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HABITAT SELECTION BY MULE DEER: EFFECTS OF MIGRATION AND POPULATION DENSITY

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

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May 1995

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HABITAT SELECTION BY MULE DEER: EFFECTS OF MIGRATION AND POPULATION DENSITY

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ABSTRACT

I investigated effects of migration and population density on habitat and diet selection in a population of mule deer (Odocoileus hemionus) in southern California from 1989 to 1991. All male deer were migratory, whereas females exhibited a mixed strategy with both migrant and resident individuals. No difference occurred in sizes of home ranges for migratory or resident deer. Home-range size of deer was smaller in summer than in winter, however. Size of home range was positively associated with proximity to human disturbance and the amount of avoided habitat (use < available) in the home range. Deer avoided human disturbance in all seasons. Clear tradeoffs existed for deer in montane southern California with respect to whether they migrated. Migratory females were farther from human disturbance and used high-quality habitats more often than did their nonmigratory conspecifics. Nonetheless, during migration deer were at increased risk of predation, and in years of low precipitation (low snow) had higher rates of mortality than did resident deer. Thus, in areas with extremely variable precipitation and snow cover, a mixed strategy for migration can be maintained. Migration patterns of deer resulted in drastic shifts of population density between seasons as deer migrated into and out of ranges. Quality of diet (as indexed by fecal crude protein) for deer in a low-density area was higher than that of a high-density area in winter, when deer densities were most different. Diet quality was similar in summer when both areas had similar densities of deer. Contrary to predictions of the ideal-free distribution, diet quality was different between the two areas in autumn when population densities were similar; this may have been due to an elevated availability of graminoids on the high-density area. Niche breadth, as measured by diet diversity, differed in a manner opposite to the predictions of the ideal-free distribution. During winter, when differences in density between the two study areas were most evident, niche breadth along the dietary axis in the low-density group was twice

the size of this measure for the high-density area. Theoretical models for changes in niche dimension need to consider such empirical outcomes.

TABLE OF CONTENTS

LIST OF FIGURES

Figure Page

LIST OF TABLES

Table Page

ACKNOWLEDGMENTS

This project was funded by grants from the California Department of Fish and Game, the National Rifle Association, and the San Bernardino County Fish and Game Commission. Housing and logistic support were provided by the U. S. Forest Service and travel was made possible by grants from the University of Alaska Fairbanks. Financial support during analyses and preparation of my dissertation were provided by a graduate assistantship from the Department of Biology and Wildlife, University of Alaska Fairbanks, and a fellowship from the University of Rhode Island's Center for Vector-Borne Disease.

I thank Dr. R. T. Bowyer, my advisory committee chairman, for his dedication to this project and my degree. His assistance, guidance, encouragement, and example helped me understand the meaning and value of good science. I also thank the members of my advisory committee, Drs. F. Dean, E. Follmann, J. Fox, and J. Kie for providing advice on all aspects of this project and for their tireless review of this dissertation. Each in their own way provided invaluable assistance and helped me develop many of the ideas found in this manuscript.

In the Department of Biology and Wildlife I would like to thank Drs. F. Chapin, J. Fox, S. MacLean, and R. White for helpful suggestions during the development of this project. I am deeply indebted to the staff of the department and that of the Institute of Arctic Biology, their never-ending patience and ability to solve all of my University problems and calm my paranoia were truly appreciated. Fellow graduate students M. Berger, M. Biddlecomb, V. Bleich, W. Eastland, N. Eikelmann, K. Gerhardt, H. Hanson, H. Meyer, J. Meyer, J. Rachlow, J. Sellinger, M. Smith, and K. Wilson shared my trials, soothed my anxieties, and filled my life in Alaska with many fond memories and much

happiness. I also thank the "Hotel Bowyer": Terry, Karolyn, Bryan, and Jeffrey. There kindness and generosity will not be forgotten.

California Department of Fish and Game Warden-Pilot R. Anthes' skill in the air and gentle manner, kept me safe and mostly free of air sickness for three years. B. Davitt at Washington States Habitat Laboratory ably performed all laboratory analyses for this project. J. Davis, J. DeWald, D. Inmann, S. Loe, T. Paulek, S. Sferra, A. Spina, and S. White provided many helpful suggestions and assistance when they were desperately needed. I also thank M. Neel for lending her botanical wizardry to this project. I especially thank Jenny Rechel for providing computing facilities, field assistance, many thoughtful discussions, and most importantly friendship; she filled my time in California with joy.

Also in California the residents, past and present, of Heartbar Station, especially Lisa Clark, David Johnson and Dan Snow, opened up their lives and made me a part. I will never forget Heartbar and the special people who lived there. In that regard Vernon, Theresa, Anastacia, and Theran Bleich helped me in ways too numerous to mention, their kindness, and giving were there to keep me well fed and happy both in California and Alaska.

At the University of Rhode Island I thank Dr. T. Mather for providing support and assistance during the completion of this dissertation. I also thank the gang at the Environmental Data Center, N. Andrew, C. Baker, J. Barrette, R. Cameleo, J. Conrad, R. Duhaime, C. LaBash, A. Tsu, and especially Dr. P. August. They all provided me with numerous suggestions during analyses and most importantly provided a kind and supportive environment. The camaraderie and professionalism I experienced at the EDC helped justify my decision to make science my life.

Finally I would like to thank my family Bob, Joanne, Jude, Steve, Ashley, Stephen, Kyle, Amanda, and most especially my parents Robert and Pauline. The support and encouragement they provided me throughout my life made all things possible. I dedicate this to them with love. As Richard Bach said, "There is no such thing as a problem without a gift for you in its hands. You seek problems because you need their gifts." The trials of this dissertation have only strengthened my conviction that you are all the greatest gifts in my life.

CHAPTER I

HABITAT SELECTION AND SURVIVAL OF MULE DEER: TRADEOFFS ASSOCIATED WITH MIGRATION

I examined tradeoffs related to migration in a population of mule deer (Odocoileus hemionus) in southern California from 1989 to 1991. All male deer I radio-collared were migratory, whereas females exhibited a mixed strategy with both migrant and resident individuals. Increased movements of deer were associated with decreased temperatures and increased weekly precipitation. No within season differences in the sizes of home ranges occurred for either migrant or resident deer. Home-range size of deer was smaller in summer than in winter, however. Size of home range was positively associated with proximity to human development and the amount of avoided habitat in the home range. Deer avoided human developments in all seasons. Further, males and resident females used areas farther than random from water in summer, whereas migratory females selected areas nearer to water. In summer, migratory females selected meadows, riparian habitats, and pine forests, whereas resident females avoided meadow and riparian habitats and used pine forests less than did migratory females. Males used habitats in a way similar to migratory females, although they avoided meadow and riparian areas. Clear tradeoffs existed for deer in montane southern California with respect to whether they migrated. Migratory females were farther from human disturbance and used high-quality habitats more often than did nonmigratory conspecifics. Nonetheless, deer were at increased risk of predation during migration, and in years of low precipitation (low snow) had higher rates of mortality than did resident deer. Thus, in areas with extremely variable precipitation and snow cover, a mixed strategy for migration can be maintained.

Key words: California mule deer, Odocoileus hemionus californicus, migration, habitat selection, home range, tradeoffs, survival, southern California

Patterns of migration have evolved to take advantage of spatial and temporal variation in the environment (French et al., 1989). Selection should favor those individuals that migrate, if by migrating, their reproductive success is enhanced (Baker, 1978). Because of environmental fluctuation and individual differences in the costs of migration, several strategies related to migration can occur in the same species or even in the same population (Fretwell, 1972). Indeed, mule deer (Odocoileus hemionus) are extremely variable throughout their distribution in whether they migrate. Many investigators have observed resident populations of deer (Bowyer, 1986; Eberhardt et al., 1984), migrant populations (Garrot et al.; 1987; Gilbert et al., 1970; Zalunardo, 1965), or populations with both resident and migrant individuals (Kufeld et al., 1989; Loft et al., 1984; Pac et al., 1988).

The question of why some individuals in a population migrate and others do not has been examined by several authors. Theoretical models concerning whether individuals migrate have been built around optimization theory (Cohen, 1967) and the concept of evolutionarily stable strategies (Parker and Stuart, 1976). The ultimate currency of most models is reproductive success. Lifetime reproductive success is a function of both survivorship and birth rate (Caughley, 1977), and the adaptive significance of migration can best be understood by examining the selective forces acting on these life-history parameters (Dingle, 1980). Forage quality and availability affect survivorship and birth rate, as does risk of predation; authors have implicated each as an ultimate factor affecting migration (Fryxell and Sinclair, 1988; Taylor and Taylor, 1977).

Although one defining characteristic of migration is a shift in habitat use (Baker, 1978), this assessment is complicated by various sex and age classes of deer potentially selecting habitats differentially. Bowyer (1986) and Loft et al. (1987) noted that young had substantially different habitat requirements, especially for concealment cover, than did adult deer. Moreover, Bowyer (1984) and Scarbrough and Krausman (1988) reported sexual differences in use of forages or habitats by mule deer. Further, McCullough (1979) postulated that differential use of resources by sex accounted for the weak relationship observed between recruitment rate of white-tailed deer (O. virginianus) and the number of male deer on the George Reserve, Michigan, whereas this inverse relationship was strong for adult females and recruited young.

Essential for understanding patterns of migration is the concept of the home range. Although home range is one of the most commonly measured variables in animal ecology, most studies have concentrated on the measurement of home-range size rather than its biological basis (Bowers et al., 1989; Hundertmark, in press). Home-range sizes within local populations of mule deer are extremely variable; home ranges of 33 ha (Loft et al., 1984) and 9,300 ha (Eberhardt et al., 1984) have been noted. Although habitat composition (Riley and Dood, 1984), availability of water (Eberhardt et al., 1984), and interspecific competition (Loft et al., 1991, 1993) have been implicated, few studies have quantitatively examined factors that affect home-range size in mule deer or other ungulates.

Although descriptions of movements for many populations exist, few authors have examined the tradeoffs involved in the migration strategies of mule deer or other large herbivores. Deer populations in the San Bernardino Mountains of southern California exhibit a mixed pattern of migration with both migrant and resident components (T. Paulek, in litt.). This afforded a unique opportunity to quantitatively assess the costs and benefits of migration.

I evaluated the causes and consequences of migration by a population of mule deer by: 1) quantifying the timing and extent of movements; 2) examining the proximate factors associated with migration; 3) quantifying the seasonal use of habitat by various classes of deer; and 4) determining how migration was related to patterns of habitat selection by mule deer. I tested whether migratory mule deer benefited from decreased intraseasonal movements, increased used of high-quality habitats, and decreased predation compared with nonmigratory conspecifics.

