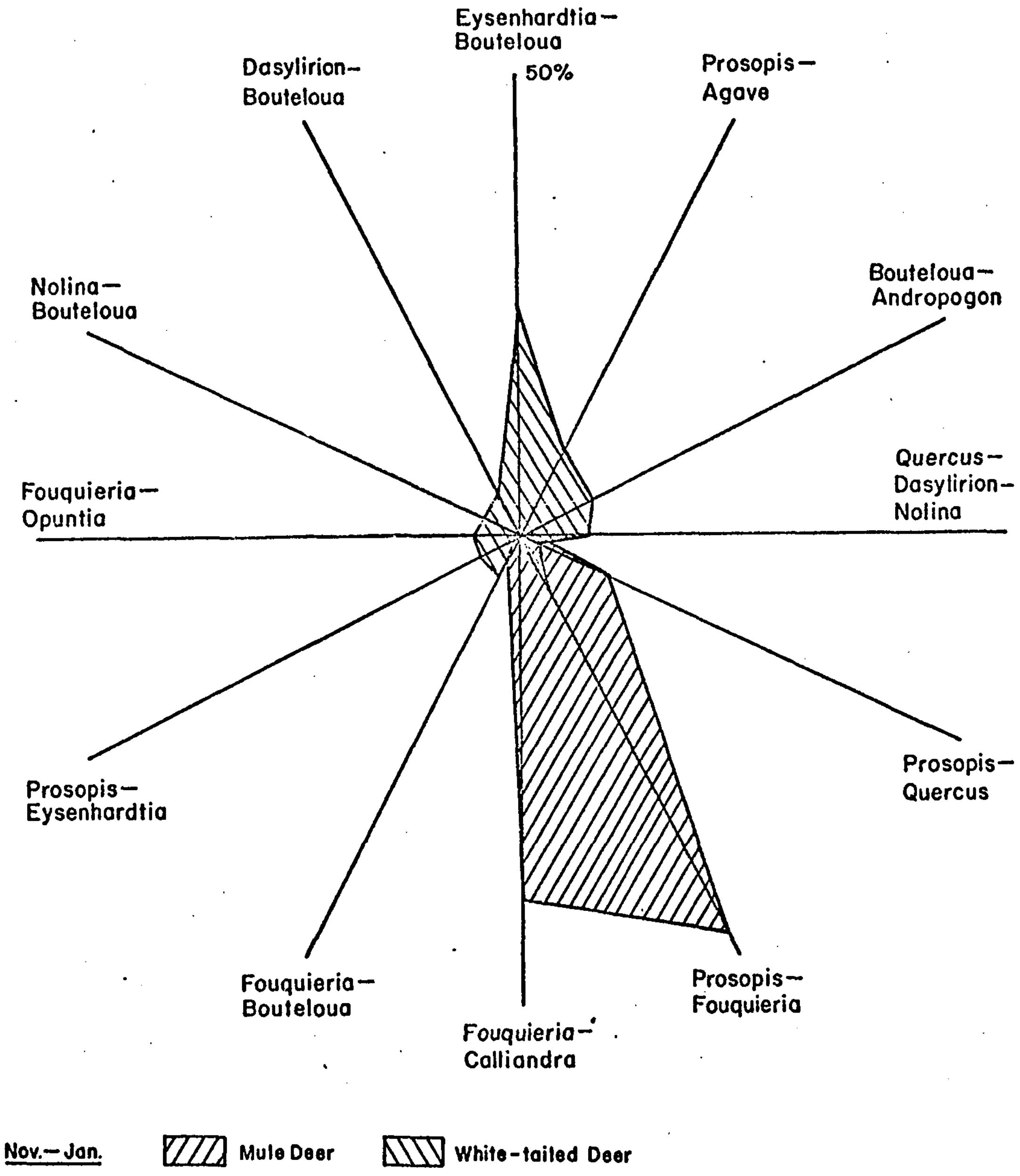
b: May-July

Figure 2.--Continued Habitat selection of mule deer and white-tailed deer according to habitat type at the San Cayetano Mountains, southeast Arizona.



c: August-October

Figure 2.--<u>Continued</u> Habitat selection of mule deer and white-tailed deer according to habitat type at the San Cayetano Mountains, southeast Arizona.



d: November-January

Figure 2.--<u>Continued</u> Habitat selection of mule deer and white-tailed deer according to habitat type at the San Cayetano Mountains, southeast Arizona.

Habitat selection of mule deer and white-tailed deer during May, June, and July is presented in Figure 2b. Most mule deer (79 per cent) were observed in the Prosopis-Fouquieria habitat type; some mule deer used the Quercus-Dasylirion-Nolina, Fouquieria-Eysenhardtia, and Nolina-Bouteloua habitat types. White-tailed deer utilized a greater diversity of dominant vegetation than did mule deer, and no vegetative type appeared to be predominantly preferred. Quercus, Dasylirion, Nolina, Bouteloua, Prosopis, Fouquieria, and/or Eysenhardtia were the plant species, which white-tailed deer were primarily associated with. Use of areas dominated by Eysenhardtia was a result of this plant's importance as a food item during the hot, dry months. There was dual use on the Prosopis-Fouquieria, Quercus-Dasylirion-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 all seasons.

Figure 2c illustrates habitat selection of mule deer and white-tailed deer for the hot, rainy season (August, September, October). Mule deer were found predominantly in the habitats dominated by Prosopis; 63% of mule deer observations were from these habitats. Mule deer also made use of the Quercus-Bouteloua and Fouquieria-Bouteloua habitats, 11 and 7 per cent, respectively. White-tailed deer showed greatest preference for the

Dasylirion-*Bouteloua* (33 per cent) and *Quercus*-*Bouteloua* (14 per cent) habitats, but also utilized those habitats associated with *Eysenhardtia*, *Nolina*, *Fouquieria*, and *Prosopis*. Overlap in habitat selection between mule deer and white-tailed deer occurred on the *Quercus*-*Bouteloua*, *Fouquieria*-*Bouteloua*, *Prosopis*-*Fouquieria*, and *Prosopis*-*Agave* habitat types. Overlap in habitat selection was estimated at 31 per cent for the months of August, September, and October.

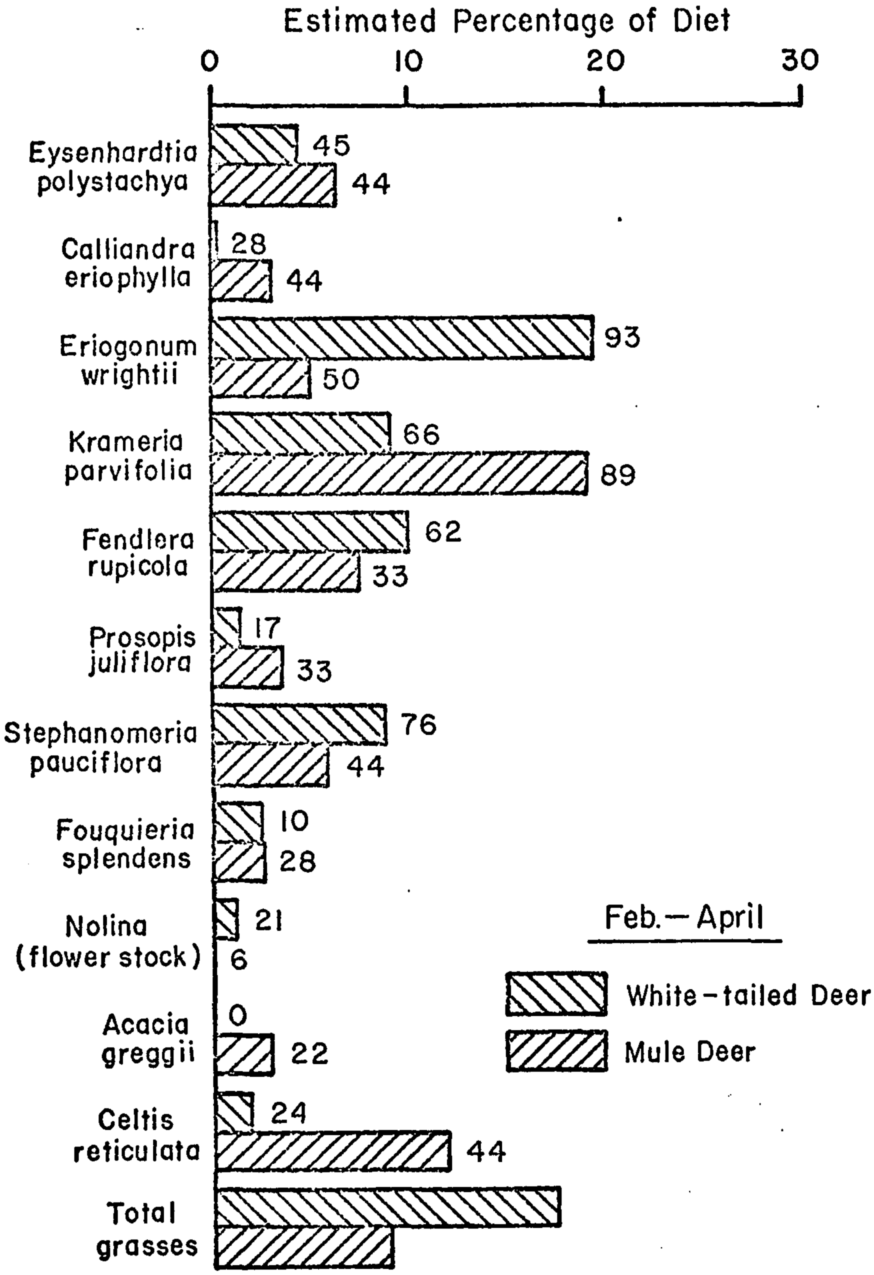
Habitat selection by mule deer and white-tailed deer for the months of November, December, and January is presented in Figure 2d. Mule deer utilized the *Prosopis*-*Fouquieria* (48 per cent) and *Fouquieria*-*Calliandra* (39 per cent) vegetations almost exclusively during this season; the only other vegetative type that mule deer frequented was *Quercus*-*Prosopis* (10 per cent). White-tailed deer displayed definite preference for the *Eysenhardtia*-*Bouteloua* habitat type (26 per cent). This preference was associated with high use of *Eysenhardtia* *polystachya* for food. White-tailed deer also used those habitats with which *Quercus*, *Dasylirion*, *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 per cent, the smallest for all four seasons.

Considering all seasons mule deer were associated with a fewer number of habitat types than white-tailed deer. Only 10 habitat types were used to any degree by mule deer, while white-tailed deer used all 18 of the above mentioned habitat types. Prosopis and/or Fouquieria were the plant species that mule deer were primarily associated with, and they were occasionally observed in the oak (Quercus) habitats. White-tailed deer did not display any particular preference for a certain habitat type but appeared to utilize all habitats. Overlap in habitat selection between mule deer and white-tailed deer ranged from 12 to 39 per cent with an average over all seasons of 28 per cent.

Food Habits

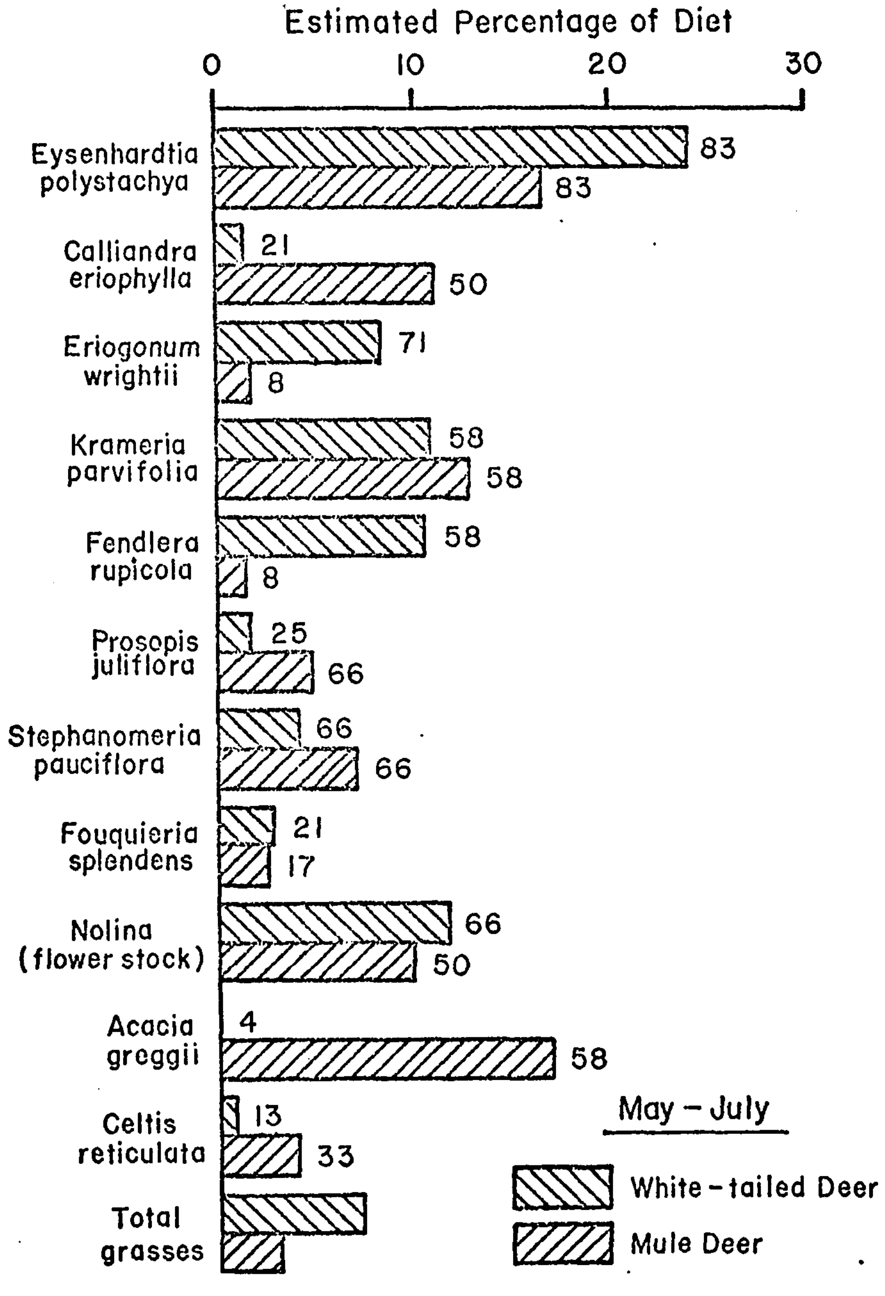
Food habits of mule deer and white-tailed deer at the San Cayetano Mountains were studied primarily by fecal analysis. A total of 189 fecal samples (84 from mule deer and 105 from white-tailed deer) were analyzed. The data from these analyses are presented in Appendix B and in Figures 3a through 3d.

Food preferences of mule deer (18 samples) and white-tailed deer (29 samples) during the cool, dry months of February, March, and April are given in Figure 3a. Eriogonum wrightii was the single most important food item for white-tailed deer during this season; it comprised an



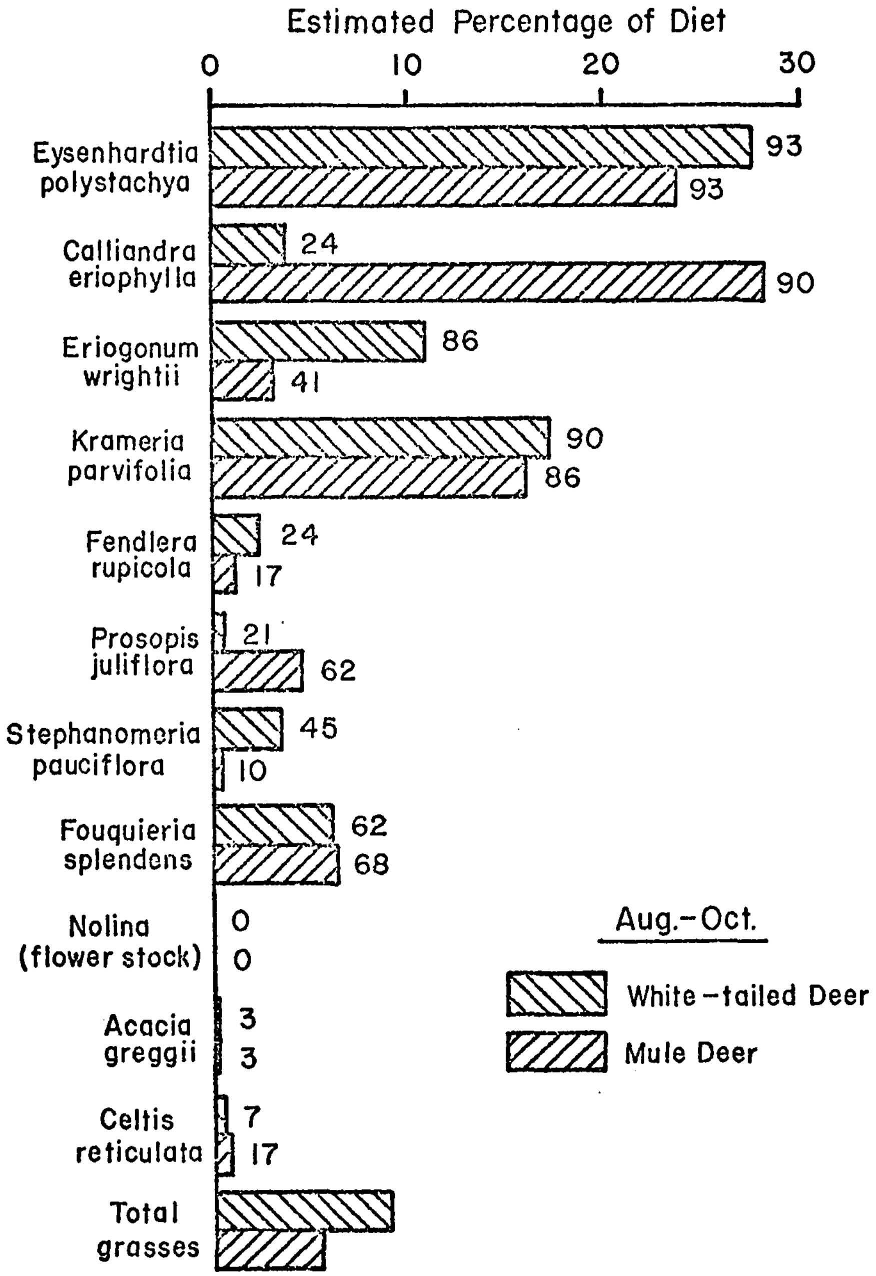
a: February-April

Figure 3. Food preferences of mule deer and white-tailed deer at the San Cayetano Mountains, southeast Arizona -- The numbers at the end of each bar are the frequency of occurrence of each plant species in the samples for the designated season.



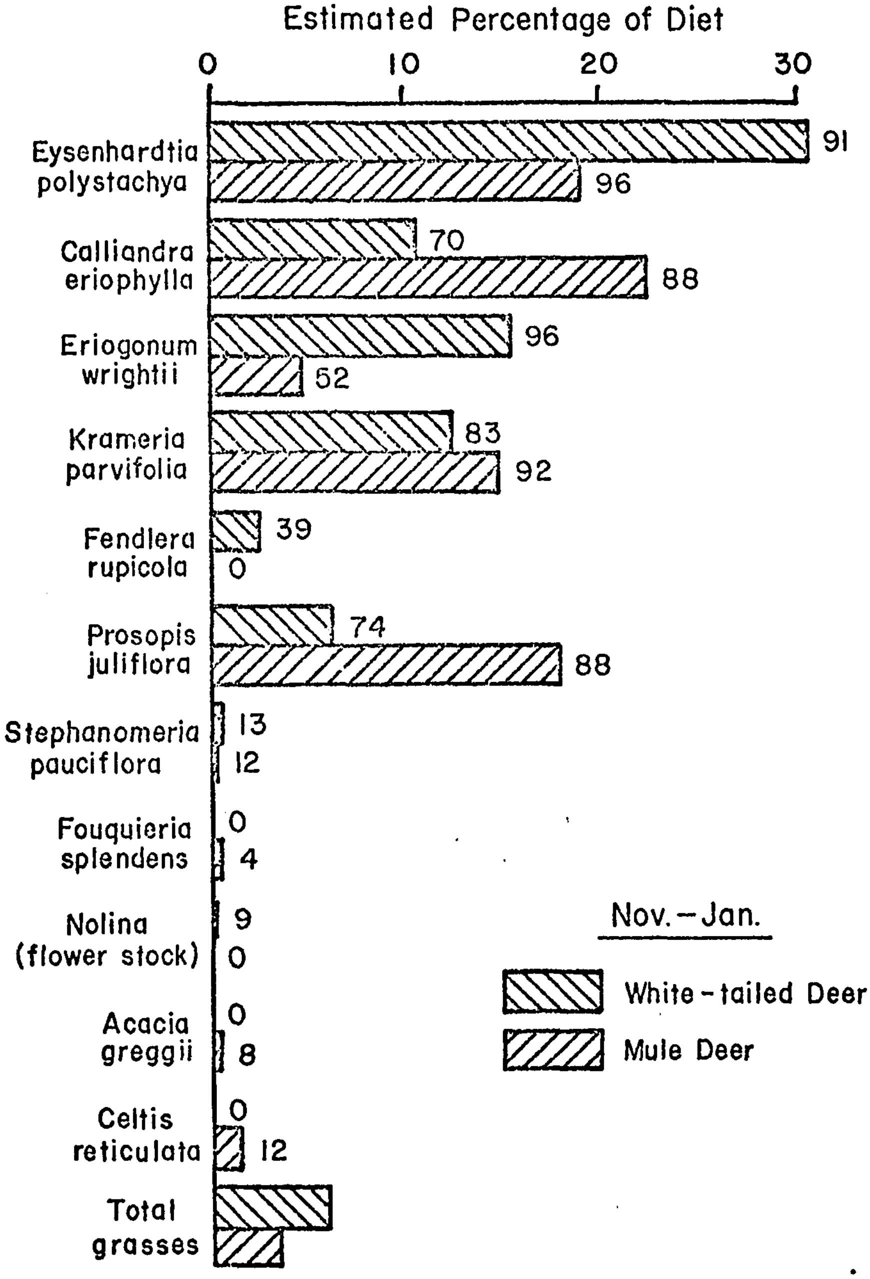
b: May-July

Figure 3.--Continued Food preferences of mule deer and white-tailed deer at the San Cayetano Mountains, southeast Arizona -- The numbers at the end of each bar are the frequency of occurrence of each plant species in the samples for the designated season.



c: August-October

Figure 3.--Continued Food preferences of mule deer and white-tailed deer at the San Cayetano Mountains, southeast Arizona -- The numbers at the end of each bar are the frequency of occurrence of each plant species in the samples for the designated season.



d: November-January

Figure 3.--<u>Continued</u> Food preferences of mule deer and white-tailed deer at the San Cayetano Mountains, southeast Arizona -- The numbers at the end of each bar are the frequency of occurrence of each plant species in the samples for the designated season.

estimated 19 per cent of the diet. Grasses were utilized extensively also; they made up 18 per cent of the diet. Other important foods to white-tailed deer were *Fendlera rupicola* (10 per cent), *Krameria parviflora* (9 per cent), and *Stephanomeria pauciflora* (9 per cent). The major constituents of mule deers' diet were *Krameria parvifolia* and *Celtis reticulata* during February, March, and April; they accounted for 19 and 12 per cent, respectively. Grasses were not as abundant in mule deer samples as in white-tailed deer samples; they amounted to 9 per cent. *Fendlera rupicola* (8 per cent) was also abundant in mule deer samples. Of the twelve major foods pictured in Figure 3a, there was dual usage by mule deer and white-tailed on all but *Acacia greggii*. Considering the entire diets of both species (Appendix B) there was 56 per cent overlap in their estimated diets.

Food preference data for the hot, dry season (May, June, and July) are presented in Figure 3b and represent 24 fecal samples from white-tailed deer and 12 from mule deer. The most important food item for white-tailed deer was *Eysenhardtia polystachya*; it amounted to almost a quarter of their diet. The flower stalks of *Nolina microcarpa* (12 per cent) were also highly preferred during this season. Other species important in the white-tailed deer diet were: *Krameria parvifolia* (11 per cent), *Fendlera rupicola* (11 per cent), and *Eriogonum wrightii* (8 per cent). Five plant species contributed to the major portion of mule deer's diet; they were *Acacia greggii* (19 per cent), *Eysenhardtia polystachya* (16 per cent), *Krameria parvifolia* (13 per cent), *Calliandra eriophylla* (11 per cent), and *Nolina* flower stalks (10 per cent). There was considerable overlap in use of *Eysenhardtia polystachya*, *Krameria parvifolia*, and *Nolina microcarpa* during the hot, dry months. The total estimated overlap in food habits between mule deer and white-tailed deer was 55 per cent, the smallest for all seasons.

White-tailed deer showed preference for three species during the hot, rainy season (Figure 3c). *Eysenhardtia polystachya* comprised 28 per cent, *Krameria parvifolia* 17 per cent, and *Eriogonum wrightii* 11 per cent. Grasses were used moderately by white-tailed deer. *Calliandra eriophylla* and *Eysenhardtia polystachya* were the most important food for mule deer during August, September, and October, making up 28 and 24 per cent of the total diet, respectively. *Krameria parvifolia* (16 per cent) was also preferred during these months. White-tailed deer and mule deer both made moderate use of *Fouquieria splendens*; it accounted for 6 per cent of the diet of both deer species. Dual use by mule deer and white-tailed deer was primarily on *Eysenhardtia polystachya* and *Krameria parvifolia*. Total overlap in food preferences was estimated at 67 per cent, the greatest overlap of all seasons.

Figure 3d presents food preferences of mule deer and white-tailed deer during the moist part of the winter. *Eysenhardtia polystachya* contributed the largest portion to the white-tailed deer diet; its contribution was estimated at 31 per cent. *Eriogonum wrightii* (16 per cent), *Krameria parvifolia* (13 per cent), and *Calliandra eriophylla* were also important items for white-tailed deer. Mule deer diets were composed mainly of *Calliandra eriophylla* (22 per cent), *Eysenhardtia polystachya* (19 per cent), *Prosopis juliflora* (18 per cent), and *Krameria parvifolia* (15 per cent). Overlap in food habits of mule deer and white-tailed deer occurred mostly on three species: *Eysenhardtia polystachya*, *Krameria parvifolia*, and *Calliandra eriophylla*, in that order. Total overlap was estimated at 60 per cent.

Considering all seasons the plant species that white-tailed deer used most were, in the order of importance: (1) *Eysenhardtia polystachya*, (2) *Eriogonum wrightii*, (3) *Krameria parvifolia*, (4) *Fendlera rupicola*, (5) *Bouteloua chondrosiodes*, (6) *Stephanomeria parvifolia*, (7) *Calliandra eriophylla*, and *Nolina microcarpa* (flower stalks). Similarly the primary food items of mule deer in order of importance were: (1) *Eysenhardtia polystachya*, (2) *Calliandra eriophylla*, (3) *Krameria parvifolia*, (4) *Prosopis juliflora*, (5) *Acacia greggii*, (6) *Celtis reticulata*, and *Nolina microcarpa* (flower stalks). Three plant species were, therefore, very important to both mule deer and white-tailed deer, and these species contributed to the majority of the dual use. The differences in the major food items between mule deer and white-tailed deer can be explained by plant versus deer distributions. For example, *Eriogonum wrightii*, *Fendlera rupicola*, and *Stephanomeria parvifolia* were found to be 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-talied deer. *Prosopis juliflora*, *Acacia greggii*, and *Celtis reticulata*, which were important to mule deer only, were distributed at the lower elevations where mule deer primarily existed.

A comparison of mule deer and white-tailed deer food preferences according to the major growth forms was made (Table 2). These analyses show that white-tailed deer utilized approximately twice as much grasses and herbs as mule deer. Shrubs were utilized the most and equally by both deer species. Flower stalks and fruits were also used similarly by mule deer and white-tailed deer, but mule deer used approximately three times as much food from tree species than did white-tailed deer. Apparently, mule deer browse more than white-tailed deer in this area, or utilize more browse species.