MATERIALS AND METHODS

Study area.--This study was conducted in the San Bernardino Mountains, which compose part of the Transverse Ranges of coastal California. These mountains are oriented on an east-west axis and extend ca. 95 km from Cajon Pass on the west to Yucca Valley, in the Mojave Desert, on the east. The mountain range is bounded by the Mojave Desert on the north and by Banning Pass 40 km to the south. Most deer I studied lived in the upper drainage of the Santa Ana River, a 32,000-ha area in the southwestern portion of that mountain range (centered at 34°10' 34" N, 116°53' 57" W; Fig. 1). This watershed is bounded on the north by Moonridge and Big Bear City, and on the east and south by the crest of the San Bernardino Mountains. Tributaries of the Santa Ana River include Mill, Bear, Cienega, and Wildhorse creeks, and many other smaller streams. The river leaves the mountain range near Redlands and flows westward across the coastal plain, toward Los Angeles.

Slopes associated with the Santa Ana drainage generally are steep and topographically diverse, limiting human access to some areas. Elevations range from 610 to 3,500 m at the summit of Mount San Gorgonio. Highway 38 parallels the Santa Ana River for part of its length. Numerous dirt and paved roads also occur in the study area, as do recreational campgrounds and ca. 200 special-use cabins managed by the United States Forest Service. Vehicular access to north-facing slopes south of Highway 38 is limited because this area is wilderness and lacks roads. Most of the lands within the watershed are administered by the San Bernardino National Forest, although some private

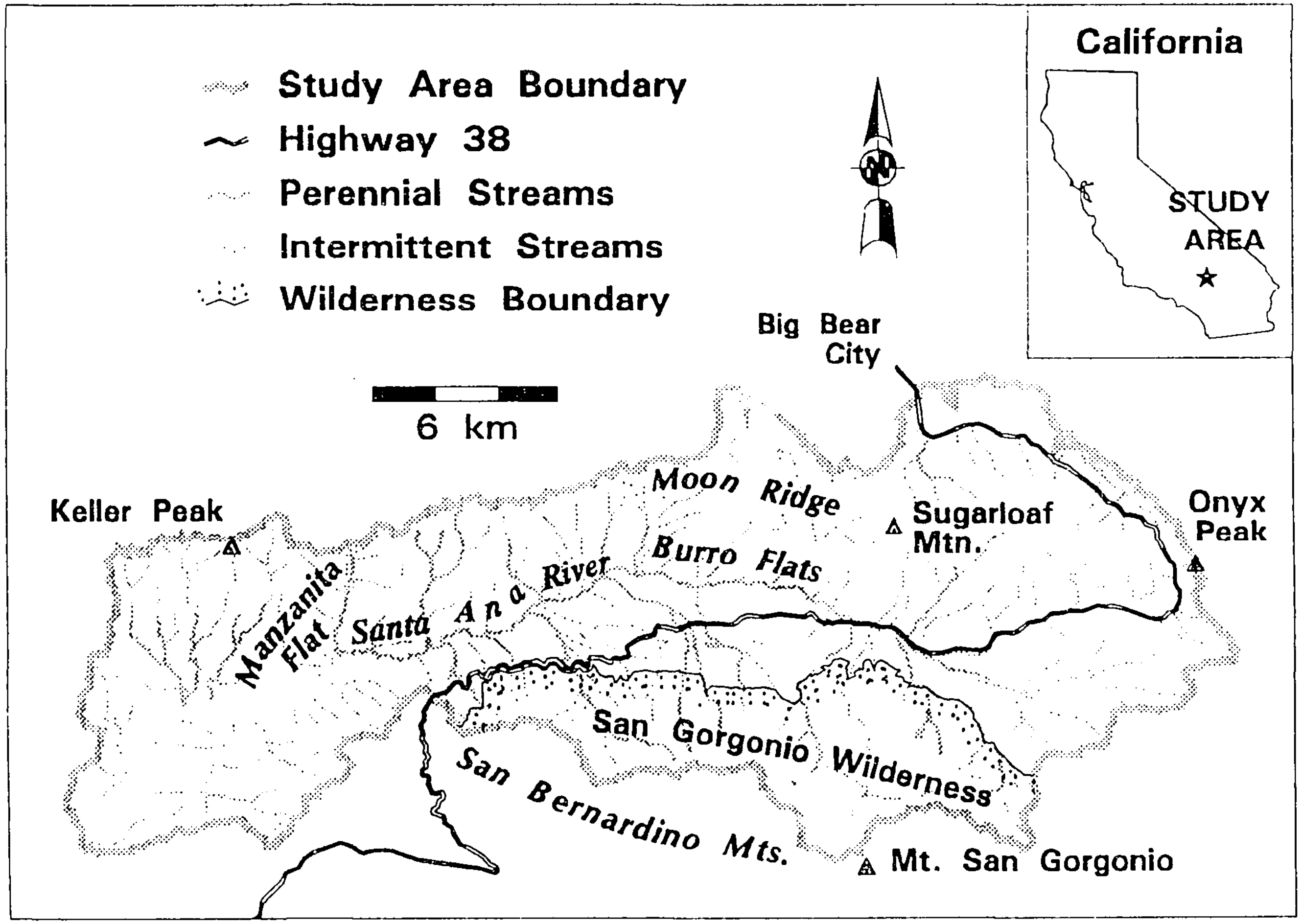

Fig. 1.--The study area in San Bernardino Co., California, depicting significant land features. Radio-telemetered deer monitored in this study were captured on Manzanita Flat to the East and Burro Flats in the center of the area.

holdings occur along the lower Santa Ana River, and in the community of Angelus Oaks.

The climate within the drainage of the Santa Ana River is typical of cismontane southern California. Annual temperatures range from >40°C during summer at low elevations, to <-20°C on the highest peaks in winter. Rainfall occurs primarily during the cooler winter months. During late summer, thunder showers become increasingly common at higher elevations, and temperatures are somewhat cooler. Above 1,500 m, winter precipitation occurs primarily as snow; however, on south-facing slopes snow cover is transitory. Annual precipitation is extremely variable but generally is >600 mm. During this investigation, 1989 (392 mm) and 1990 (469 mm) were drought years, whereas precipitation was average in 1991 (736 mm).

The study area encompasses a variety of vegetation types typical of cismontane southern California (K. E. Mayer and W. F. Laudenslayer, in litt.). Foothills at lower elevations support the coastal-scrub habitat composed primarily of Eriogonum fasciculatum, Artemesia californica, and Salvia. Above the coastal scrub is mixed-chaparral habitat typified by broad-leaved sclerophyllous shrubs primarily of the genera Arctostaphylos, Rhamnus, Ceanothus, Cercocarpus, and Quercus. Pure stands of chamise chaparral dominated by Adenostoma fasciculatum also are present and intergrade with mixed chaparral at moderate elevations. Stands of sagebrush (Artemesia tridentata) habitat exist at elevations >1,500 m. Plant nomenclature follows Munz (1974).

Limited areas of montane riparian and meadow habitat occur within the mesic areas of the drainage. Plant genera typical of riparian habitat include Salix, Populus, Quercus, Platanus, Rhus, Sambucus, and Alnus. Juncus and Carex are abundant in meadows. Montane-hardwood habitat typically occurs on mountainous slopes and valley bottoms ≥1,500 m. Both deciduous and evergreen oaks (Quercus) dominate the overstory, whereas Arctostaphylos, Ceanothus, and Cercocarpus are abundant in the shrub layer. Various conifer-dominated habitats also occur in the area, including Jeffrey-Ponderosa pine (Pinus jeffreyi-P. ponderosa), mixed pine, pinyon pine (P. monophyla), and juniper (Juniperus occidentalis).

Annual and perennial grasslands occur throughout the drainage on south-facing slopes. These grasslands are dominated by Agropyron, Bromus, and Sisymbrium, and are primarily a result of past fire and mechanical disturbance of habitat. Bare ground or talus slopes often occur in areas with highly erosive soils and are commonly a result of past fires. Evidence of historical fires occurs throughout the study area. Most of the Santa Ana drainage west of the confluence of Bear Creek and the Santa Ana River (e.g., Manzanita Flat) burned in 1970 and again in 1980. Several small (<0.5 km^2), controlled burns have been conducted east of Bear Creek since 1980. Excluding these controlled burns and small (<1 ha) wildfires, the remainder of the drainage has not burned in this century.

The study area contains several large, mammalian carnivores including bobcat (Lynx rufus), coyote (Canis latrans), and mountain lion (Felis concolor). Bowyer (1987) demonstrated that coyotes in southern California may be effective predators on adult deer, and such predators probably affect habitat selection by deer (Bowyer, 1986; Hirth, 1977).

Several other species of ungulates occur within the study area, including bighorn sheep (Ovis canadensis), domestic cattle (Bos taurus), and feral asses (Equus asinus). The range of bighorn sheep (>100 animals) is centered on the crest of Mt. San Gorgonio, although individuals have been observed along the eastern end of the Santa Ana drainage and north of Big Bear Lake. A livestock allotment encompassed most south-facing slopes in the study area. Although cattle were present in the area only during the summer and autumn of the 1st year of this study, the detrimental effects of past grazing by cattle were evident throughout the area. At least 80 feral asses occurred in the Big Bear watershed north of Moonridge. Although there are no apparent barriers to movements by feral asses, none were observed in the drainage of the Santa Ana river during this study. Quantitative estimates of population sizes for deer in the San Bernardino Mountains are lacking, but the herd is thought to be near its carrying capacity.

Sampling procedures and analyses.--In January 1989 and January 1990, I captured deer using a helicopter and drive nets (Beasom et al., 1980). Capture teams of at least eight people were stationed at three sites around the study area where 30.5 by 2.4-m tangle nets were erected. Deer were then driven into the nets with a helicopter. Personnel restrained these deer with leather hobbles and blindfolds to prevent injury. Teams were trained to handle deer quickly and efficiently, and animals usually were restrained <10 minutes. Selected deer were fitted with telemetry collars equipped with mortality sensors (6-h delay, Model 500, Telonics, Mesa, AZ). In total, 43 deer were captured (34 animals in 1989 and 9 in 1990) of which 29 were fitted with radio collars (22 adult females and seven adult males). Three collared deer remained outside the study area for the duration of the study, and were not considered in analyses.

All aspects of animal handling complied with field methods adopted by the American Society of Mammalogists (Ad Hoc Committee on Acceptable Field Methods, 1987) and were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks. No deaths of deer occurred during capture, and only one mortality may have resulted from capture-related factors.