Another comparison that was made concerning mule deer and white-tailed deer food habits was the number of

Table 2. Per cent of mule deer and white-tailed deer diets from the major growth forms.

	Season							
	Feb.-April		May-July		Aug.-Oct.		Nov.-Jan.	
Growth Forms	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

WT = White-tailed deer, MD = Mule deer.

different plant species identified in the analysis of each fecal sample. This analysis was performed to compare the diversity of each species' diet. The least squares analysis of variance for these comparisons is given in Table 3. The results of this analysis show that there is a statistically significant difference ($F_{(1,177)} = 64.59$) between the number of plant species per fecal sample for mule deer and white-tailed deer. The difference between the seasons is also statistically significant ($F_{(5,177)} = 3.35$) at the .05 level. The interaction between the species and season effects is not statistically significant ($F_{(5,177)} = 1.55$) at the .05 level of significance. The number of different plant species in a fecal sample is, therefore, significantly influenced by the season and deer species from which the sample comes. The means, confidence intervals ($t_{.05}\ S_{\bar{x}}$), and sample sizes for each season by species category are given in Table 4. The means for white-tailed deer are consistently greater than those for mule deer. In comparing the means for mule deer versus white-tailed deer for each season, the technique of least significant different (lsd) was used, since these comparisons are orthogonal (independent) and the probability of a Type I error remains constant. For all seasons the difference between the mean number of plant species per fecal sample for white-tailed deer was

Table 3. Least squares analysis of variance on the number of plant species per fecal sample from deer at the San Cayetano Mountains from August, 1969 to January, 1972.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F-Ratio
Species	1	115.00	115.00	64.59*
Season	5	29.82	5.97	3.35*
Sp. x Sea.	5	13.81	2.76	1.55
Experimental Error	177	315.15	1.78	

*Denotes significant F-value at the .05 level of significance.

Table 4. Mean number of plant species per fecal sample for deer at the San Cayetano Mountains from August, 1969 to January, 1972.

Deer Species	Season					
	Dec.-Jan.	Feb.-Mar.	Apr.-May	June-July	Aug.-Sept.	Oct.-Nov.
Mule Deer	7.71 ± .68[a] (17)	8.46 ± .80 (13)	7.17 ± 1.33 (6)	7.73 ± .89 (11)	8.73 ± .89 (11)	7.50 ± .54 (26)
White-tailed Deer	9.12 ± .68 (17)	9.86 ± .61 (21)	10.29 ± .76 (14)	8.78 ± .66 (18)	9.95 ± .64 (19)	9.31 ± .71 (16)

[a]Values are: Mean ± (t.05)(Standard Error)
(Sample Size)

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 are presented in Table 5. The overlap in spatial distributions ranged from 22 per cent to 37 per cent with a mean of 32 per cent. 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; the range was from 12 to 39 per cent with a mean of 28 per cent. The greatest overlap in habitat selection was during May through July, and the least was during the months of November, December, and January. Since the same slope exposure-altitude intervals may display different vegetation (habitat), I 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. A better estimate of the true overlap for these two parameters is, therefore, the product of the probabilities of their respective overlaps (S x H in Table 5). These indices are quite low in comparison to the others, and I believe these indices present a more accurate picture of

Table 5. 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 x H)	Food Habits (F)	Coefficient of Competition (S x H x F)
Feb.-April	.22	.31	.07	.56	.04
May-July	.33	.39	.13	.55	.08
Aug.-Oct.	.37	.31	.11	.67	.07
Nov.-Jan.	.37	.12	.04	.61	.02
Seasonal Ave.	.32	.28	.09	.60	.05

where mule deer versus white-tailed deer are found at the San Cayetano Mountains.

Throughout the study there was much dual use of the forage plants by mule deer and white-tailed deer. This is affirmed by the high overlap in food habits between the two species. Overlap in food habits ranged from 55 per cent to 67 per cent with an average of 60 per cent. This overlap was greatest during the months of August, September, and October and smallest during May, June, and July.

Levins (1968, p. 52) advocates the use of the coefficient of competition, which is the product of all the individual indices of overlap. Coefficients of competition for the four seasons are presented in Table 5 (S x H x F). These coefficients are presumably measures of direct competition, and they convey no information about the phenomenon of competitive exclusion. The coefficients of competition are very low, but the similarity in food preferences of the two species and the contiguously allopatric nature of their distributions lead me to believe that they competitively exclude each other at the San Cayetano Mountains. I personally believe that the coefficients of competition are conservative, because of the way in which they are calculated. Since the coefficients of competition are a product of the indices of overlap, and these indices are always less than 1.00, the more ecological parameters one studies the smaller the coefficients of competition will become. The problem is that some of these parameters may not be particularly meaningful when considering the possibility of direct competition. The result, therefore, is a lower coefficient than is actually the case in the field.

Recruitment

Results from sex-age classifications, which are related to recruitment to the populations of mule deer and white-tailed deer, are presented in Table 6. White-tailed deer showed higher recruitment to their populations than mule deer for the first two years. The magnitude of this difference was 9.3 and 13.2 per cent for 1969-70 and 1970-71, respectively. Populations of both species declined drastically during the drought of late 1970 and early 1971, so the number of deer classified was quite low. Even so, mule deer appeared to have much higher recruitment after the drought period. During the winter of 1971-72 mule deer had a doe-fawn ratio of 100:56 and white-tailed deer, 100:06. Total recruitment for the entire study was slightly in favor of white-tailed by 4.4 per cent.

Table 6. Doe-fawn counts of deer at the San Cayetano Mountains for the months of November through February, 1969-1972.

	White-tailed Deer			Mule Deer		
Year	Does	Fawns	Fawns/ 100 Does	Does	Fawns	Fawns/ 100 Does
1969-70	60	18	30.0	34	7	20.7
1970-71	66	20	30.3	41	7	17.1
1971-72	18	1	5.5	9	5	55.6
Totals	144	39	27.0	84	19	22.6

COEXISTENCE: DOS CABEZAS MOUNTAINS

Field work was conducted on the Dos Cabezas study area from August, 1969, to March, 1972. Mule deer and white-tailed deer were sympatric from approximately 6,500 to 8,000 feet in elevation. Data from the Dos Cabezas Mountains were divided into three seasons, since the area was high enough in elevation that the winter season was reasonably long. This division into three seasons 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 this time there was no evidence in either fecal analysis or direct observations that deer were using twigs of deciduous plants to any extent. By the first of April the deciduous plants began to sprout and were available for deer to feed upon. 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. The three seasons were, therefore, April to mid-July, mid-July to the end of October, and November through March.

Spatial Distributions

Spatial distributions of deer at the Dos Cabezas Mountains are given in Figure 4 and Table 7, and represent 1,762 deer observations throughout the duration of the study. A total of 389 white-tailed deer were observed in 173 groups or 2.2 white-tails per group. Likewise, 1,373 mule deer were observed in 284 groups for 4.8 mule deer per group. Mule deer were, therefore, more gregarious than white-tailed deer at the Dos Cabezas Mountains. Sightings of all deer groups are presented in Figure 4, where distributions of mule deer and white-tailed deer are related to altitude and vegetative zone. Each dot represents an observation of a group of mule deer and each cross a group of white-tailed deer, and not sightings of individual deer. These data are a compilation of all sightings of deer groups for all seasons from 1969 to 1972. Distributions of white-tailed deer appeared to be more restricted than mule deer, for observations of this species tended to be clumped. This restriction of white-tailed deer was not associated with any particular vegetative zone, but they were almost always found above 6,500 feet in elevation. Distributions of mule deer were more scattered than white-tailed deer, and they were much less restricted. Mule deer utilized all three vegetative 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

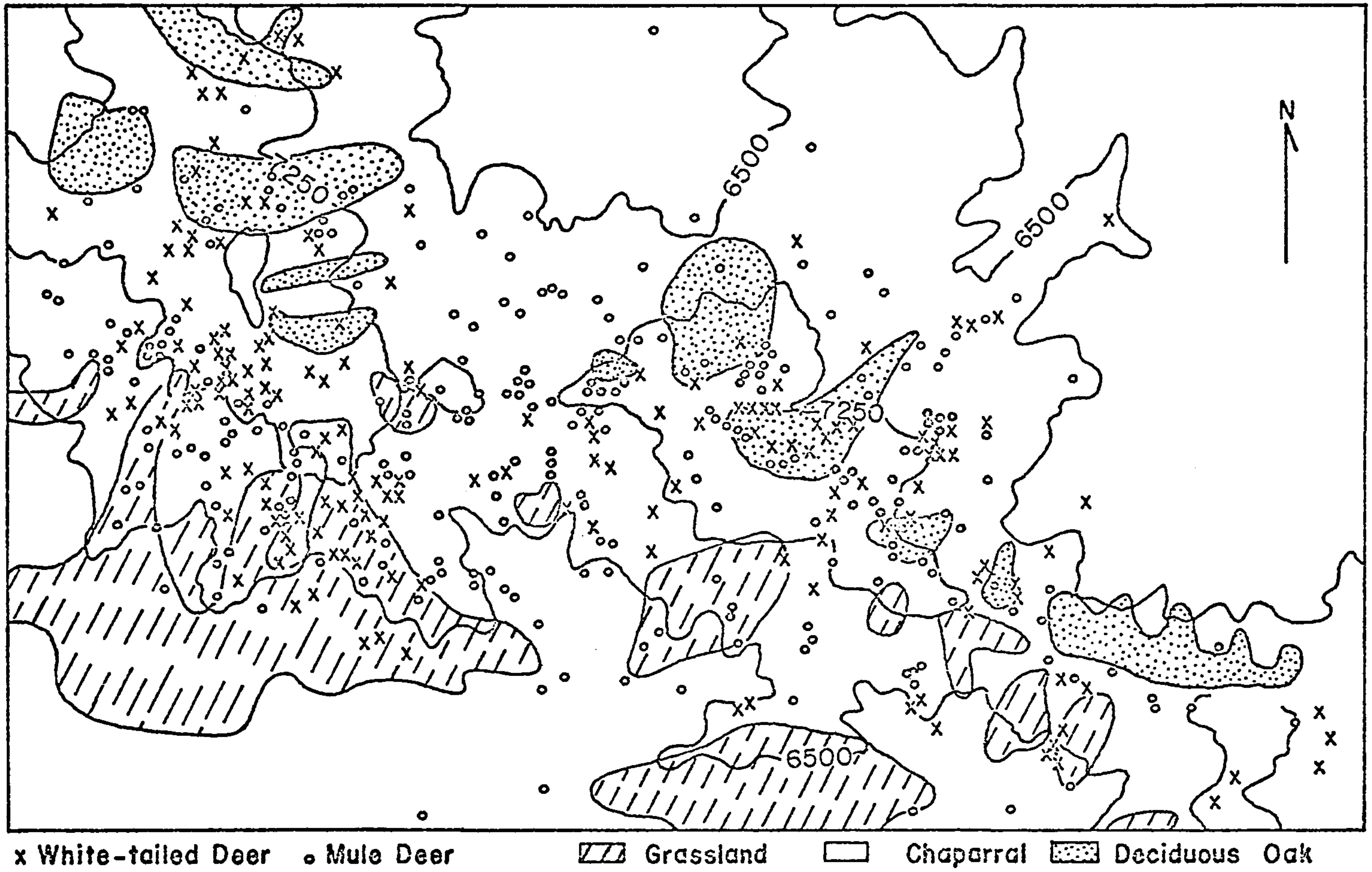


Figure 4. Distributional patterns of mule deer and white-tailed deer in relation to altitude and vegetative zone at the Dos Cabezas Mountains, southeast Arizona -- Each circle and cross represents a sighting of a group of white-tailed deer and mule deer, respectively, and not individual deer.

Table 7. Percentages of mule deer and white-tailed deer observed on the various slope exposure-altitude intervals at the Dos Cabezas Mountains from August, 1969 to March, 1972.[a]

Altitude Interval	Deer Species[b]	Slope Exposure[c]						
		S	SW	SE	Ne	NW	NE	N
				a: April to Mid-July				
7,500- 8,000	WT	3.2	2.4	5.6	2.4	4.0	4.8	5.6
	MD	.8			.6	.8	4.8	3.7
7,000- 7,499	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
6,500- 6,999	WT	3.2	8.8	8.8	4.0		2.4	
	MD	9.1	8.5	3.3	6.0	2.1	2.5	
6,000- 6,499	WT			3.2	2.4		1.6	
	MD	2.1		3.3	.8	1.2	2.1	
5,500- 5,999	WT			1.6	.8			
	MD	.2			5.0	.8		
				b: Mid-July to October				
7,500- 8,000	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
7,000- 7,499	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
6,500- 6,999	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
6,000- 6,499	WT	1.9	3.8					
	MD	.6	1.3	3.4	.3		1.6	
5,500- 5,999	WT							
	MD				2.8			

Table 7.--Continued

Altitude Interval	Deer Species	Slope Exposure						
		S	SW	SE	Ne	NW	NE	N
					c: November to March			
7,500- 8,000	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
7,000- 7,499	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
6,500- 6,999	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	
6,000- 6,499	WT	1.9			1.9			
	MD		3.7	.9	1.2			
5,500- 5,999	WT							
	MD				.9			.3

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

[b] WT = White-tailed deer, MD = Mule deer.

[c] S = South, SE = Southeast, SW = Southwest, Ne = Neutral, NW = Northwest, NE = Northeast, N = North.

on the study area, and the nature of their distributions presented in Figure 4 shows that their populations were sympatric in the Dos Cabezas Mountains. Overlap between mule deer and white-tailed deer populations occurred on the three major vegetative zones. Because Figure 4 is a compilation of the entire data, a subdivision of these data by season, altitude, and slope exposure is more meaningful.

For the period of April to mid-July 125 observations of white-tailed deer and 481 observations of mule deer were made. During these months both species used all slopes to some extent (Table 7a). The southeast and neutral slopes appeared to be used the most as were the elevations from 6,500 to 7,500 feet. Overlap between mule deer and white-tailed deer, according to the various slope exposure-altitude intervals, was 66 per cent.