Deer with telemetry transmitters were relocated ca. every 10 days from 1 January 1989 to 27 November 1991 with a fixed-winged aircraft using the equipment and techniques described by Krausman et al. (1984). The timing of all aircraft flights for locating telemetered animals was between 0700 and 1800 h, Pacific Standard Time. When the location of a deer was determined, the geographic position of that animal was estimated using a LORAN-C navigation system. In total, telemetered deer were relocated 1,521 times, of which 523 relocations were on winter range, and 929 on summer range; 69 relocations were of deer migrating between ranges.

Because both aerial-telemetry and LORAN-C positioning have inherent errors, I estimated the circular error associated with aerial-telemetry and LORAN-C locations in the study area. First, LORAN-C locations were corrected for directional bias using the techniques of Patric et al. (1988). The circular error then was estimated by calculating 90% C. L. for the mean locations of radio collars placed at five known locations. Based upon 40 relocations, the circular error for aerial telemetry was 177 m. I then considered all habitat occurring within that 177-m circle as an estimate of habitat used by a particular deer at that location.

A habitat map was developed for the area from a LANDSAT-TM scene with 25-m resolution of cells. Using Terra Mar (Terra Mar, Inc., Garden Grove, CA) software, the drainage was classified into nine spectral classes representing habitat types. The classified image was then verified using a combination of 1:9,200 color aerial photographs, and ground truthing. This final image was transferred to ARC/INFO (Environmental Systems Research Institute, Redlands, CA), the Geographic Information System (GIS) used in this study.

A three-dimensional terrain surface of the study area was generated from 30-m resolution, 7.5-minute digital elevation models (United States Geological Survey) using the GRID module of ARC/INFO. This terrain surface provided information on elevation, slope, and aspect. Additionally, the surface model was used to derive an index of terrain diversity for the area. Although many methods exist to assess diversity of terrain (Beasom et al., 1983; Bleich, 1993; Nelleman, 1991, and others), these methods are often labor intensive or may not allow for adequate evaluation of the components of terrain diversity (i.e., variation in both slope and aspect). Thus, for each location evaluated, terrain diversity was estimated using the GIS by calculating the standard deviation in slope and the mean angular deviation of aspect (Zar, 1984) in a circle of 177 m radius. An index to diversity of terrain was then calculated as the product of these two deviations.

In addition to the habitat map, terrain model, and derived information, all available geographic data on soils, fire history, water, and human developments were digitized from 7.5-minute quadrangle maps of the study area. Spatial information on human developments included the location of dirt and paved roads, special-use cabins, and campgrounds.

For each radio-collared animal, a data set of locations that was not significantly ($\underline{P} \leq 0.05$) autocorrelated was entered into the GIS. Data sets were analyzed for autocorrelation using the multiresponse sequence procedure (MRSP) of BLOSSOM statistical software (Slauson et al., 1991; Solow, 1989). If data within a season were significantly autocorrelated, data points were eliminated from analysis using a bootstrap procedure until sufficient autocorrelation was eliminated ($\underline{P} > 0.05$). Using this procedure, 49 data points (3.2% of total data set) were removed from habitat-selection and home-range analyses.

Degree of autocorrelation also was used as a means of identifying seasonal shifts in range by deer. Because serial autocorrelation is evaluated with MRSP by testing the null hypothesis that there is no difference between distance traveled between sequential locations and nonsequential ones, significant autocorrelation can occur if an animal moves less or more between sequential than between nonsequential locations. Data sets for each animal were initially divided into seasons based on annual changes in temperature and precipitation; summer was defined as 15 April to 15 November, whereas the remainder of the year was considered winter. If large movements at the beginning or end of a season caused significant autocorrelation, then those data points were moved to the appropriate data set. Locations that fell sequentially between seasonal data sets were considered transitional points (i.e., migratory movements) between summer and winter ranges.

I generated circles with a radius of 177-m for each of 1,382 deer locations to estimate deer use of habitat. The GIS included 30-m cells of habitat in circles only if the center of the habitat cell was inside the circle. Thus, a boundary of ± 15 m existed around each circle where precise measurement of habitat availability was not possible. Further, the GIS also was used to estimate distance from each telemetry location to water, Highway 38, dirt roads, cabins, and campgrounds. Distance to such developments was used as an index to potential disturbance of deer by humans. Data on the GIS were projected into similar geographic units for analyses, Universal Transverse Mercator meters (UTM--Snyder, 1984).

Statistical analyses.--Data sets not distributed normally were tested with the appropriate nonparametric rank statistic. I used PC SAS (SAS Institute, 1988), BLOSSOM (Slauson et al., 1991), and CALHOME (Kie et. al., 1994) in my analyses.

I considered deer migratory if they exhibited directional movements and their seasonal home ranges did not overlap (McCullough, 1964; Schoen and Kirchhoff, 1985). For migratory deer, I determined mean date of departure from summer and winter ranges by subdividing migration into 1-week intervals and calculating a weighted mean and pooled variance for the date deer were first observed outside their seasonal ranges. This method is an adaptation of a technique to estimate mean date of birth (Caughley, 1977).

The mean easting and northing, based on the seasonal UTM-coordinates of the locations for a deer, were used as a measure of the center of activity (Hayne, 1949). Minimum distances to water (perennial streams, intermittent streams, or springs) and human developments (highway, paved roads, dirt roads, cabins or campgrounds) for these centers of activity were determined using the GIS, and entered into analyses of home-range size. Additionally, straight-line distance between seasonal centers of activity was used as an index to the distance traveled during migrations, recognizing that these straight-line distances underestimate the total distances moved by these animals (Bowyer, 1981). Fidelity to seasonal ranges for individual deer was tested using the multiresponse randomized block procedure of Blossom (MRBP--Mielke, 1991; Slauson et al., 1991). I tested the null hypothesis that the distribution of locations for an individual in a particular season did not differ between years.

Home ranges were calculated seasonally for nonautocorrelated data sets using a beta-test version of the program CALHOME (Kie et al., 1994). The 95% minimum-convex polygons (MCP--Mohr, 1947) were reported for comparison with other studies; a 95% home-range polygon also was estimated using the adaptive-kernel method (Worton, 1989). The beta-test version of CALHOME first estimated the optimum smoothing parameter for the adaptive-kernel model (Kie et al., 1994; Worton, 1989). The program then calculated the results using 80%, 100%, and 120% of that optimum. CALHOME then reported the adaptive-kernel home ranges using whichever smoothing parameter minimized the least-squares cross-validation scores (Worton, 1989).

To detemine adequate sample size for estimating home ranges, I evaluated how home-range size varied with increasing sample size. Five individuals with the greatest number of locations and no significant home-range shifts between years were used in this analysis. I selected subsets of the locations for an individual combined by season for all years, and created incrementally larger subsamples until the maximum number of locations for an individual was attained. The maximum number of locations ranged between 23 and 27 for winter and 47 and 53 for summer. I sampled each individual in this manner for five replicates of each sample size. The 95% adaptive-kernel home range was then estimated for each subsample of each individual. Home-ranges and the sample size used to estimate them were analyzed using the nonlinear regression proceedure of SAS (PROC NONLIN) to estimate the equation for sample size and estimated home-range size: home-range size $= A(1 - \underline{e}^{-\underline{bn}})$, where A is the asymptote of the equation, $\underline{e}$ is the base of the natural log, $\underline{n}$ is sample size, and $\underline{b}$ is a constant. Based on these equations, I determined that, on average, estimated home-range size reached 90% of the asymptote value for each individual at sample sizes of ca. 25 and 15 locations for summer and winter, respectively. To meet these criteria, I combined seasonal locations for individuals between all years where significant shifts in home range did not occur. Fifteen seasonal home ranges lacked adequate sample size for estimation of their size and were eliminated from analyses. Mean (± $\underline{SD}$) number of locations for estimating home-ranges of the remaining deer was 40 ± 10.7 and 20 ± 4.6 for summer and winter, respectively.

I used Spearman's rank correlation ($\underline{r}_S$) to examine relationships between movements of deer and climatic variables (Zar, 1984). A ranked analysis of variance (ANOVA--Conover and Iman, 1981; PROC GLM, SAS--Institute, Inc., 1988) was used to test for differences in home-range size for various sex and movement (i.e., migratory-nonmigratory) categories of telemetered deer. I used a Bonferroni correction for multiple comparisons (Rice, 1989). Additionally, I used stepwise regression analysis (α to enter = 0.15, α to remove = 0.20) to evaluate variables associated with the size of home ranges (Zar, 1984); home-range size was $\log_{10}$ transformed for this analysis. Home-range composition for regression analysis was estimated from all habitats contained within a 177-m buffer of the 95% home-range estimate for a deer.

The percent of each of nine habitat types contained within a circle with a radius of 177 m was used in analyses of habitat selection; these analyses relied primarily on one-way multivariate analysis of variance (MANOVA--Johnson and Wichern, 1988) comparing habitat use by deer with habitat at random locations. This approach had the advantage of simultaneously comparing all habitat components considered in analyses (Aebisher et al., 1993). Finally, habitat selection (use > available) was estimated by subtracting percent availability of a habitat from percent habitat use. This measure was used because it is intuitively simple; a positive value implies selection, whereas a negative one indicates avoidance (use < available). Available habitat was defined as all habitats occuring within the study area. Because the amount of habitat available at the level of the landscape did not differ between groups of animals or seasons, changes in habitat use represent changes in habitat selection for intergroup and interseason comparisions. Because I was interested in habitat selection at the level of the population, I combined locations of deer for this analysis. I assumed that these noncorrelated samples of individuals on different days under differing environmental conditions represented independent samples (Hjeljord et al., 1990; Molvar and Bowyer, 1994). This procedure is conservative because it increases the variability of my data set; however, it also increases sample sizes.

Survival of deer was estimated using the Kaplan-Meier, staggered-entry model (Pollock et al., 1989). Differences in survivorship were tested with a log-rank test as recommended by Pollock et al. (1989).

RESULTS

Movements and distribution.--All deer (one male, seven females) captured below 1,500 m in elevation at Manzanita Flat were migratory. These deer moved seasonally from mixed chaparral and chamise habitats at low elevation in the western end of the study area to high-elevation areas of mixed pine in the San Gorgonio Wilderness and adjoining areas (Fig. 2). The mean (± SD) distance traveled between winter and summer ranges for these eight animals was 12.6 ± 5.3 km and ranged from 8.6 to 19.8 km. Seventeen deer

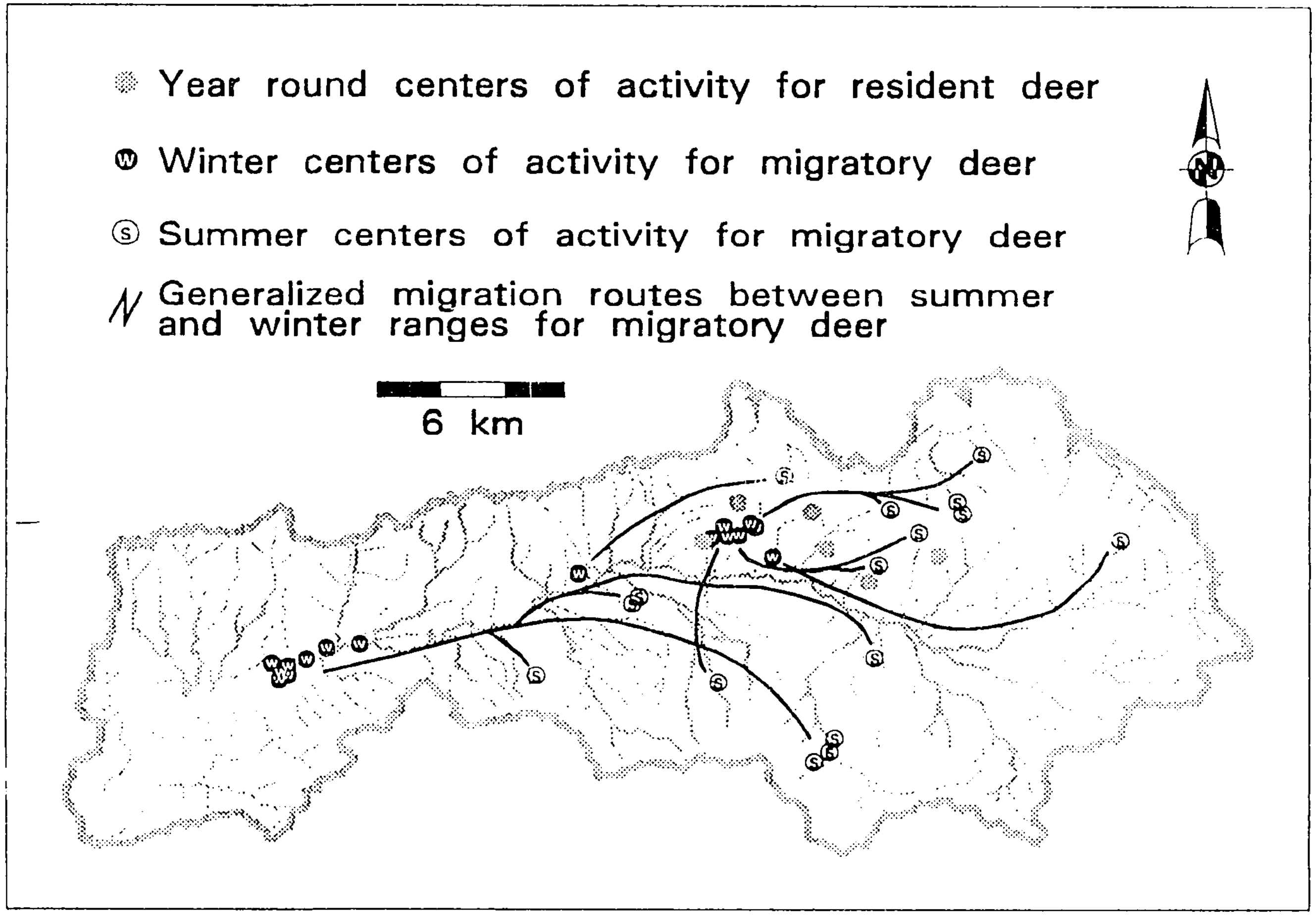

Fig. 2.--Seasonal distribution and generalized migration routes of radio-collared deer, San Bernardino Co., California, 1989-1991.

five males, 12 females) were captured on south-facing slopes >1,500 m at Burro Flats in habitats dominated by live oak and chaparral. Of the five males, three migrated and two died before their status could be determined. Of the 12 females, three migrated during each year of study, four migrated in some years but not in others, and five were year-round residents of Burro Flats. Deer that migrated from Burro Flats exhibited up-canyon movements in summer to high-elevation habitats near Sugarloaf Mountain, Onyx Peak, and the San Gorgonio Wilderness. The mean (± SD) distance moved for these deer was 8.1 ± 2.9 km (range = 4.4-11.3 km).

For migratory deer, departure from winter to summer range occurred between the 1st week in March and the 2nd week of May during 1989-1991. Departure from summer range occurred between the 1st week in October and the 3rd week in January. Mean week of migration was relatively constant for the duration of the study (Table 1). No significant difference occurred among years in when deer departed from summer range (ANOVA, $F = 2.46$, d.f. = 1, 22, $P > 0.05$); however, time of departure from winter range did differ among years (ANOVA, $F = 4.61$, d.f. = 2, 30, $P < 0.05$), with deer departing winter range signficantly earlier in 1989 than in 1990 or 1991 (Tukey's multiple-comparison test, $P < 0.05$). Timing of departure from winter range did not differ ($P > 0.05$) between 1990 and 1991.

Based on a Wilcoxon two-sample test, no significant difference occurred between categories of deer in distance traveled between sequential locations; however, I did observe some differences within seasons (Fig. 3). During spring, resident females moved less than did migratory females or migratory males ($Z = -2.24$, d.f. = 1, $P < 0.05$; $Z = 2.13$, d.f. = 1, $P < 0.05$, respectively). Males moved more than did migratory and resident females during autumn ($Z = 2.47$, d.f. = 1, $P < 0.05$), when rut was underway. Additionally, males moved more than did migratory females during winter ($Z = 2.09$,

Table 1.--Mean date of departure for spring and autumn migrations of mule deer, San Bernardino Co., California 1989-1991.

Year	Departure from	Mean date ± SD	n
1989	Winter range	10 April ± 9.8 days	10
1989	Summer range	1 December ± 18.4 days	13
1990	Winter range	29 April ± 23.7 days	14
1990	Summer range	17 November ± 20.2 days	11
1991	Winter range	1 May ± 14.0 days	9

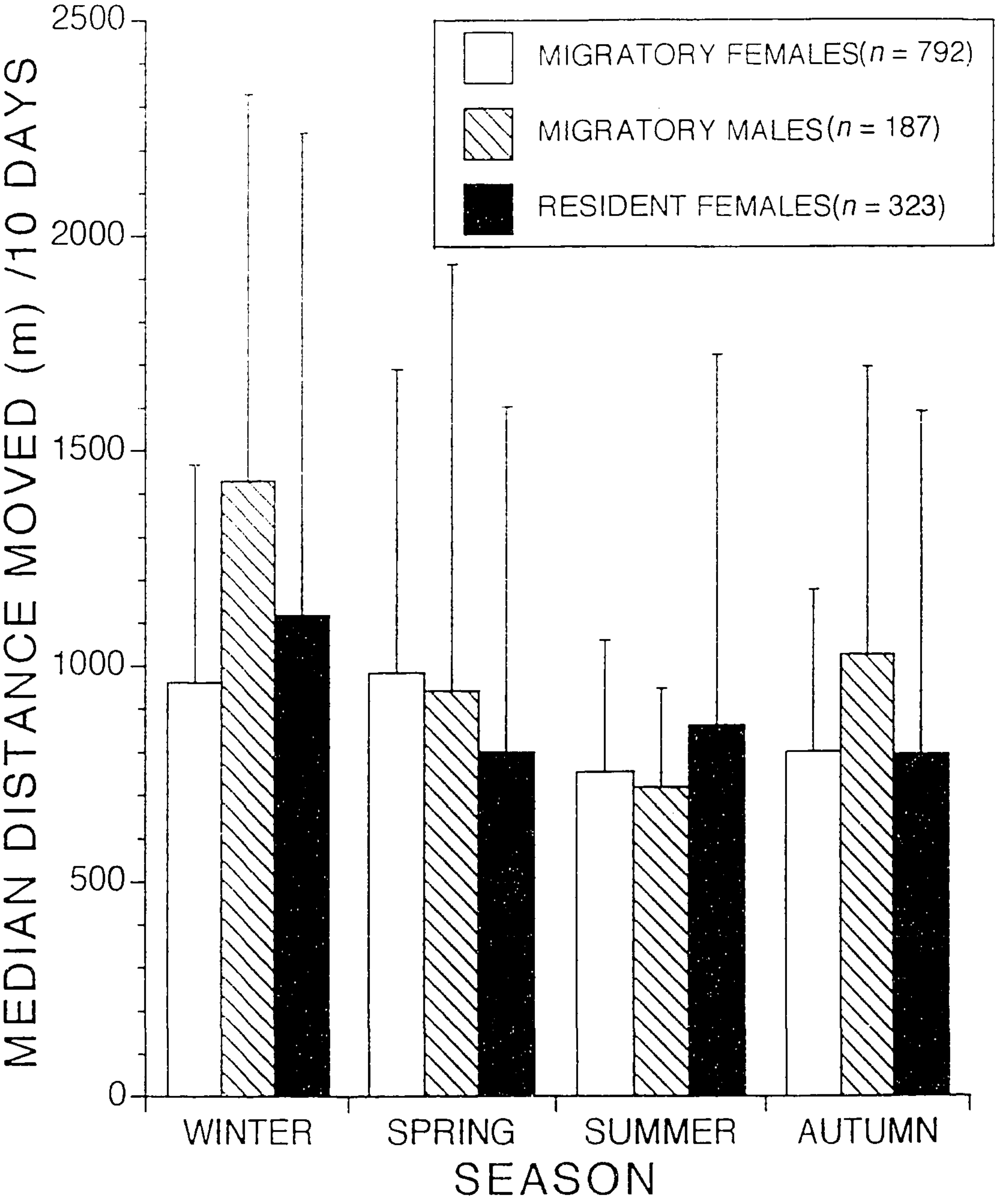

Fig. 3.--Median distance between consecutive telemetry locations by season for various classes of mule deer, San Bernardino Co., California, 1989-1991. Error bars indicate one-half the interquartile distance.

d.f. = 1, P <0.05) and less than resident females during summer (Z = -2.16, d.f. = 1, P <0.05). Other seasonal comparisons were not significant (P >0.05).

All sex and movement classes of deer exhibited seasonal differences in distance traveled between sequential radio-telemetry locations for 1989-1991(Kruskal-Wallis test; males, X^2 = 17.47, d.f. = 3, P<0.001; migratory females, X^2 = 12.09, d.f. = 3, P <0.01; resident females, X^2 = 7.87, d.f. = 3, P <0.05), with the greatest movements occurring in winter and spring when temperatures were coolest and precipitation highest (Figs. 3, 4). Indeed, I observed negative correlations for movement of deer between sequential relocations and mean daily temperature (r_s= -0.13, n = 1,336, P <0.001), maximum temperature (r_s = -0.12, n = 1,336, P < 0.001), and minimum temperature (r_s = -0.16, n = 1,336, P <0.001), whereas a positive correlation occurred between movement and total precipitation (r_s = 0.11, n = 1,336, P <0.001).