From mid-July to the end of October, 106 and 320 observations of white-tailed and mule deer were made, respectively. Spatial distributions of the two species according to the various slope exposure-altitude intervals show that there was no real preference for any particular slope exposure (Table 7b). However, mule deer observations were more frequent on north-facing slopes between 6,500 and 7,500 feet in elevation. There was considerably overlap between the two species from 6,500 to 8,000 feet in elevation. Overlap for this time period was estimated at 64 per cent.

During the winter months 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 7c). Most deer were observed between 6,500 and 7,500 feet in elevation. White-tailed deer were found on south- and southwest-facing slopes more than mule deer, and mule deer on southeast and neutral slopes. As in other seasons there was considerable overlap between mule deer and white-tailed deer populations; this overlap was estimated at 57 per cent.

The sympatric nature of mule deer and white-tailed deer is also reflected in the association coefficients from the formula

$$I_{ai} = 2\left[\frac{J_i}{A + B} - .5\right]$$

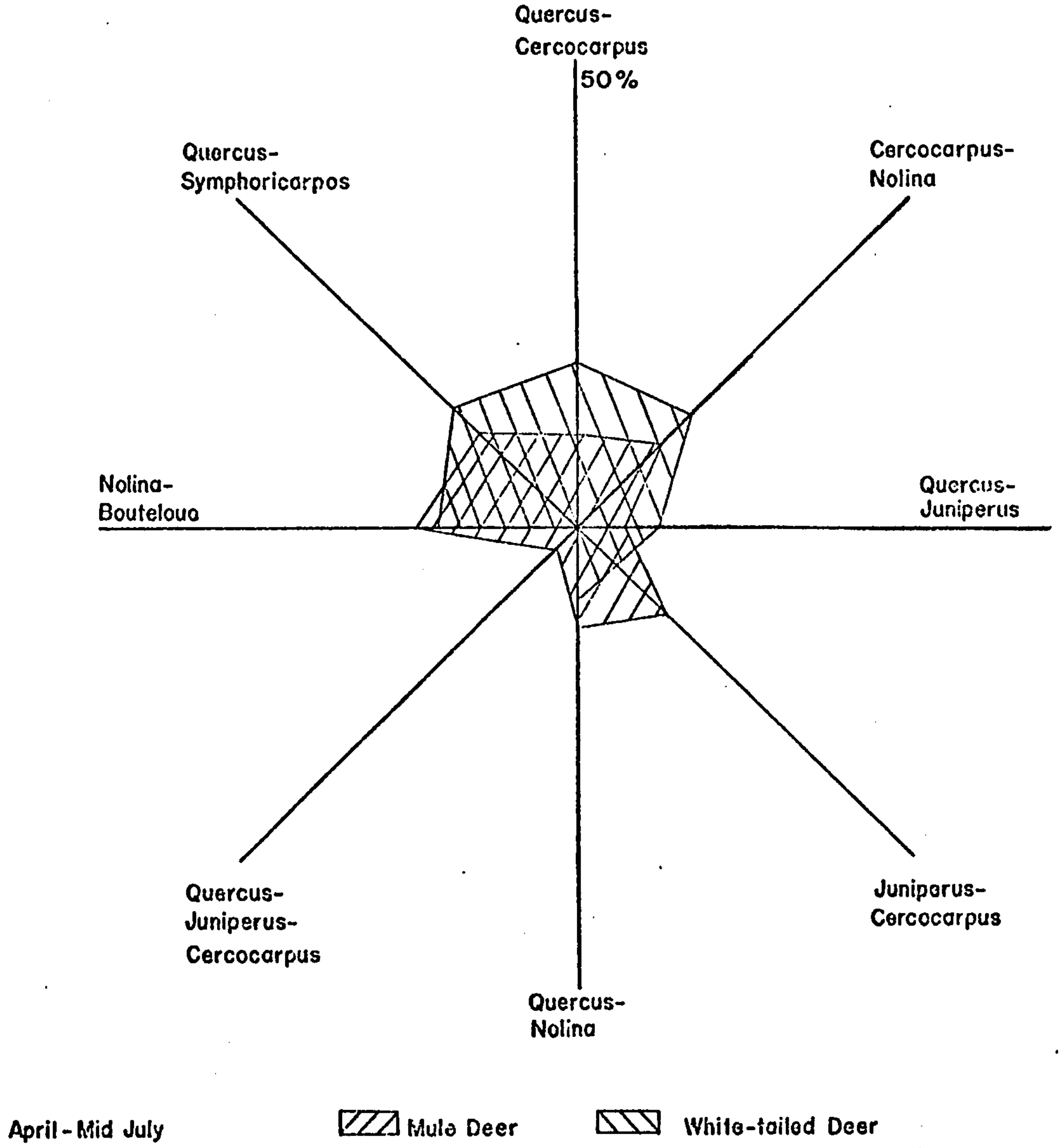
after Southwood (1966). These coefficients for the varous seasons are as follows: April to mid-July, +.858; mid-July through October, +.878; and November through March, +.872. These coefficients are extremely high and reflect the positive association between mule deer and white-tailed deer at Dos Cabezas. There is sufficient evidence, therefore, that mule deer and white-tailed deer were sympatric in their distributions.

Habitat Selection

Habitat selection of mule deer and white-tailed deer at the Dos Cabezas Mountains was ascertained on the basis of 1,784 deer observations in 19 habitat types. Both species used predominantly eight of these habitat types. These habitat types are: (1) *Quercus*-*Cercocarpus*, (2) *Cercocarpus*-*Nolina*, (3) *Juniperus*-*Cercocarpus*, (4) *Quercus*-*Juniperus*, (5) *Quercus*-*Nolina*, (6) *Quercus*-*Juniperus*-*Cercocarpus*, (7) *Nolina*-*Bouteloua*, and (8) *Quercus*-*Symphoricarpos*.

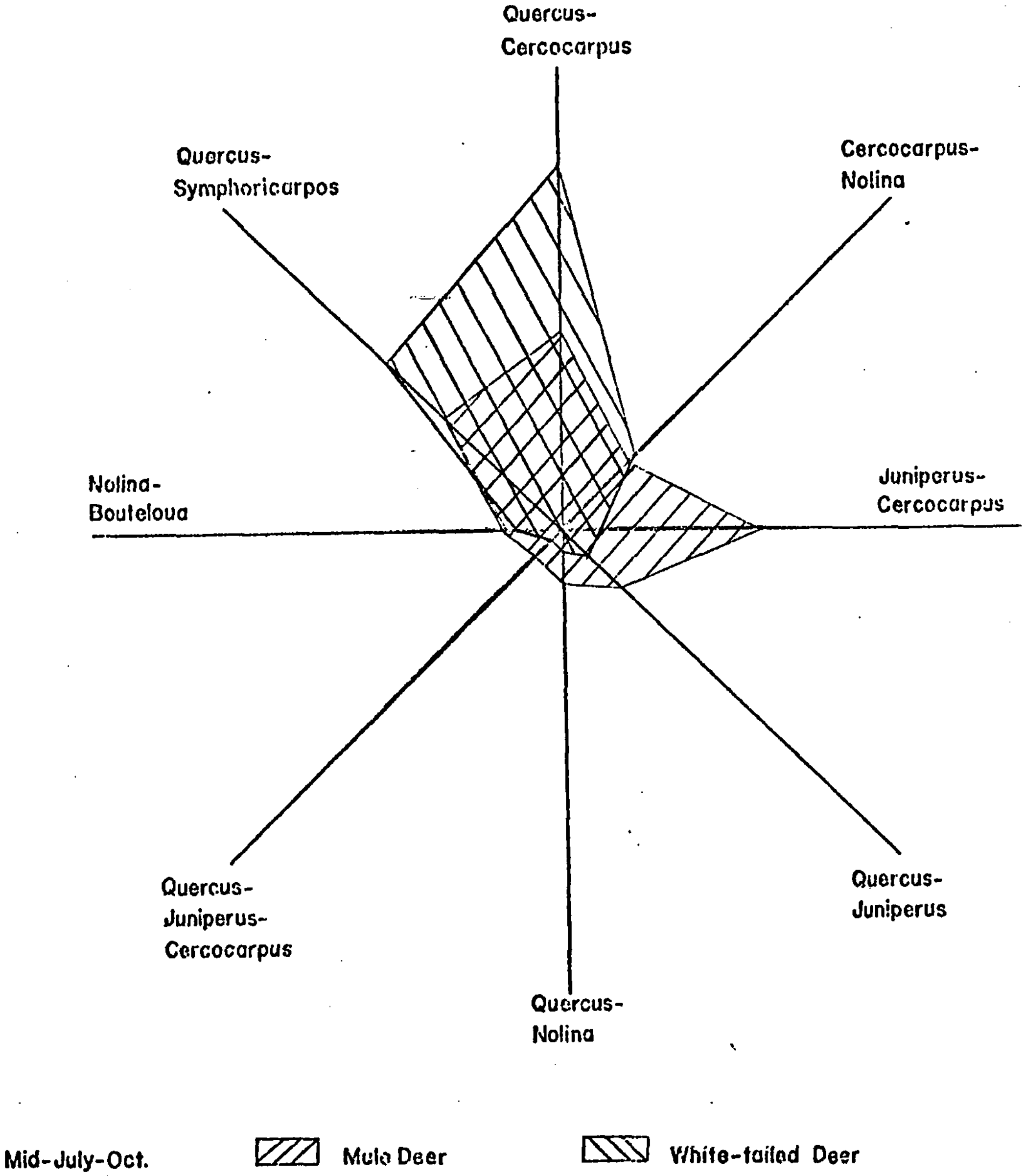
Habitat selection of mule deer and white-tailed deer for April to mid-July is presented in Figure 5a and represents 118 and 482 white-tailed deer and mule deer observations, respectively. Overlap in habitat selection for this season was estimated at 76 per cent. White-tailed deer utilized a higher percentage 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 white-tailed deer. The *Quercus*-*Juniperus*-*Cercocarpus* habitat type was not used much by either species.

For the period of 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



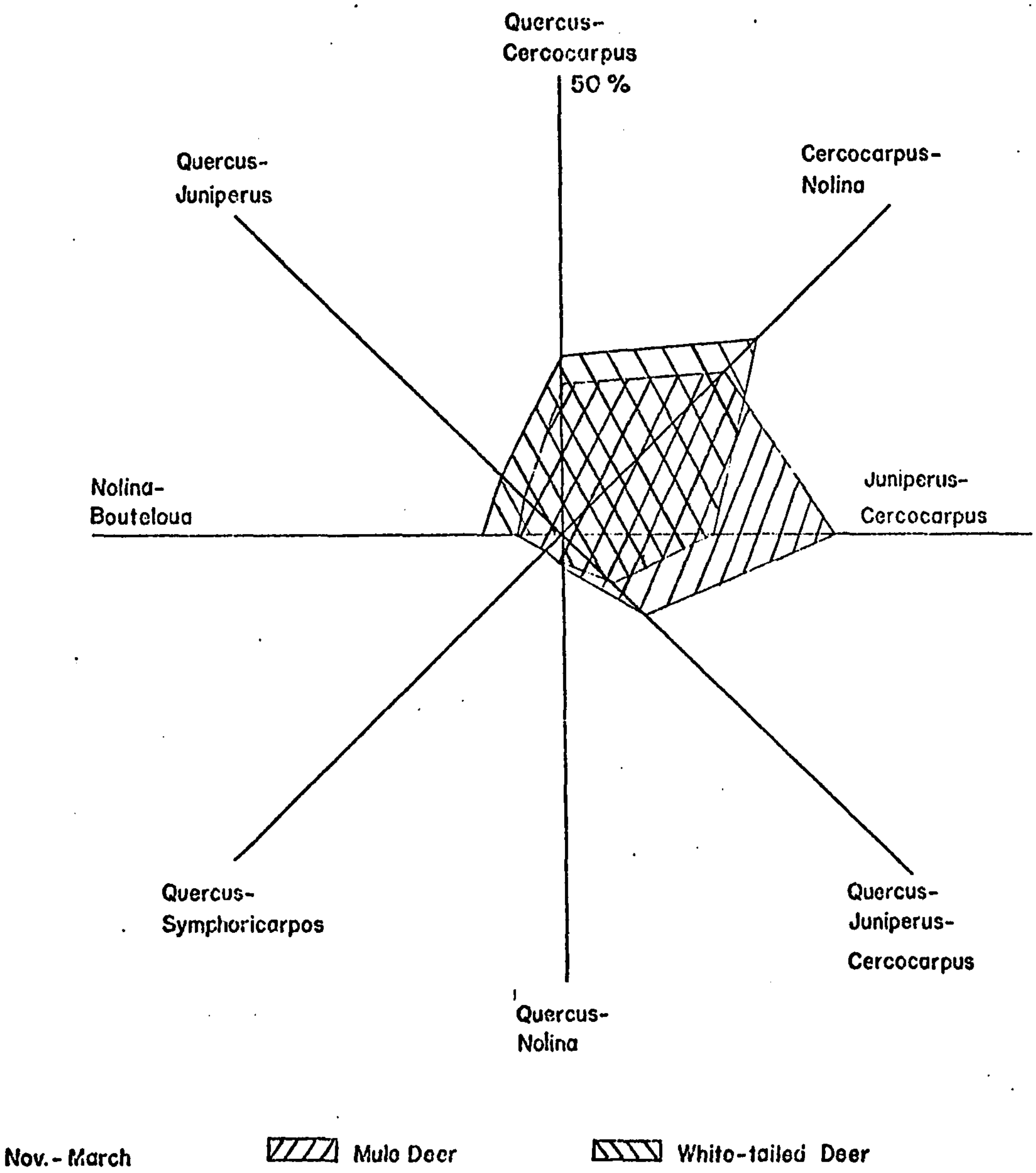
a: April to Mid-July

Figure 5. Habitat selection of mule deer and white-tailed deer according to habitat type at the Dos Cabezas Mountains, southeast Arizona.



b: Mid-July to October

Figure 5.--<u>Continued</u> Habitat selection of mule deer and white-tailed deer according to habitat type at the Dos Cabezas Mountains, southeast Arizona.



c: November to March

Figure 5.--Continued Habitat selection of mule deer and white-tailed deer according to habitat type at the Dos Cabezas Mountains, southeast Arizona.

in the previous season (Figure 5b). 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 for this season was lowest of all the seasons, 66 per cent.