Home ranges.--Radio-telemetered deer demonstrated high fidelity to seasonal home ranges. Based on MRBP analyses, only 24% of 74 tests for home-range fidelity showed significant changes in the position of seasonal home ranges of deer between years; every deer tracked >1 year had highly overlapping home-ranges. Most annual changes in home ranges occurred for migratory deer; in only one instance did a resident deer have a significant shift in home-range location between years.

A chi-square test (d.f. = 1) indicated that no difference (P >0.25) occurred between either sex (X^2 = 0.89) or season (X^2 = 0.76) in the number of home-range shifts between years. One group of three female deer with summer ranges near Sugarloaf Mountain, however, accounted for nearly one-half of the shifts in home-range location observed between years. These deer did not migrate in winter 1989, migrated to Burro Flats in winter 1990, and delayed their movements to winter ranges on Burro Flats until March 1991, when late-winter snows forced them from their high-elevation (>2,500 m)

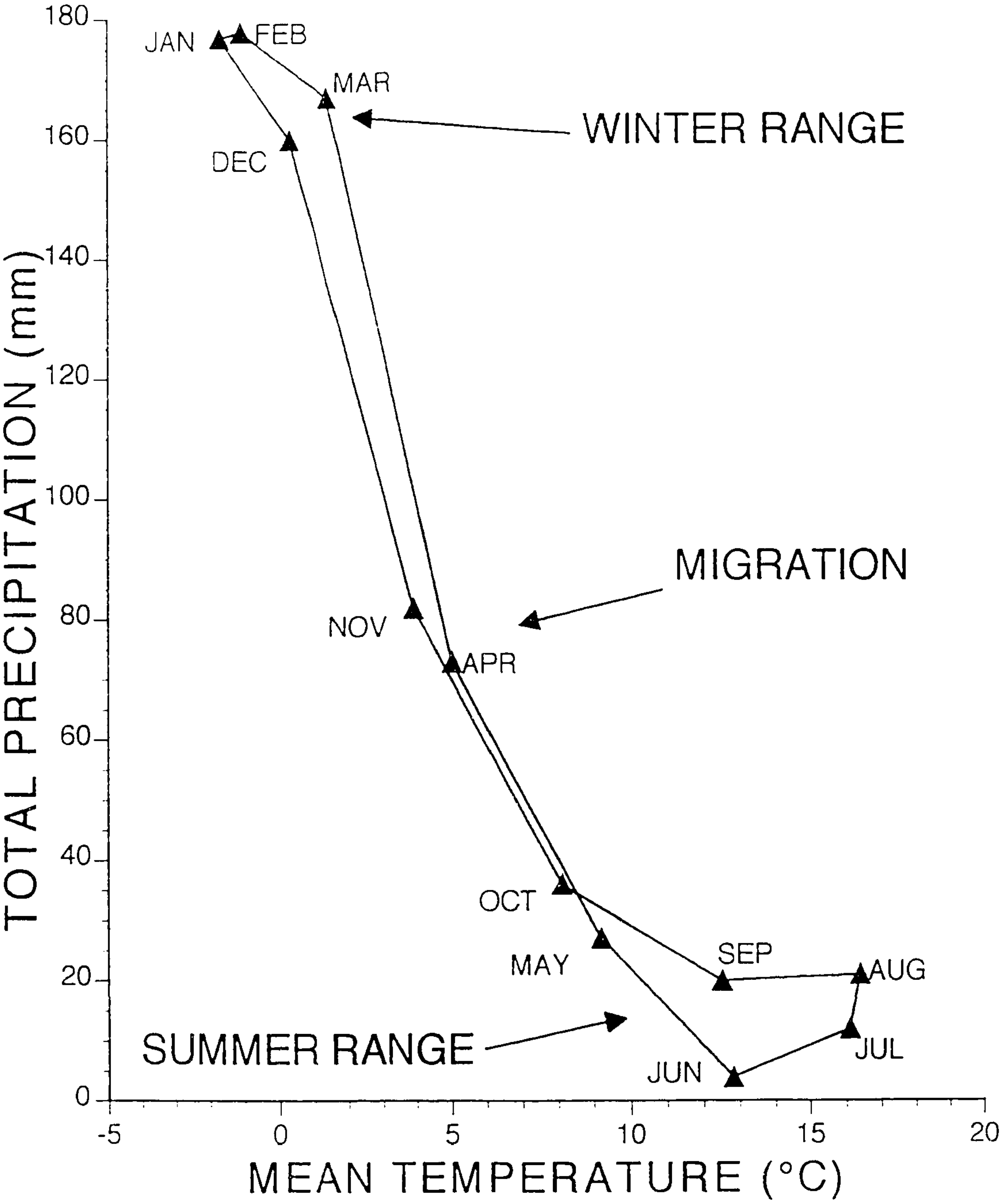

Fig. 4.--Climograph of mean monthly temperature and precipitation at Angelus Oaks, California (1,600 m elevation), 1989-1991.

summer ranges. All other migratory deer had distinct winter and summer ranges in each year.

Seasonal home ranges of telemetered deer were extremely variable. Using the adaptive-kernel method, mean (± $\underline{SD}$) home-range size was 788.6 ± 691.8 ha (minimum covex polygon = 443.9 ± 413.0 ha, $\underline{n} = 33$). No significant difference in sizes of home ranges occurred between categories of deer (Table 2), but home ranges were significantly smaller in summer than in winter.

Two deer with summer ranges in the San Gorgonio Wilderness had significantly smaller home ranges (185 ha, $\underline{t} = 6.73$, $\underline{d.f.} = 14$, $\underline{P} < 0.001$; 304 ha, $\underline{t} = 4.69$, $\underline{d.f.} = 14$, $\underline{P} < 0.001$) than deer with home ranges elsewhere in the study area ($\underline{X} = 578.33 \pm 226.43$ ha, $\underline{n} = 15$). I used stepwise-multiple regression to determine if home-range size was related to the vegetative composition of the home range, distance from the center of activity to water, and to human developments for deer in summer and winter. These independent variables explained substantial variation in the size of deer home ranges in summer ($\underline{R}^2_a = 0.81$, $\underline{d.f.} = 16$, $\underline{F} = 9.59$, $\underline{P} < 0.001$; $\hat{\underline{Y}} = 2.7633 - 0.0002$ distance to human development + 0.0177 % sagebrush + 0.04017 % chamise - 0.00010 distance to water + 0.000710 % bare ground). Partial regressions indicated that human disturbance ($\underline{r}^2 = 0.29$), % chamise ($\underline{r}^2 = 0.24$), and % sagebrush ($\underline{r}^2 = 0.15$) were most influential in affecting home-range size; other variables were less important ($\underline{r}^2 < 0.09$). During winter, size of home ranges also were predicted well by habitat variables ($\underline{R}^2_a = 0.90$, $\underline{d.f.} = 15$, $\underline{F} = 35.4$, $\underline{P} < 0.001$; $\hat{\underline{Y}} = 2.0933 + 0.01889$ % pine + 1.4191 % meadow + 0.0172 % bareground). Partial regressions indicated meadow ($\underline{r}^2 = 0.90$), bareground ($\underline{r}^2 = 0.80$), and pine ($\underline{r}^2 = 0.53$) were all influential.

Table 2.--Differences in home-range size of mule deer associated with sex, season, and migratory status, San Bernardino County, California, 1989-1991.

Population subset	n	95% Adaptive-kernel home range (ha)		95% Minimum convex-polygon home range (ha)	
		X	SD	X	SD
Summer					
Migratory males	3	392.3	196.7	257.3	43.8
		F = 0.85[a]			
Migratory females	9	554.2	277.4	314.7	165.2
		F = 0.11			
Resident females	5	599.8	189.5	331.0	72.6
Winter					
Migratory males	3	396.0	108.3	230.3	108.3
		F = 2.68			
Migratory females	7	1357.3	981.1	766.6	551.9
		F = 0.37			
Resident females	6	1028.6	944.7	555.5	651.3
All deer					
Summer	17	539.1	240.0	309.4	126.0
		F = 5.16*			
Winter	16	1,053.8	902.1	586.9	551.9

[a] Statistics are multifactor ANOVAs. F-values and significance levels presented are for tests of means above and below the respective statistic; *P ≤0.05 after Bonferroni correction (Rice, 1989).

Habitat use.--Kolmogorov-Smirnov tests showed that deer distributed themselves differently than random with regard to distance from human developments (Fig. 5). In general, deer were farther than random ($n = 1,773$) from potential human disturbance in summer and winter (migratory females: summer, $KS_a = 5.01$, $P < 0.001$, winter, $KS_a = 2.83$, $P < 0.001$; resident females: summer, $KS_a = 1.60$, $P < 0.05$, winter, $KS_a = 1.76$, $P < 0.01$; migratory males: summer, $KS_a = 2.61$, $P < 0.001$, winter, $KS_a = 1.70$, $P < 0.01$). Moreover, I observed differences in how classes of deer distributed themselves with respect to potential disturbance. Migratory females were farther from human development than were migratory males (summer, $KS_a = 3.39$, $P < 0.001$; winter, $KS_a = 1.72$, $P < 0.01$) and were observed farther from such disturbance than were resident females in summer ($KS_a = 4.59$, $P < 0.001$) only. Also, migratory males were farther from developments than were resident females in summer ($KS_a = 2.02$, $P < 0.001$). Male ($KS_a = 2.12$, $P < 0.001$) and female ($KS_a = 4.22$, $P < 0.001$) deer that were migratory were observed closer to human developments in winter than in summer, whereas resident females showed no trend ($P > 0.05$).

All deer differed from random with regard to distance from water in both seasons (Fig. 6). Migratory females were observed closer than random ($n = 1,773$) from water in summer ($KS_a = 5.52$, $P < 0.001$) and farther than random in winter ($KS_a = 3.40$, $P < 0.001$). Resident females were distributed farther than random from water in both seasons (resident females: summer, $KS_a = 4.89$, $P < 0.001$; winter, $KS_a = 2.13$, $P < 0.001$). Migratory males were farther than random from water in summer ($KS_a = 5.13$, $P < 0.001$), whereas they were not significantly different from at random with regard to water in winter ($P > 0.05$). Additionally, migratory females were observed closer to water than resident females ($KS_a = 2.12$, $P < 0.001$) or migratory males ($KS_a = 2.12$, $P < 0.001$) in summer; they occurred farther from water than did resident females ($KS_a = 2.12$,

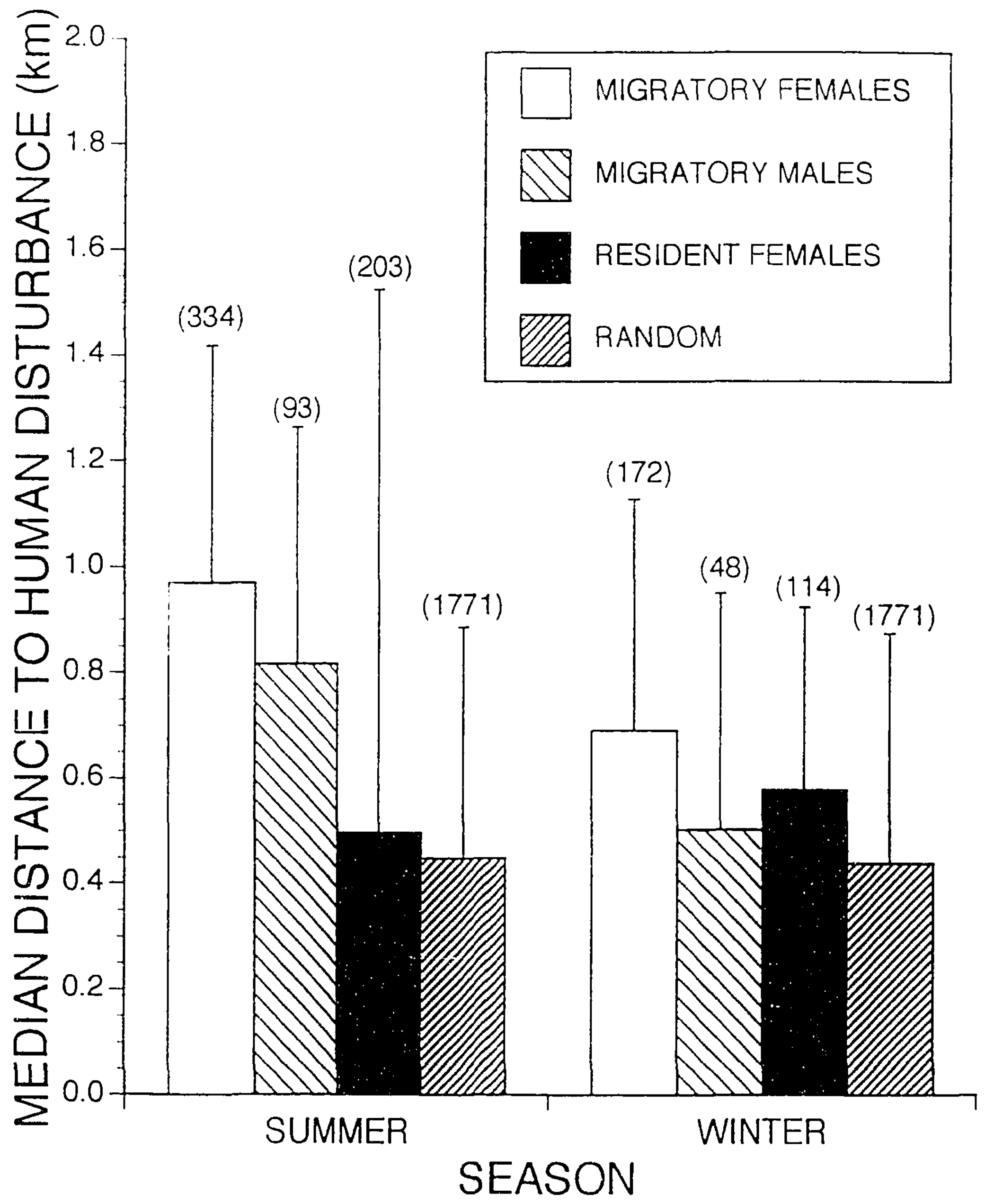

Fig. 5.--Median distance to human disturbance for various classes of mule deer in summer and winter, San Bernardino Co., California, 1989-1991. Error bars indicate one-half the interquartile distance; sample sizes are above error bars.

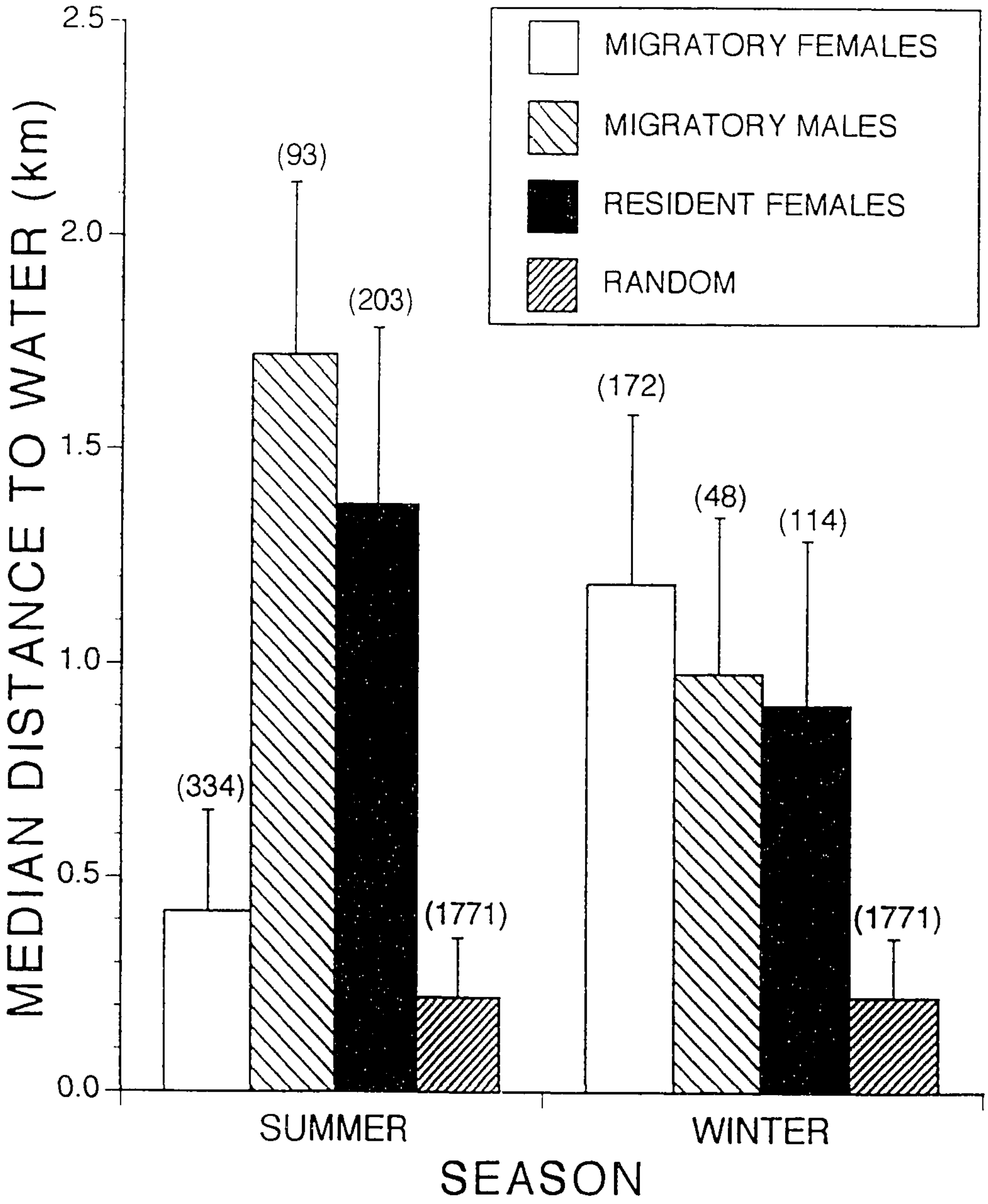

Fig. 6.--Median distance to water for various classes of mule deer in summer and winter, San Bernardino Co., California, 1989-1991. Error bars indicate one-half the interquartile distance; sample sizes are above error bars.

$\underline{P}$ <0.001) or migratory males ($\underline{KS_a}$ = 2.12, $\underline{P}$ <0.001) in winter. Finally, migratory males were observed farther from water than were resident females in summer, although I observed no difference between these two groups in winter ($\underline{P}$ >0.05).

All categories of deer differed from random in their use of terrain. Generally, migratory deer occurred at higher elevations on more north-facing slopes during summer than in winter (Table 3). Resident deer, however, remained on steep, south-facing slopes year round. Further, male deer were observed at higher elevations during summer than were females (Table 3).

For random sites, highly rugged areas as measured by changes in slope occurred at lower elevations (correlation between variation in slope and elevation, $\underline{r_s}$ = -0.26, $\underline{n}$ = 1,771, $\underline{P}$ <0.001) and in areas of steeper slope (correlation between variation in slope and mean slope, $\underline{r_s}$= 0.21, $\underline{n}$ = 1,771, $\underline{P}$ <0.001), whereas areas of highly diverse terrain, as measured by changes in aspect, occurred at higher elevations (correlation between angular deviation in aspect and elevation, $\underline{r_s}$ = 0.90, $\underline{n}$ = 1,771, $\underline{P}$ <0.001). Telemetered deer did not differ from random with respect to use of rugged terrain as measured solely by angular deviation (Table 4). Migratory females in both seasons, and resident females in winter, differed from random in their use of rugged terrain; this difference represents selection or avoidance of areas of highly changing slope. Finally, migratory females occurred on the least-rugged slopes in summer, and on the most-rugged terrain in winter (Table 4).

Deer use of habitats differed significantly between seasons (Fig. 7, Fig. 8, Table 5), with migratory deer radically changing their patterns of habitat use. Generally, migratory deer selected habitats dominated by pine forests in summer and by oak and chaparral in winter. Additionally, migratory females used riparian and meadow habitats to a greater extent in summer than in winter. Habitat use by resident females remained relatively

Table 3. Mean (±,SD) use of various terrain characteristics by subsets of telemetered mule deer, San Bernardino Co., California, 1989-1991. Z-values from Wilcoxon two-sample test are given between categories of deer.