There were 152 observations of white-tailed deer and 616 observations of mule deer for the winter months (November-March). Mule deer again utilized the Juniperus-Cercocarpus habitat much more than white-tailed deer (Figure 5c). High 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 between both species. There was, therefore, a great amount of overlap in habitat selection between mule deer and white-tailed deer. This overlap was estimated at 82 per cent, the largest of all the seasons. Both species displayed a change in habitat selection during the winter months compared to other months. The Quercus-Symphoricarpos habitat type was rarely used during these months, whereas it was very important on other months. Since the two dominants of this habitat type provide good food and cover during spring and summer, deer found these areas most desirable during these months.

But, both *Quercus gambelii* and *Symphoricarpos ereophilus* are deciduous, so these areas were quite undesirable in the winter months when these dominant plants were leafless and dormant. The *Quercus-Nolina* habitat type was not used much by either species, but the *Quercus-Juniperus-Cercocarpus* type was. This was the only season during which the latter was of any importance to either mule deer or white-tailed deer.

Food Habits

Food habits of mule deer and white-tailed deer at Dos Cabezas Mountains were ascertained on the basis of 263 pellet group samples, 153 from mule deer and 110 from white-tailed deer. The majority of the information from these fecal samples after microscopic analysis is presented in Appendix C. Seven food items were the most important and comprised the bulk of the diets of both mule deer and white-tailed deer (Figure 6). These items in the order of importance are: *Cercocarpus breviflorus*, *Juniperus deppeana*, *Eriogonum wrightii*, *Quercus gambelii*, *Quercus emoryi*, seeds of *Juniperus deppeana*, and flower stalks of *Nolina microcarpa*. For the months of April through mid-July 35 fecal samples from white-tailed deer and 47 from mule deer were analyzed. *Cercocarpus breviflorus*, *Juniperus deppeana*, *Eriogonum wrightii*, *Quercus gambelii*, grasses, and flower stalks of *Nolina microcarpa* were the most important food

Figure 6. Food habits of mule deer and white-tailed deer for all seasons at the Dos Cabezas Mountains, southeast Arizona -- The numbers at the end of each bar are the frequency of occurrence of each plant species in the samples for the designated season.

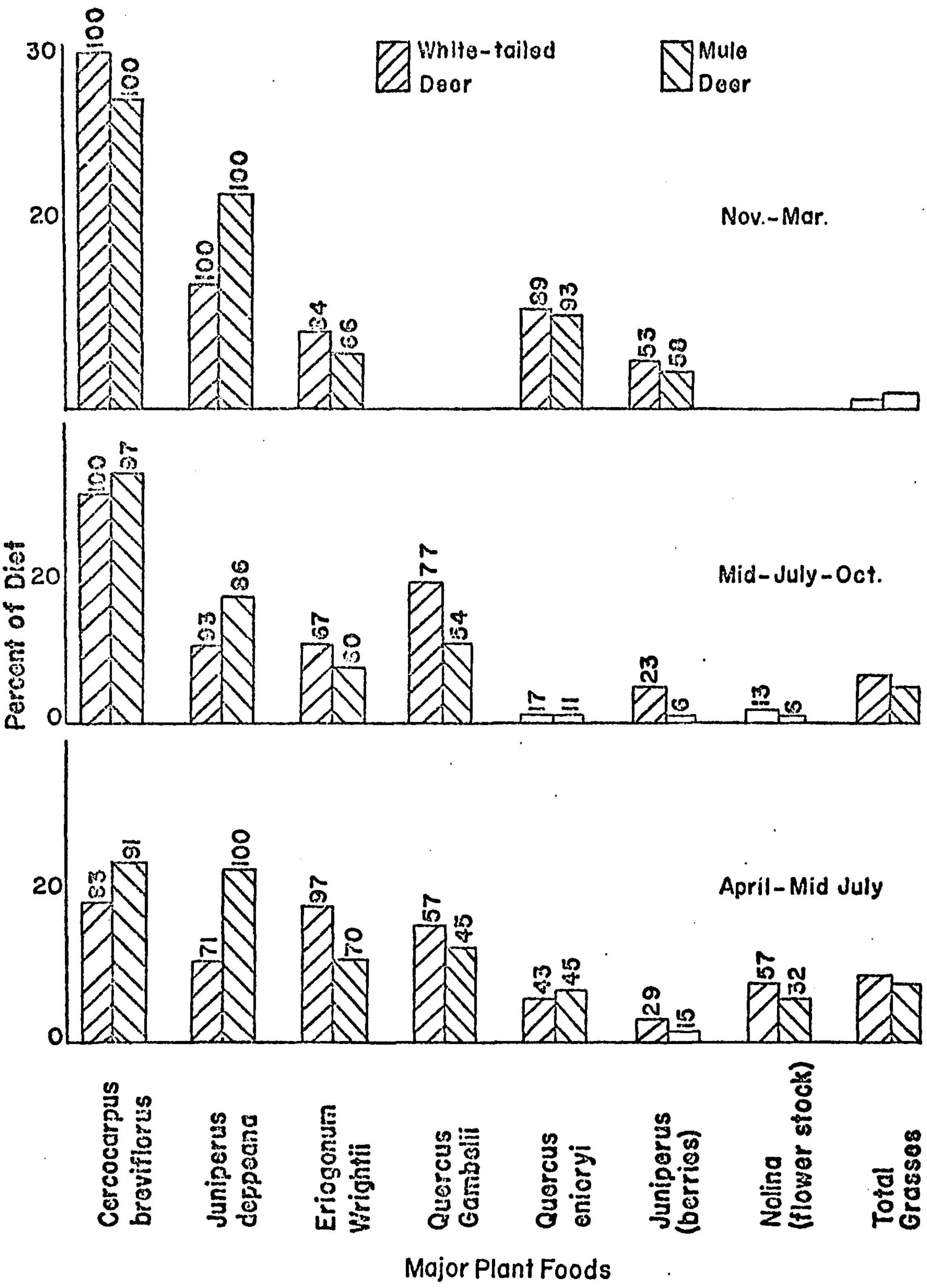


Figure 6. Food habits of mule deer and white-tailed deer for all seasons at the Dos Cabezas Mountains, southeast Arizona.

items for both mule deer and white-tailed deer. The primary difference in use of these plants was that mule deer utilized about twice as much Juniperus deppeana as did white-tailed deer, and Eriogonum wrightii was more important to white-tailed deer than mule deer. Use of all other major plant foods was very similar. The flower stalks of Nolina microcarpa were important food items during these months only. There was even some intra- and interspecific conflict observed over use of this choice food item. Grasses were of greatest importance during this season compared to other seasons. Overlap in food habits for this season was quite high and was estimated at 74 per cent, the lowest for all seasons. There was considerable dual use on all of the major plant foods (Figure 6).

For the rainy season (mid-July to October) 30 fecal samples from white-tailed deer and 35 from mule deer were analyzed. With the coming of the summer rains Cercocarpus breviflorus was the single most important food item for both mule deer and white-tailed deer from mid-July through October. Quercus gambelii, Juniperus deppeana, and Eriogonum wrightii were also important sources of food during this time period. However, Juniperus deppeana was again more important to mule deer, and white-tailed deer utilized Quercus gambelii to a greater extent. Quercus emoryi and the flower stalks of Nolina microcarpa were scarcely exploited as food. As Figure 6 shows, there was much overlap in food habits between both species; this overlap was estimated at 77 per cent. Food habits of both species were most diverse during this season, and a great many herbs and grasses were used (Appendix C).

For the months of November through March fecal samples sizes were 45 and 71 for white-tailed deer and mule deer, respectively. *Cercocarpus breviflorus* was the primary food source for both mule deer and white-tailed deer. *Juniperus deppeana*, *Quercus emoryi*, and *Eriogonum wrightii* were all of secondary importance. Seeds of *Juniperus deppeana* were used during these months also. As in the other seasons, *Juniperus deppeana* was much more important to mule deer than white-tailed deer. *Quercus gambelii* and the flower stalks of *Nolina microcarpa* were not used at all during the winter months. The lack of use of *Quercus gambelii* for the winter months was associated with dormancy and the low use of habitats dominated by this species. Use on most plant species was very similar. Since deer were restricted to evergreen browse during the months from November through March, their food habits were less variable than in other months. The months of February and March were considered the most critical for deer at the Dos Cabezas Mountains because of this restriction. Overlap in food habits was extremely high; it was estimated at 84 per cent, the highest for all seasons.

Considering all seasons the plant species that white-tailed deer used most, in order of importance, were: (1) Cercocarpus breviflorus, (2) Eriogonum wrightii, (3) Juniperus deppeana, (4) Quercus gambelii, and (5) Quercus emoryi. Similarly the primary food items of mule deer, in order of importance were: (1) Cercocarpus breviflorus, (2) Juniperus deppeana, (3) Eriogonum wrightii, (4) Quercus gambelii, and (5) Quercus emoryi. All the plant species that were important food items for white-tailed deer were also important to mule deer; the order of importance was the only difference.

A comparison of food habits of mule deer and white-tailed deer according to the major growth forms failed to show any outstanding differences (Table 8). They did not partition the food source in any obvious way. Choice of foods was evidently determined by availability and not by any other detectable criterion. Food availability, especially grasses and herbs, was greatly influenced by overgrazing by livestock.

As was done for the data from the San Cayetano Mountains, the number of plant species per fecal sample was subjected to a least squares analysis of variance. The results from this analysis are presented in Table 9. These data indicate that the species of deer and season both have statistically significant effects on the number of plant species per fecal sample. The interaction between

Table 8. Per cent of mule deer and white-tailed deer diets from the major growth forms.

	Season					
	April to Mid-May		Mid-July to October		November to March	
Growth Forms	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

WT = White-tailed deer, MD = Mule deer.

Table 9. Least squares analysis of variance on the number of plant species per fecal sample from deer at the Dos Cabezas Mountains from August, 1969 to January, 1972

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F-Ratio
Species	1	96.62	96.62	57.67*
Season	5	175.93	35.19	21.00*
Sp. x Sea.	5	54.20	10.84	6.47*
Experimental Error	251	420.54	1.68	

*Denotes significant F-value at the .05 level of significance.

these two effects was also statistically significant ($F_{(1,1251)} = 6.47$). A review of the species by season means (Table 10) shows that white-tailed deer utilized a greater number of plant species than mule deer in all but one season. The one season in which white-tailed deer utilized fewer plant species, on the average was February and March, and this was the reason for a significant interaction between the species and season effects. A comparison of the means in Table 10 on a seasonal basis indicates that white-tailed deer utilized a statistically significant greater number of plant species per fecal sample than did mule deer in all but one season. This period was during February and March, the most critical time of the year for deer with respect to the food supply.

Niche Overlap

The indices in overlap in spatial distributions, habitat selection, and food habits between mule deer and white tailed deer are summarized in Table 11. These indices reflect the sympatric nature of their populations in the Dos Cabezas Mountains. The overlap in spatial distributions according to altitude and slope exposure ranged from 57 to 66 per cent with an average of 62 per cent. Overlap for this parameter was lowest for those studied. Overlap in habitat selection ranged from 66 to 82 per cent with an average of 75 per cent. Since deer

Table 10. Mean number of plant species per fecal sample for deer at the Dos Cabezas Mountains from August, 1969 to January, 1972.

Deer Species	Season					
	Dec.-Jan.	Feb.-Mar.	Apr.-May	June-July	Aug.-Sept.	Oct.-Nov.
Mule Deer	7.19 ± .51[a] (27)	6.50 ± .69 (16)	9.79 ± .62 (19)	8.20 ± .61 (20)	9.75 ± .61 (20)	8.75 ± 1.08 (8)
White-tailed 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)

[a] Values are: Mean ± (t.05)(Standard Error)
(Sample Size)

Table 11. 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 x H)	Food Habits (F)	Coefficient of Competition (S x H x F)
Apr. to Mid-July	.66	.76	.51	.74	.37
Mid-July to Oct.	.64	.66	.42	.77	.28
Nov. to March	.57	.82	.47	.84	.39
Seasonal Ave.	.62	.75	.46	.78	.35

must use the same habitats at the same slope exposure-altitude intervals simultaneously, a look at the product of the indices of spatial distributions and habitat selection is informative. Again these indices are quite high, being around 40 to 50 per cent. Overlap in food habits ranged from 74 to 84 per cent with an average of 78 per cent, high for the three 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 highness of these indices, it appears that mule deer and white-tailed deer are quite similar in their use of space and food at the Dos Cabezas Mountains.

Levins' (1968) coefficients of competition for the Dos Cabezas Mountains are given in Table 11 (S x H x F). They indicate that there is considerable direct competition between mule deer and white-tailed deer at the Dos Cabezas Mountains. Although I believe that these coefficients are conservative, for the reasons mentioned previously, it is interesting to note that the coefficient for the critical time of the year (November-March) is highest and that for the optimal season (mid-July to October) is the lowest.

Recruitment

Results from herd composition counts related to recruitment to the populations of mule deer and white-tailed deer are presented in Table 12. Mule deer had a

Table 12. Herd composition counts of deer at the Dos Cabezas Mountains for the months of November through February, 1969-1972.

	White-tailed Deer			Mule Deer		
Year	Does	Fawns	Fawns/ 100 Does	Does	Fawns	Fawns/ 100 Does
1969-70	41	17	41.5	205	89	43.4
1970-71	30	8	26.7	123	34	27.6
1971-72	31	6	19.4	103	38	36.9
Totals	102	31	30.4	431	161	37.4

higher recruitment to the population than did white-tailed deer for the duration of the study. The magnitude of this difference was not significant until the last year when recruitment for mule deer was close to twice as great as that for white-tailed deer. Since a drought period preceded the last year's figures, this difference is quite informative. Overall recruitment for mule deer was seven per cent higher than for white-tailed deer.