Population subset	Terrain characteristic			
	n	Elevation (m)	Slope (degrees)	North facing slopes (%)
Random	1771	2,040.62 ± 586.11	20.88 ± 8.15	53.55 ± 37.3
Summer				
Migratory males	103	2,552.03 ± 228.36[ab]	21.50 = 5.96	62.90 ± 38.66[ab]
		7.36*	5.74*	-2.51*
Migratory females	334	2,269.99 ± 359.64[ab]	17.69 ± 5.11[ab]	76.34 ± 27.30[ab]
		-1.55	9.27*	-11.81*
Resident females	203	2,293.00 ± 204.79[ab]	22.75 ± 6.34[a]	38.42 ± 33.73[ab]
Winter				
Migratory males	64	1,754.33 ± 406.68[a]	21.12 ± 6.50	20.47 ± 28.06[a]
		6.87*	-0.47	-4.57*
Migratory females	172	1,308.33 ± 348.33a	21.67 ± 6.79	35.12 ± 26.90[a]
		12.66*	1.65	-5.45*
Resident females	114	2,119.79 ± 245.49	22.60 ± 6.64[a]	21.19 ± 29.43[a]

*P <0.05, following Bonferoni correction (Rice, 1989).

[a] Denotes within group means differed significantly (P <0.05) from random.

[b] Denotes within group means differed significantly (P <0.05) between seasons.

Table 4. Mean (±, SD) use of rugged terrain by subsets of telemetered mule deer, San Bernardino Co., California, 1989-1991. Ruggedness as measured by variation in slope, aspect, and a composite index is presented with F-values from a MANOVA comparing subset use of all terrain measures.

		Measures of terrain ruggedness		
Population Subset	n	Standard deviation of slope	Angular deviation of aspect	Composite ruggedness index
Random		44.7 ± 29.9	130.0 ± 16.7	5,834.0 ± 3,971.0
Summer				
Migratory males	103	42.4 ± 19.6	131.8 ± 16.2	5,633.2 ± 2,910.2
		24.80***	1.05	24.55***
Migratory females	334	32.3 ± 16.8^{ab}	129.9 ± 13.5	4,221.0 ± 2,317.0^{ab}
		12.36***	2.61	13.88***
Resident females	203	37.1 ± 17.6	132.1 ± 15.8	4,928.3 ± 2,566.0
Winter				
Migratory males	64	46.4 ± 29.7	130.9 ± 16.3	6,024.4 ± 3,743.9
		19.74***	0.53	20.52***
Migratory females	172	74.3 ± 48.2^{a}	132.2 ± 14.3	9,792.7 ± 6,500.1^{a}
		82.69	2.62	85.80***
Resident females	114	34.3 ± 16.2a	129.5 ± 15.4	4,462.8 ± 2,294.0^{a}

*P <0.05, **P <0.01, ***P <0.001

[a] Denotes within group means differed significantly (P <0.05) from random.

[b] Denotes within group means differed significantly (P <0.05) between seasons.

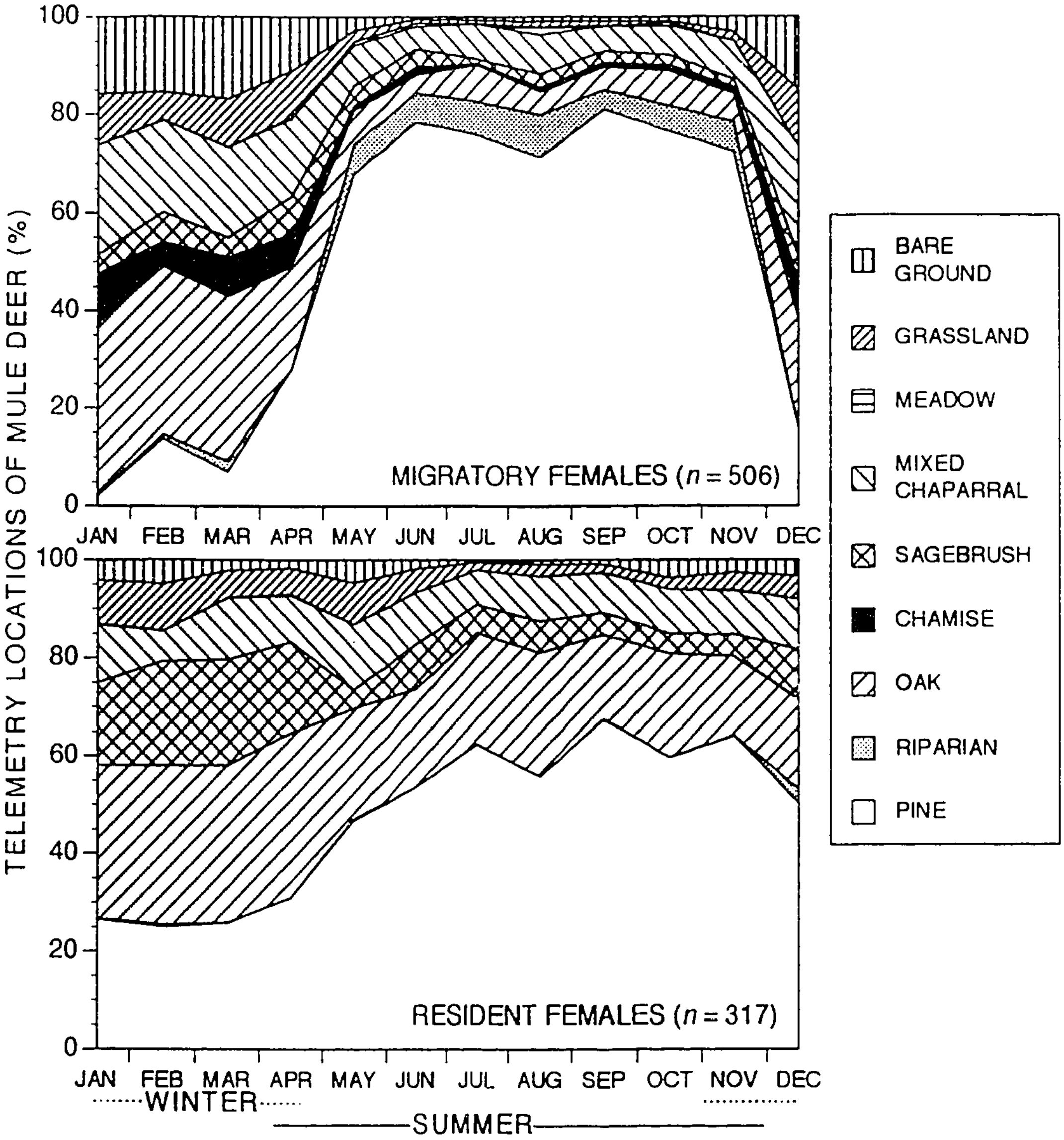

Fig. 7.--Percent of telemetry locations in various habitat types for migratory (above) and resident (below) female mule deer, San Bernardino Co., California, 1989-1991.

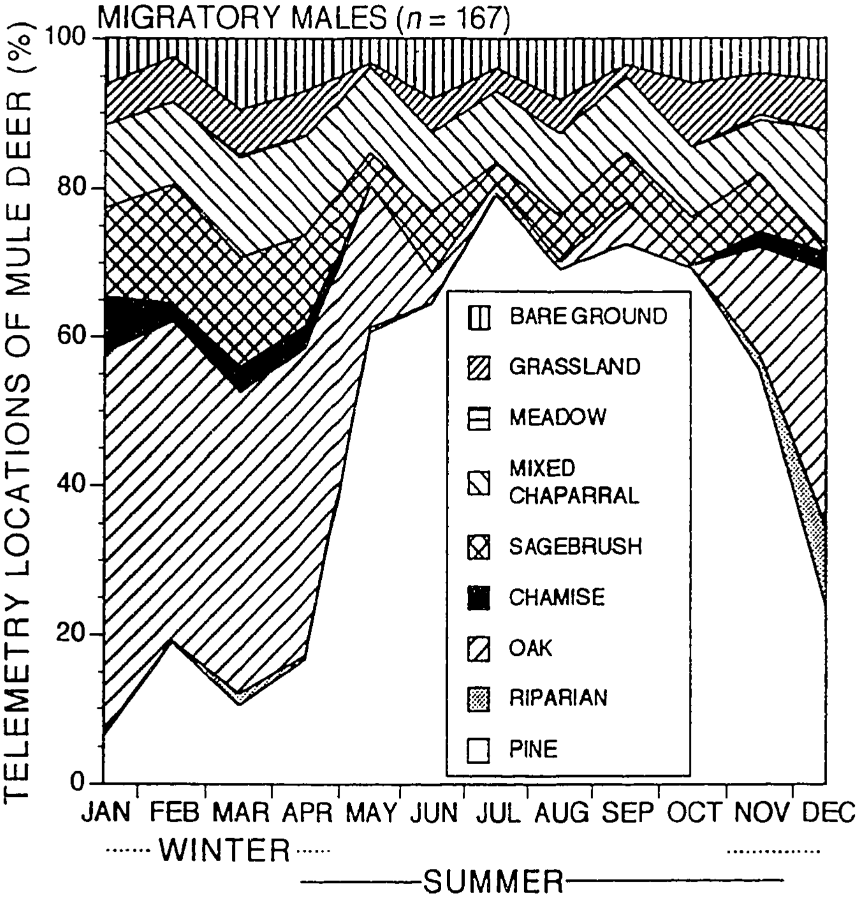

Fig. 8.--Percent of telemetry locations in various habitat types for male mule deer, San Bernardino Co., California, 1989-1991.

Table 5. Mean (±, SD) percent use of habitat types by subsets of telemetered mule deer, San Bernardino County, California, 1989-1991. F-values from a MANOVA comparing subsets of all habitat types.

Population		Habitat type			
Subset	n	Pine	Oak	Riparian	Meadow
Summer					
All deer	800	65.0 ± 30.0	8.7 ± 15.8	2.7 ± 8.1	0.3 ± 2.0
Sex					
Migratory males	103	70.9 ± 22.3a	4.3 ± 11.6a	0.2 ± 0.7a	0.0 ± 0.0a
Migratory females	334	75.9 ± 23.7a	5.1 ± 9.8a	6.0 ± 11.7a	0.6 ± 2.7a
F-value		7.61**	1.34	36.14***	9.65**
Migratory status					
Resident females	203	56.9 ± 33.2a	21.6 ± 21.8[a]	0.1 ± 0.6	0.1 ± 0.3
Migratory females	334	75.9 ± 23.7	5.10 ± 9.8	6.0 ± 11.7	0.6 ± 2.7
F-value		63.73***	154.97***	73.97***	13.55***

(Continued)

Table 5. Continued.