Forage Utilization

A summary of the utilization surveys on *Cercocarpus breviflorus* according to year and slope exposure is given in Table 13. Surveys for the two years were carried out on the same plots. These surveys were conducted on *Cercocarpus breviflorus* only, since it is the key browse plant for deer at the Dos Cabezas Mountains (see Figure 6). Use of the annual growth of this species was extremely high. For all plots sampled the use on *Cercocarpus breviflorus* averaged 75 per cent of the annual leader growth. Use on this species was much higher in 1971 than in 1972; estimated use was 81 and 70 per cent, respectively. Statistical treatment of these data by analysis of variance shows that this difference in the yearly use is statistically significant ($F_{(.05)\ (1,8)} = 29.55$). This difference in per cent use for the two years is probably the result of differences in productivity of *Cercocarpus*

Table 13. Estimates of the utilization of the annual growth of *Cercocarpus breviflorus* by deer and cattle at the Dos Cabezas Mountains.

	Slope Exposure[b]					
Year	S	SE	Ne	NW	NE	Year Means
1971	75.4 ± 3.9[a] (2-100)	83.4 ± 2.7 (1-50)	84.7 ± 1.8 (2-100)	81.5 ± 2.5 (3-115)	80.1 ± 3.7 (1-50)	80.9 (9-415)
1972	61.9 ± 5.0 (2-75)	71.3 ± 5.3 (1-40)	82.7 ± 3.7 (2-70)	67.4 ± 3.5 (3-115)	71.2 ± 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)

[a] Values are: Mean $\pm t_{.05} S_{\bar{x}}$
(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.

[b] S = South, SE = Southeast, Ne = Neutral, NW = Northwest, and NE = Northeast.

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 per cent use for the following winter.

Use of Cercocarpus breviflorus for the various slope exposures was quite variable. Statistical analysis of these differences show that the effect of the slope exposures, on which surveys were carried out, was statistically significant ($F_{(.05)\ (4,8)} = 7.50$). Ranking the slope exposures in order of highest to lowest use (neutral, southeast, northeast, northwest, and south), reveals no explainable reason for these differences. I believe these differences are related to the specific areas where the surveys were made and their associated deer densities rather than slope exposure.

Cercocarpus breviflorus was utilized by cattle as well as deer at Dos Cabezas, so it was a highly preferred forage plant for all large herbivores in the area. The high percentage of use (up to 85 per cent in some areas) of the annual growth of this species indicates that food is a limiting factor during the late months of the winter in certain parts of the mountain. The high use of Quercus emoryi by deer during the winter months (Figure 6) also suggests a food shortage, since its forage value is quite low.

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 them to be aware of each other's presence. The maximum distance between individuals that any behavioral interactions became apparent was usually less than 50 yards, but this depended on the density of shrubs and trees. A summary of the observations of behavioral interactions between mule deer and white-tailed deer on both study areas is presented in Table 14. Encounters between the two species was more frequent at the Dos Cabezas area than at the San Cayetanos, 11 per cent of all deer-group observations at the former compared to 3 per cent at the latter. The difference in these frequencies reflects the sympatric nature of their populations at Dos Cabezas and the almost mutually exclusive nature at the San Cayetanos.

Most encounters (48 per cent) between mule deer and white-tailed deer occurred during April, May, or July; the hot, dry months of the year. In 59 per cent of these encounters I could not determine from my observations which species was dominant. When dominance could be ascertained (41 per cent of the encounters), mule deer were always

Table 14. Summary of behavioral interactions between mule deer and white-tailed deer, Dos Cabezas and San Cayetano Mountains.

Date	Herd Composition of Mule Deer[a]	Herd Composition of White-tailed Deer[b]	Dominant Species	Type of Dominance[c]
		Dos Cabezas Mountains		
8/19/69	2B, 2D	1D	NA	
12/ 6/69	1B, 5D, 1F	1D, 1F	NA	
12/21/69	3D, 1F	2D, 1F	NA	
12/21/69	1D, 2F	1B, 1D, 1F	NA	
2/ 7/70	8D, 5F	2D, 1F	NA	
2/27/70	2D	2D	MD	Active
7/25/70	2D	2D	NA	
9/ 8/70	2B	5B	MD	Passive
12/13/70	2D, 2F	1D	NA	
1/16/71	4D, 2F	1B, 1D, 1F	NA	
4/ 5/71	11D, 3F	1B, 3D	MD	Active
4/22/71	4D, 2F	4D, 1F	MD	Active
4/23/71	3D	1D	NA	
5/ 8/71	6D	4D	NA	
5/ 8/71	12D, 2F	2D	MD	Passive
5/18/71	1B, 12D, 2F	1D	MD	Active
5/19/71	5B, 15D, 3F	1B, 4D	NA	
6/ 6/71	8D	3B	MD	Passive
6/ 6/71	12D, 1F	3D, 1F	MD	Active
6/30/71	1D	2B	NA	
6/30/71	9D, 3F	1D, 1F	MD	Passive
		San Cayetano Mountains		
3/22/70	2D	2B, 4D, 1F	NA	
9/13/70	5D	2B	NA	
1/10/71	1B	1B, 1D, 1F	NA	
5/26/71	2D	1D	MD	Passive

Table 14.--Continued

Date	Herd Composition of Mule Deer[a]	Herd Composition of White-tailed Deer[b]	Dominant Species	Type of Dominance[c]
6/11/71	1D	1D	MD	Active
11/24/71	3D	2B	NA	

[a] B = bucks, D = does, F = fawns.

[b] "NA" means that dominance could not be determined from the interactions observed. "MD" means that mule deer were dominant.

[c] "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 Giest (1961).

dominant. Dominance of mule deer over white-tailed deer did not appear to depend upon the sex of the respective species' groups (Table 14). 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. In this case "passive" is 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 move out of the way of mule deer. Mule deer would continue their feeding without any apparent disturbance or aggression toward white-tailed deer. "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 described by Cowan and Giest (1961) and Dorrance (1966). The "crouch" occurs in part with hunched posture, low-rumped position, stiff and stilted walk, and ears laid back and turned with concave side exposed laterally. The "snort" occurs in the crouch position with the neck extended, head downward, hairs erect, and the tail held outwards or upwards. Dominance of mule deer over white-tailed deer was never displayed by attack. When mule deer displayed dominance over white-tailed deer, they did so in seeking a choice food item (i.e., flower stalks of <u>Nolina</u>

microcarpa during May or June) or over a choice bedding area out of the wind. On four occasions mule deer displaced, by threat, white-tailed deer feeding on flower stalks of Nolina 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 from my field notes of an observation made in the Dos Cabezas Mountains on September 8, 1970.

> I located a group of five white-tailed bucks and two mule deer bucks. Antler points for the five white-tailed deer were: 4 x 4, 3 x 3, 2 x 2, 2 x 2, and 1 x 1; and for the mule deer 3 x 3 and 2 x 2. This whole group of deer was feeding together early in the morning. There was much intraspecific aggression among the white-tails, especially the 4 x 4 white-tailed deer toward the others. The mule deer were obviously dominate; they moved about as they pleased, while the white-tailed deer made room for them to feed upon various mountain mahogany (Cercocarpus 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. Although the 4 x 4 white-tailed deer was very aggressive and dominant over the other white-tails, he was subordinate to the mule deer. From these observations I was able to detect a "peck-order" from the largest (3 x 3) mule deer down to the smallest (1 x 1) white-tailed deer. The last I saw of the group they were still all together.

The dominance of mule deer over white-tailed deer witnessed throughout this study is not surprising, since mule deer are nearly twice the size of white-tailed deer.

This size difference may account for mule deer's dominance in all circumstances observed during the study.

VEGETATIONAL SURVEYS

Surveys on *Quercus emoryi* and *Q. oblongifolia* were conducted at the Dos Cabezas and San Cayetano Mountains, respectively. These surveys were designed to determine the successional status of the oak communities and to detect any possible vegetative changes in past years. Individuals of the above species were categorized as to height and per cent decadence. Height was used as an indication of age and decadence as an indication of condition.

The height distribution of *Quercus emoryi* sampled at the Dos Cabezas Mountains is given in Figure 7. The majority (83 per cent) of these plants were over eight feet tall, and none of the plants sampled were in the seedling class of 0-2 feet. Several of the individuals of *Quercus emoryi* that were examined were completely dead (17 per cent). These data indicate that most of the oaks were in the older age classes and that reproduction was poor to non-existent.

The height distribution of *Quercus oblongifolia* sampled at the San Cayetano Mountains is presented in Figure 8. Practically all (94 per cent) of the individuals of this species were eight feet tall or taller, and none of the plants sampled were in the seedling class of 0-2

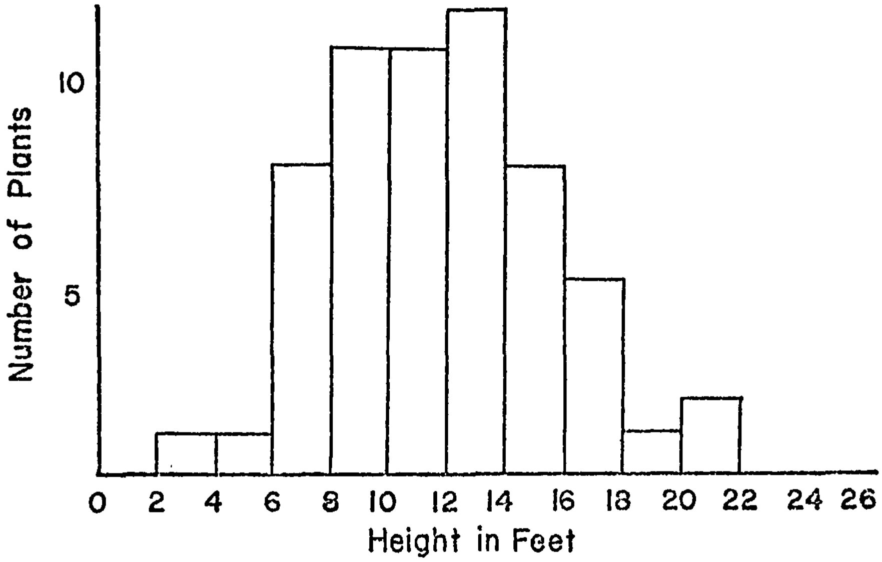


Figure 7. Height distribution of Quercus emoryii sampled at the Dos Cabezas Mountains, southeast Arizona.

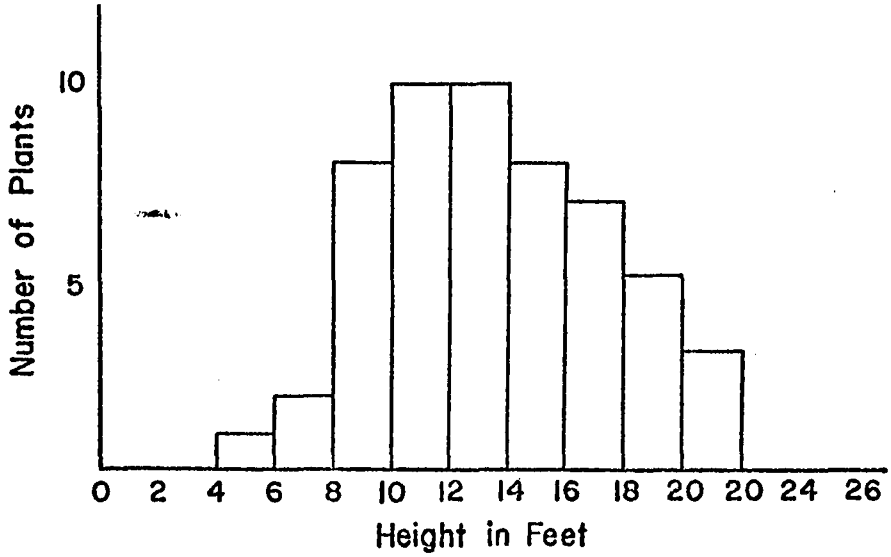


Figure 8. Height distribution of Quercus oblongifolia sampled at the San Cayetano Mountains, southeast Arizona.

feet. Many of these plants that were examined were dead (20 per cent), and others were observed to be in poor condition. As was found for _Q. emoryi_ at the Dos Cabezas Mountains, most of the oaks at the San Cayetano Mountains belonged to the older age classes, and reproduction was poor.

The above results suggest that _Q. Emoryi_ and _Q. oblongifolia_ at the Dos Cabezas and San Cayetano Mountains, respective, are declining and probably will not maintain their status as dominants in the present plant communities. According to Daubenmire (1968, p. 105) these plants would be classified as "disappearing relics" of an earlier stage of succession. But since 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 lower oak zone on my study areas is shifting upward in elevation as has been 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 southern Arizona (Powell, Jantzen, and Cosper, 1961) (see Appendix B). 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 to be quite variable, and the altitude and vegetative type where this association occurs is often different from one mountain area to another. This fact is well displayed by the present study in that populations of these two species were sympatric at the study area (Dos Cabezas) with higher altitudes and more mesic vegetation and climate, but mutually exclusive at the area (San Cayetanos) with lower altitudes and more xeric vegetation and climate. This phenomenon makes it difficult to answer the question: What factor or combination of factors determines where mule deer populations dwindle and whitetail populations begin to 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 populations of mule deer and white-tailed deer were closely associated between 4,250 and 5,250 feet in elevation. The coefficients of association after Southwood (1966) were somewhat neutral in that they indicated that there was no attraction or repulsion between the two species. Indices of overlap between mule deer and white-taileddder according to altitude and slope exposure (spatial distributions) were moderate; but they are probably 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 those habitat types that were dominated by _Prosopis juliflora_ and _Fouquieria splendens_, and they were occasionally observed in the habitats dominated by _Quercus oblongifolia_. White-tailed deer displayed a greater diversity in habitat selection than mule deer and appeared not to be associated directly with any plant species, although _Quercus oblongifolia_, _Dasylirion wheeleri_, and _Eysenhardtia polystachya_ received considerable use. Overlap in habitat selection between the two species was quite variable from one season to another. I believe that the relationship in distributional patterns (i.e., spatial distributions and habitat selection) of mule deer and white-tailed deer is most accurately quantified as a product of the indices of overlap in spatial distributions and habitat selection. These products may be called coefficients of distributional overlap. And, since these coefficients are around 10 per cent or lower for the data from the San Cayetanos, the two species are contiguously allopatric, a term discussed by Miller (1967).

Although the populations of mule deer and white-tailed deer were primarily separated at the San Cayetanos, there were several key forage plants found common to both of their distributions. These plants (Eysenhardtia polystachya, Krameria parvifolia, and Calliandra eriophylla) were subjected to a great deal of dual use by both deer species. Since Eriogonum wrightii was found primarily within the range of white-tailed deer, it was utilized mostly by this species. The same analogy can be applied to Prosopis juliflora and distributions of mule deer. The indices of overlap in food habits were high, ranging from 55 to 67 per cent. The low coefficients in distributional overlap and high indices of overlap in food habits lead me to conclude that mule deer and white-tailed deer tend to competitively exclude each other at the San Cayetano Mountains. The concepts of the competitive exclusion principle as outlined by Cole (1960), Hardin (1960), and Miller (1967) support this conclusion. The principles of competitive exclusion imply that the removal of one species allows 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). I doubt, however, whether white-tailed deer would extend their range considerably if mule deer were removed, because cattle have extremely overutilized the areas inhabited by mule deer. This principle also suggests that two similar species mutually avoid each other and select habitats in which each is competitively superior over the other. 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 _M. pennsylvanicus_ in Montana. _Microtus pennsylvanicus_ and _Cleitherionomys gapperi_ competitively exclude each other (Morris, 1969; Grant, 1969) as does _Peromyscus_ and _Mus_ (Sheppe, 1967).

Levins' (1968, p. 52) coefficients of competition substantiate the conclusion of competitive exclusion between mule deer and white-tailed deer at the San Cayetano Mountains. These coefficients indicate that there is little or no direct competition between the two species for all seasons.

Contrary to the situation in the San Cayetanos, mule deer and white-tailed deer populations at the Dos Cabezas Mountains were sympatric from 6,500 to 8,000 feet in elevation. 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 per cent. Both species were associated with those habitat types dominated by *Quercus emoryi*, *Juniperus deppeana*, *Cercocarpus breviflorus*, *Q. gambelii*, *Nolina microcarpa*, *Symphoricarpos ereophilus*, and/or *Bouteloua spp*. White-tailed deer displayed a greater preference for the *Quercus*-*Cercocarpus* and *Quercus*-*Symphoricarpos* habitat types than mule deer, whereas the *Juniperus*-*Cercocarpus* habitats were preferred more by the latter. These differences in habitat preference were slight, however, so that overlap in habitat selection was also high, ranging from 66 to 81 per cent. 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 at Dos Cabezas were important to diets of both deer species; the most prominent of these species were: *Cercocarpus breviflorus*, *Juniperus deppeana*, *Eriogonum wrightii*, and *Quercus gambelii*. There was, therefore, much overlap in their food habits. The high overlap in spatial distributions, habitat selection, and food habits coupled with the high utilization of the key forage plant (*Cercocarpus breviflorus*) during the winter months lead me to conclude that direct competition between the two species was occurring during these critical months. For 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 conclusion of direct competition between mule deer and white-tailed deer at 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 are probably the most critical months, since there would not be an abundance of deciduous forage plants to sustain deer through the hot, dry months.

The coefficients of competition indicate only if there is a potential for competition, because they convey no information about food availability or abundance. 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 utilization of <u>Cercocarpus breviflorus</u> was greater during the winter of 1970-71 than during 1971-72, there was undoubtedly 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 one density independent factor is sure to be of influence also. Plant productivity in desert areas is greatly influenced by annual precipitation, so annual precipitation could conceivably influence the degree of direct competition between these two species.

Data from both study areas indicate that mule deer and white-tailed deer are quite similar in their forage preferences. It appears that if a plant is palatable, it will be utilized by both species. This similarity in food preferences probably tells us something about the similarity of the nutritional characteristics of mule deer and white-tailed deer. However, some differences have been found. First, white-tailed deer appear to choose a greater diversity of plant species in their diet, since fecal samples for this species averaged a greater number of plant species. I interpret these results to mean that mule deer are more opportunistic in their feeding habits and are able to sustain themselves on only a few desirable species. In contrast white-tailed deer are probably 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 study areas, because plant availability was essentially equal for both species.

Secondly, white-tailed deer utilized a greater percentage of grasses and herbs than mule deer at the San Cayetano Mountains. This difference has two possible explanations: (1) it is characteristic of their food preferences, or (2) is a function of plant availability, since livestock use was much greater in mule deer habitats at the San Cayetano Mountains. No such difference in use of grasses and herbs was documented for the Dos Cabezas Mountains, but I believe this was because of extreme overuse of this area by livestock. The best habitats for white-tailed deer on both study areas were where livestock use was not extreme. Consequently, food preferences would seem to be the primary explanation (i.e., white-tailed deer graze more than mule deer). In any competitive interactions between these two 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, since this type of disturbance tends to increase grass and herb abundance (McCulloch, 1969; Hungerford, 1970) and thus favor white-tailed deer.

The previous discussion concerns competition for a common resource; Miller (1967) and Crombie (1947) have termed this component of competition as "exploitation."

Exploitation usually involves use of space and food; it is believed to be the most primitive and unstable form of interaction between species. The second component of interspecies competition is "interference" (Miller, 1967; Crombie, 1947). It 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. Since mule deer were observed to be the more dominant species, it is possible that they interfere with white-tailed deer. From the behavioral interactions that were observed between mule deer and white-tailed deer, it is hard to say how important interference is in their interactions. However, the infrequent occurrence of behavioral interactions and the usual nonaggressive nature of these encounters lead me to conclude that interference is not a very important factor in the relationship between these two species. Behavioral interactions (i.e., dominance-subordinance relationships) appear to be of considerable importance between similar pairs of small rodents (Murie, 1971; Cameron, 1971; Grant, 1969; Koplin and Hoffman, 1968).

Few papers concerned with interspecies relationships conclude that direct competition has occurred. Cameron (1971) reported interspecific competition between *Neotoma lepida* and *N. fuscipes*; similar results have been presented for Baiomys taylori and Sigmodon hispidus by Raun and Wilks (1964). Many researchers appear to be reluctant to make such a conclusion, because niche theory (Gause's Hypothesis) and the concepts of the evolution of similar species are contradicted. Data for part of the present study directly contradict Gause's Hypothesis, but I believe this contradiction can be easily explained. First, Gause's Hypothesis 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 disturbance. Interspecies competition is undoubtedly a transient phenomenon at 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 comprised 64 per cent of the population of antlered deer for mule deer and only 24 per cent 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 slowly increasing. This change is bound to be a slow process, when one considers the slow turnover rates for deer populations. There are many examples which show that 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.*, it takes at least eight generations (270 days) for one species to replace another when placed in a very simple environment (Park, 1948). Consider the difference in turnover rates between *Odocoileus spp.* and *Tribolium spp.* and the corresponding replacement time becomes quite long.

The life table for the buck segment of the mule deer population at Dos Cabezas shows that they have a thriving population (Appendix D); that is, most of the individuals in this segment of the population are young. Only 22 per cent of the mortalities were four and one-half years old or older. Samples for white-tailed deer at Dos Cabezas were inadequate but appear to indicate that their populations are declining, since 76 per cent of the mortality figures were four and one-half years old or older. 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 I 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 over 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? I believe the major factor has been a vegetative change, which has been coupled with overgrazing by livestock. Hastings and Turner (1965) give evidence that there has been an upward shift in the vegetative zones in southern Arizona during the last 100 years. Their book shows that there has been a decline in desert grasslands, because of the encroachment of desert shrubs (*Prosopis juliflora*, *Fouquieria splendens*, *Acacia greggii*, and *A. constricta*) into grassland communities. They also have evidence that the lower oak zone is retreating upward in altitude. According to Hastings and Turner, hotter and drier conditions coupled with overgrazing by livestock and fire suppression appear to be the causes of these vegetative changes. Other articles give evidence for this vegetative change in recent (Humphrey, 1958) and prehistoric years (Van Devender and King, 1971). Surveys, which were conducted during this study, on *Quercus spp.*, show that the lower oak zone is retreating upward at the San Cayetano and Dos Cabezas Mountains (Figures 7 and 8). Analysis of size classes indicate that the oaks (*Q. oblongifolia* or

Q. emoryi) are remnant populations with little or no reproduction occurring. At the San Cayetano Mountains 94 per cent of Q. oblongifolia sampled were over eight feet tall, and 84 per cent of Q. emoryi were taller than eight feet at Dos Cabezas. There is, therefore, good evidence that vegetative changes are occurring on both study areas. I believe these vegetative changes associated with overgrazing by livestock have brought mule deer and white-tailed deer into direct competition at the Dos Cabezas Mountains. Both the vegetative changes, that have been documented, 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, there are three factors that have probably been influential. These factors are: (1) a climatic change to hotter and drier conditions that has resulted in an upward shift in the vegetative zones, (2) overgrazing by livestock, and (3) fire suppression. All of these factors create environmental (vegetative) changes that would favor mule deer encroachment into white-tailed deer range. I believe that the first of these factors has been most influential, but for any given mountain area any one factor or combination of these factors may have been most influential. The above influences are probably the ultimate factors.

In most mountain areas of southern Arizona, populations of mule deer and white-tailed deer are not closely associated enough for direct competition to occur. But, in some areas they are associated closely enough for them to competitively exclude each other. I believe that competition between mule deer and white-tailed deer, when it occurs, is only a result of the above factors and is not solely responsible for past changes in distributions of the two species.

SUMMARY

Niche relationships between mule deer and white-tailed deer were studied at 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 observations were carried out. 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 studied supplemental to the other data gathered.

Spatial distributions according to altitude and slope exposure suggest that there is no attraction between mule deer and white-tailed deer at the San Cayetano Mountains, but there is also no repulsion. There appeared to be a "buffer" zone between their populations. Mule deer were associated with fewer vegetative 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 vegetative types at the San Cayetanos and did not appear to be associated with any particular plant species, although *Quercus oblongifolia*, *Dasylirion wheeleri*, and *Eysenhardtia polystachya* received considerable use. The most important forage plants for white-tailed deer at the San Cayetano Mountains were *Eysenhardtia polystachya*, *Eriogonum wrightii*, *Krameria parvifolia*, and *Fendlera rupicola*. Similarly the primary food items of mule deer were *Eysenhardtia polystachya*, *Calliandra eriophylla*, and *Krameria parvifolia*. There was much overlap in preferences of mule deer and white-tailed deer (55 to 67 per cent) particularly on *Eysenhardtia polystachya* and *Krameria parvifolia*. White-tailed deer utilized a greater diversity of forage plants than did mule deer.

Populations of mule deer and white-tailed deer were sympatric at 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*, *Cercocarpus breviflorus*, *Q*. *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 the *Juniperus*-*Cercocarpus* habitats were preferred more by the latter. Food habits of mule deer and white-tailed deer were very similar; all the plant species that were important to white-tailed deer were also important to mule deer. The most frequent forage plants, in order of importance, were *Cercocarpus breviflorus*, *Eriogonum wrightii*, *Juniperus deppeana*, and *Quercus gambelii*. White-tailed deer utilized a greater number of forage plants per fecal sample than mule deer at the Dos Cabezas Mountains. Recruitment to the population was higher for mule deer than white-tailed deer. Utilization of the annual leader growth on the key browse plant (*Cercocarpus breviflorus*) was extremely high.

Mule deer were dominant over white-tailed deer in all encounters observed during the study. In half of these instances mule deer used 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 me to conclude that mule deer and white-tailed deer tend to 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 (*Cercocarpus breviflorus*) at Dos Cabezas during the winter months leads me to conclude that direct competition between the two species was occurring during these months. 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 has been a vegetative change, which has been accompanied or produced by livestock overgrazing.

There are three factors, which have probably been influential in the historical changes in mule deer and white-tailed deer distributions: (1) a climatic change to hotter and drier conditions that has resulted in an upward shift in the vegetative zones, (2) overgrazing by livestock, and (3) fire suppression. All of these factors would favor mule deer encroachment into white-tailed deer range. I believe that interspecific competition between these two species is not solely responsible for historic changes in their distributions, but that the above factors are the ultimate causes.

APPENDIX A

RATIO OF WHITE-TAILED DEER TO MULE DEER KILLED BY HUNTERS IN SOUTHEASTERN ARIZONA

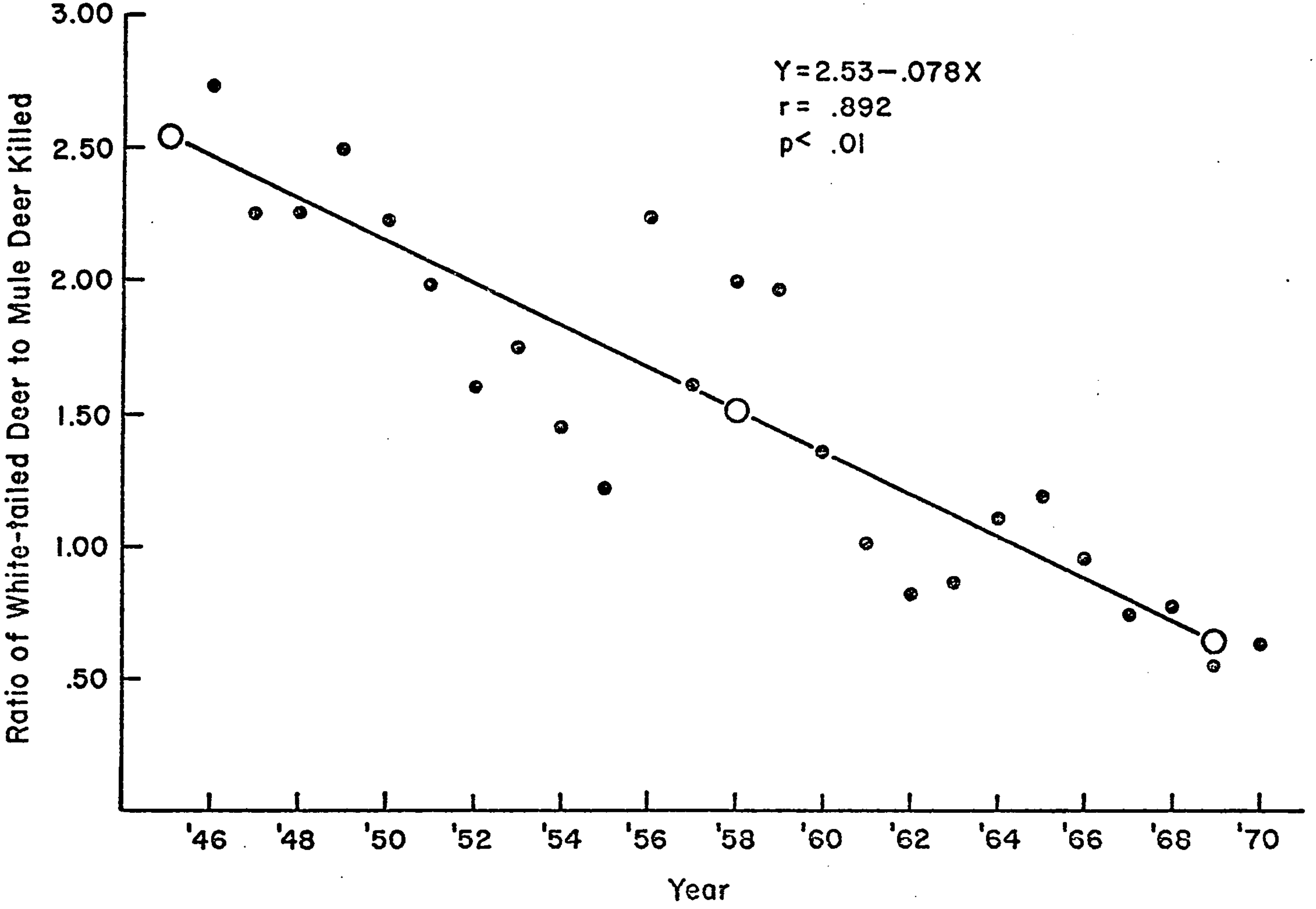


Figure 9. Ratio of white-tailed deer to mule deer killed (bucks only) in southeastern Arizona (Mgmt. Units: 29, 30, 31, 32, 33, 34, 35, and 36) from 1946 to 1970 -- These data were taken from the Arizona Game Management Data Summary published annually by the Arizona Game and Fish Department.

APPENDIX B

FOOD PREFERENCES OF DEER AT THE SAN CAYETANO MOUNTAINS

Table 15. Food preferences of mule deer and white-tailed deer at the San Cayetano Mountains from August, 1969 to January, 1972.

	Feb.-April				May-July				Aug.-Oct.				Nov.-Jan.			
	WT (29)		MD (18)		WT (24)		MD (12)		WT (29)		MD (29)		WT (23)		MD (29)	
Plant Species	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.
Eysenhardtia polystachya	4.7	45	6.3	44	24.0	83	16.4	83	27.6	93	23.8	93	30.7	91	19.0	96
Calliandra eriophylla	.2	28	3.1	44	1.2	21	11.1	50	3.7	24	28.2	90	10.6	70	22.3	88
Eriogonum wrightii	19.4	93	5.1	50	8.3	71	1.6	8	10.8	86	3.1	41	15.5	96	4.9	52
Krameria parvifolia	9.1	66	19.1	89	10.8	58	12.8	58	17.2	90	16.1	86	12.5	83	14.9	92
Fendlera rupicola	9.9	62	7.5	33	10.5	58	1.3	8	2.3	24	1.2	17	2.5	39	0.0	0
Prosopis juliflora	1.3	17	3.6	33	1.5	25	4.8	66	.6	21	4.7	62	6.2	74	17.9	88
Stephanomeria pauciflora	8.9	76	5.9	44	4.1	66	7.0	66	3.4	45	.2	10	.5	13	.3	12
Fouquieria splendens	2.4	10	2.6	28	2.9	21	2.5	17	6.1	62	6.3	68	0.0	0	.3	4
Nolina (flower stalk)	1.2	21	.1	6	11.8	66	10.0	50	0.0	0	0.0	0	.1	9	0.0	0
Argemone platyceras	T	3	0.0	0	7.0	42	.4	8	.2	7	0.0	0	0.0	0	0.0	0
Mimosa dysocarpa	0.0	0	T	6	3.9	42	0.0	0	2.4	38	3.7	45	.6	13	1.3	16
Bouteloua chondrosiodes	6.6	55	3.3	39	2.9	54	.1	17	5.3	66	3.3	45	3.0	39	2.0	40
Bouteloua curtipendula	4.3	41	3.3	33	1.7	33	1.3	25	1.3	34	.9	31	1.2	39	.5	20
Quercus oblongifolia	5.9	62	2.3	28	2.0	21	.1	17	T	3	0.0	0	1.8	30	.7	16
Artemesia ludoviciana	2.5	28	.6	11	1.6	17	0.0	0	1.3	34	.4	7	1.5	26	0.0	0
Acacia greggii	0.0	0	3.1	22	T	4	17.1	58	.1	3	.1	3	0.0	0	.4	8
Celtis reticulata	2.0	24	12.0	44	.6	13	4.0	33	.6	7	.9	17	0.0	0	1.5	12
Ferocactus wislenzenii	.4	7	0.0	0	0.0	0	0.0	0	.6	10	2.3	31	1.5	13	6.0	68
Anisacanthus therberi	.8	17	3.8	33	.9	13	1.5	17	.3	10	.3	3	.1	9	0.0	0
Commelian dianthifolia	0.0	0	0.0	0	.5	4	0.0	0	1.7	34	2.0	28	.3	9	0.0	0
Juniperus monosperma	T	3	3.4	56	0.0	0	1.3	25	0.0	0	.1	10	2.1	9	1.3	20
Unknown #20	4.3	52	4.3	44	.8	21	0.0	0	.2	21	.2	7	1.2	30	.2	12
25 other species	9.3	-	7.4	-	9.3	-	5.2	-	7.7	-	1.7	-	4.6	-	3.8	-

WT = White-tailed deer, MD = Mule deer.

APPENDIX C

FOOD PREFERENCES OF DEER AT THE DOS CABEZAS MOUNTAINS

Table 16. Food preferences of mule deer and white-tailed deer at Dos Cabezas Mountains from August, 1969 to January, 1972

	April to Mid-July				Mid-July to Oct.				Nov.-March			
	WT (35)		MD (47)		WT (30)		MD (35)		WT (45)		MD (71)	
Plant Species	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.
Cercocarpus breviflorus	17.2	83	22.4	91	29.3	100	31.7	97	45.0	100	39.5	100
Juniperus deppeana	10.0	71	21.8	100	9.3	93	16.0	86	15.9	100	27.6	100
Quercus emoryi	4.7	43	6.1	45	.7	17	.7	11	12.6	89	11.9	93
Eriogonum wrightii	16.8	97	10.2	70	8.9	67	7.6	60	9.9	84	6.7	66
Quercus gambelii	14.6	57	11.8	45	17.1	77	10.1	54	-	-	-	-
Stephanomeria pauciflora	.7	14	.9	17	3.8	47	2.5	23	1.0	31	.5	14
Symphoricarpos ereophilus	1.2	17	3.9	32	1.9	27	2.8	31	-	-	-	-
Artemesia ludoviciana	2.1	23	2.1	28	1.0	33	.6	8	1.2	40	1.3	30
Nolina (flower stalk)	6.5	47	4.3	32	.8	13	.3	6	-	-	-	-
Juniperus (berries)	2.3	29	.7	15	2.4	23	.3	6	5.2	53	4.3	58
Quercus hypoleucoides	2.7	43	1.5	13	.9	20	.4	6	.6	24	.5	20
Cowania mexicana	-	-	.4	4	.6	13	1.8	9	1.3	24	.8	20
Garrya wrightii	-	-	T	2	.6	10	-	-	.8	16	1.3	31
Rhus trilobata	.2	6	.6	11	.6	10	1.4	11	-	-	.6	28
Fendlera rupicola	1.4	23	1.5	30	1.5	33	-	-	1.1	31	.5	7
Celtis reticulata	2.5	37	1.2	17	3.0	33	1.0	11	.4	11	-	-
Acacia constricta	.2	5	.2	2	2.4	27	2.8	26	.3	2	1.8	10
Mimosa biuncifera	-	-	-	-	.6	3	2.3	11	-	-	T	1
Bouteloua curtipendula	.7	20	1.7	33	1.0	20	2.3	43	.1	4	.2	7
Bouteloua gracilis	1.2	30	1.4	26	1.4	23	.2	6	.1	4	-	-
Lycurus phleoides	1.9	31	1.4	23	2.2	37	.7	9	-	-	T	1
Andropogon cirratus	1.2	23	.6	17	.3	13	1.1	11	T	2	T	4
Eragrostis curvula	1.8	11	.5	11	.5	10	.1	3	-	-	1.5	6
33 other species	5.3	-	4.9	-	10.9	-	7.9	-	1.6	-	2.2	-

WT = White-tailed deer, MD = Mule deer.

APPENDIX D

POPULATION CHARACTERISTICS OF DEER AT THE DOS CABEZAS MOUNTAINS

Table 17. Age classification of hunting and natural mortalities of male mule deer at the Dos Cabezas Mountains.

	Age Class								
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8+
Number	3	13	34	23	9	3	2	2	4
Percentage			37	25	10	3	2	2	4

Table 18. Age classification of hunting and natural mortalities of male white-tailed deer at the Dos Cabezas Mountains

	Age Class								
	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

Table 19. Life table for male mule deer from the Dos Cabezas Mountains.[a]

x	d'x	dx	lx	qx	Lx	ex
1/2	190	470	1,000	470	765.0	1.40
1-1/2	137	339	530	639	360.5	1.19
2-1/2	34	84	191	440	99.0	1.42
3-1/2	23	57	107	532	78.5	1.60
4-1/2	9	22	50	440	34.0	1.86
5-1/2	3	8	28	286	24.0	2.11
6-1/2	2	5	20	250	17.5	1.75
7-1/2	2	5	15	330	12.5	1.17
8-1/2+	4	10	10	1,000	5.0	.50

x = age group, d'x = number of deaths, dx = number of deaths per 1,000, lx = number of survivors per 1,000, qx = mortality rate, Lx = mean number of individuals alive between the stated age class, ex = mean expectation life.

[a] Estimates for the 1/2 and 1-1/2 age classes were taken from the percentage of spike bucks and percentage of fawns (divided by 2) observed in the population. Percentages of the other age groups were taken from Table 17.

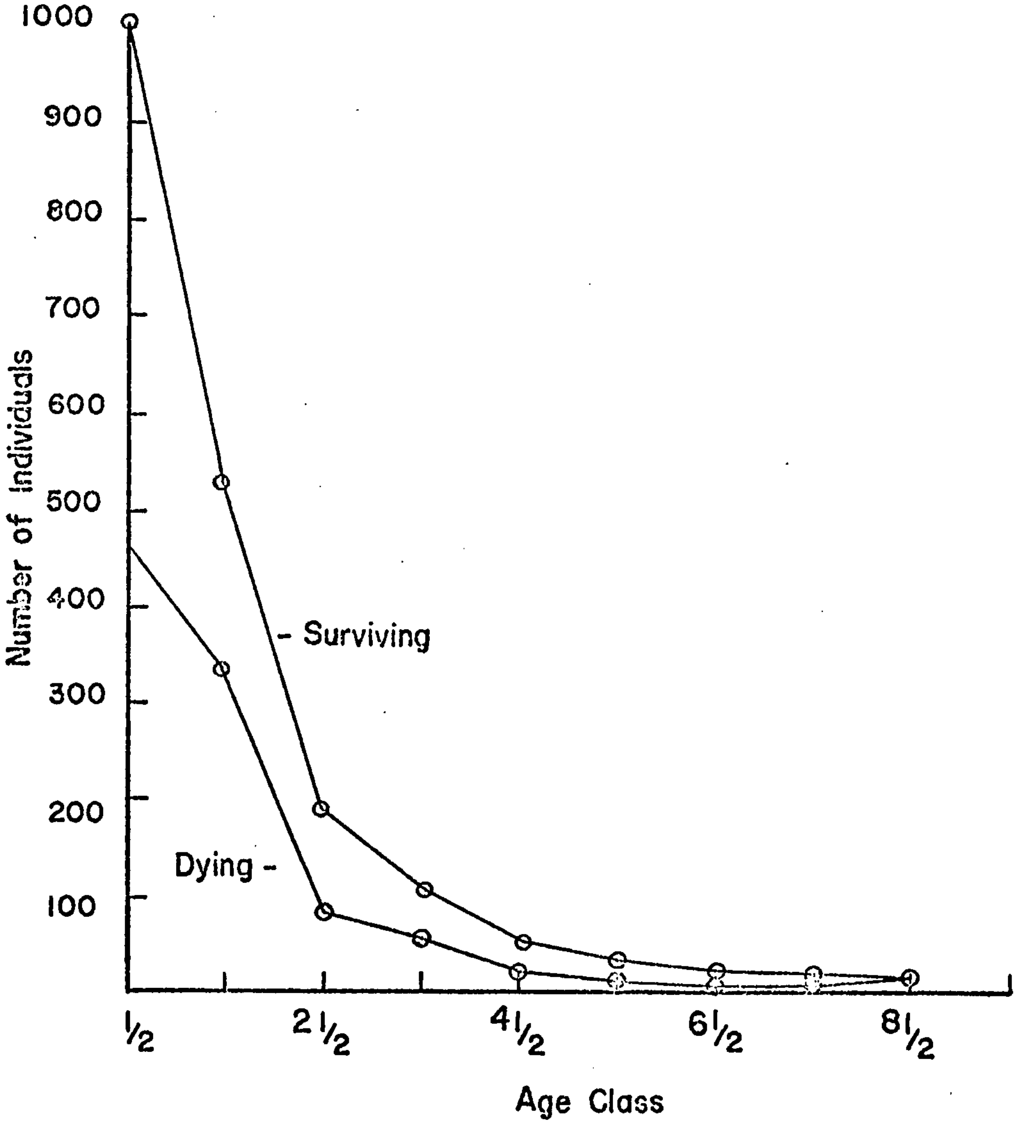


Figure 10. Mortality and survivorship curves for mule deer males at the Dos Cabezas Mountains.

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