Winter					
All deer	432	17.5 ± 25.0	30.6 ± 23.9	0.8 ± 4.1	0.2 ± 1.8
Sex					
Migratory males	64	13.3 ± 19.4	41.4 ± 22.4	1.8 *= 7.3	0.3 ± 1.3
Migratory females	172	9.1 ± 20.5	32.4 ± 23.0	1.0 ± 3.9	0.1 ± 0.1
F-value		6.14*	7.2**	0.70	0.74
Migratory status					
Resident Females	114	31.0 ± 30.6	29.4 ± 23.0	0.6 ± 3.3	0.1 ± 0.5
Migratory females	172	9.1 ± 20.5	32.4 ± 23.0	1.0 ± 3.9	0.1 ± 0.04
F-value		78.76***	3.16	2.48	0.25

(Continued)

Table 5. Continued

	n	Chamise	Sagebrush	Mixed chaparral	Grasslands	Bare ground
Summer						
All deer		0.4 ± 2.5	5.3 ± 11.7	8.9 ± 10.5	3.0 ± 7.3	5.7 ± 12.82
Sex						
Migratory males	103	0.00 ± 0.00^a	6.3 ± 12.1^a	9.6 ± 7.6	3.6 ± 7.3^a	5.3 ± 10.4
Migratory females	334	1.00 ± 3.75^a	2.96 ± 10.2	6.2 ± 10.6^a	1.1 ± 3.8^a	1.2 ± 4.6^a
F-value		12.88***	23.49***	27.73***	23.32***	55.92***
Migratory status						
Resident females	203	0.0 ± 0.0	5.82 ± 11.1A	9.5 ± 10.6	3.8 ± 10.5A	2.2 ± 6.7
Migratory females	334	1.0 ± 3.8	2.96 ± 10.2	6.2 ± 10.6	1.1 ± 3.8	1.2 ± 4.6
F-value		25.40***	28.88***	21.09***	29.84***	6.04*

(Continued)

Table 5. Continued

Winter						
All deer	432	3.7 ± 7.2	13.5 ± 18.6	14.7 ± 13.5	8.5 ± 10.2	10.4 ± 15.6
Sex						
Migratory males	64	3.7 ± 7.2	12.4 ± 15.0	13.0 ± 11.2	7.0 ± 10.0	7.1 ± 11.1
Migratory females	172	7.8 ± 8.8	4.5 ± 11.3	20.0 ± 14.0	9.5 ± 8.7	15.7 ± 17.1
F-value		20.71***	29.63***	11.68***	8.76**	17.24***
Migratory status						
Resident females	114	0.0 ± 0.0	18.8 ± 19.2	10.1 ± 14.0	6.7 ± 10.8	3.3 ± 9.9
Migratory females	172	7.8 ± 8.8	4.5 ± 11.3	20.0 ± 14.0	9.5 ± 8.7	15.7 ± 17.1
F-value		172.31***	88.87***	42.41***	15.27***	79.02***

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] Denotes within group means differed significantly ($P < 0.05$) between seasons.

constant throughout the year, although some seasonal changes occurred. Similar to migratory deer, resident females selected more pine-dominated habitats in summer than in winter, interchanging use of pine forests with oak woodlands between seasons. Further, resident deer used more grassland and sagebrush in winter than in summer. Differences in habitat use between categories of deer occurred for nearly all habitat-class comparisons (Table 5). Migratory females used significantly more pine and riparian habitats and less brush and grassland in summer than did migratory males. Migratory females used more brush-dominated habitats and less tree-dominated ones than did migratory males in winter. Additionally, resident females selected significantly less pine, riparian, and meadow habitats and more oak and brush-dominated habitats than did migratory females in summer Resident females selected more sagebrush and pine and less chamise-chaparral than did migratory females in winter.

Based on a general-linear model comparing habitat composition at locations of deer with habitat at random sites, significant differences occurred in the selection of habitat types by adult mule deer (Fig. 9). During summer ($d.f. = 1, 1,972$), resident females selected pine ($F = 16.32$, $P < 0.001$), oak ($F = 6.41$, $P < 0.05$), and grassland habitats ($F = 14.24$, $P < 0.001$), while avoiding riparian areas ($F = 26.15$, $P < 0.001$), chamise ($F = 39.23$, $P < 0.001$), mixed chaparral ($F = 7.68$, $P < 0.01$) and meadows ($F = 5.26$, $P < 0.05$). Areas dominated by sagebrush were used as available ($P > 0.05$). Similarly, during winter ($d.f. = 1, 1,883$), resident females selected oak forests ($F = 23.47$, $P < 0.001$) and avoided riparian areas ($F = 8.59$, $P < 0.01$) and chamise chaparral ($F = 20.48$, $P < 0.001$). Contrary to summer patterns of habitat selection, resident females strongly selected sagebrush ($F = 125.58$, $P < 0.001$) and avoided pine forests ($F = 16.24$, $P < 0.001$), while using all other habitats in proportion to their availability.

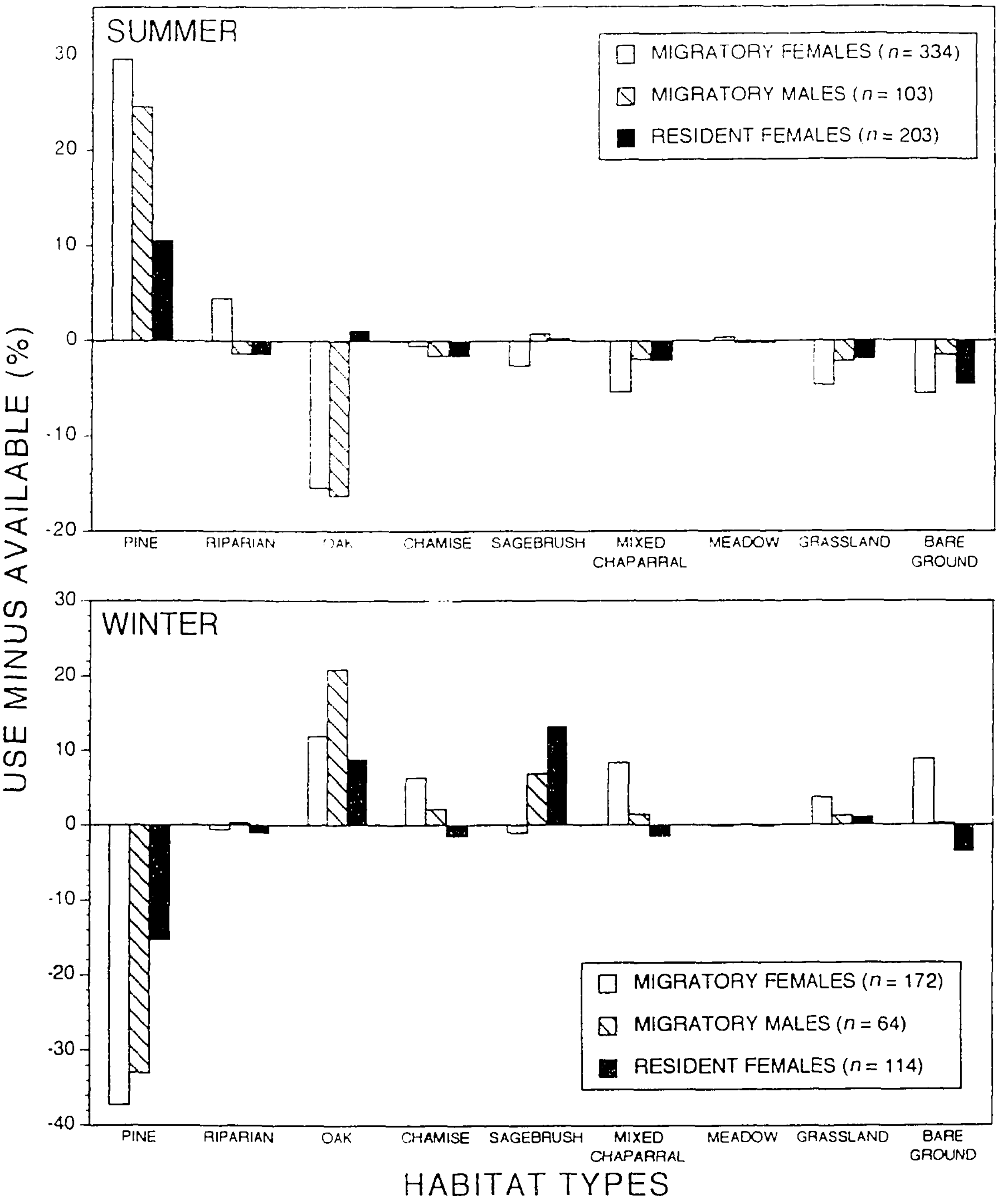

Fig. 9.--Selection (percent use minus percent availability) for habitat types by classes of mule deer, San Bernardino Co., California, 1989-1991.

During winter, migratory females (d.f. = 1, 1,941) and males (d.f. = 1, 1,833) were similar in their selection of habitats. Both groups selected areas with oak woodlands (migratory females: F = 62.73, P <0.001; males: F = 48.73, P <0.001), and chamise (migratory females, F = 295.07, P <0.001; males, F = 12.47, P <0.001), while avoiding pine forests (migratory females, F = 235.84, P <0.001; males, F = 57.59, P <0.001), and using meadow and riparian areas as available. Migratory females selected mixed chaparral (F = 68.81, P <0.001), and grassland (F = 43.15, P <0.001), male use of these habitats did not differ from available. Additionally, males selected sagebrush habitats (F = 25.53, P <0.001), and migratory females avoided these areas (F = 4.89, P <0.05).

In summer, migratory females (d.f. = 1, 2,103) selected all habitat types differently from their availability. Migratory females selected pine forests (F = 227.98, P <0.001), meadows (F = 10 28, P <0.01) and riparian areas (F = 121.22, P <0.001), while avoiding oak woodlands (F = 80.15, P <0.001), chamise (F = 7.01, P <0.01), sagebrush (F = 25.50, P <0.001), mixed chaparral (F = 101.20, P <0.001), and grasslands (F = 116.42, P <0.001). Males (d. f. = 1, 1,872) also selected pine habitats (F = 42.79, P <0.001) and avoided oak woodlands (F = 32.42, P <0.001) and grasslands (F = 8.35, P <0.01). Unlike migratory females, males avoided meadows (F = 5.01, P <0.05) and riparian areas (F = 11.72, P <0.001), and used all other habitats as available in summer.

Mortality.--Female deer showed marked differences in rates of survival between migration classes (Fig 10). In years with low precipitation (1989-1990), survivorship was significantly lower in migratory deer than for resident deer. Conversely, in 1991, a year of normal precipitation, resident females had somewhat higher rates of mortality than did migratory females, although this difference was not statistically significant (Fig. 10). The timing of mortalities also was different between the two groups. Mortalities for migratory females occurred within 1 month of migration, whereas mortalities for resident females

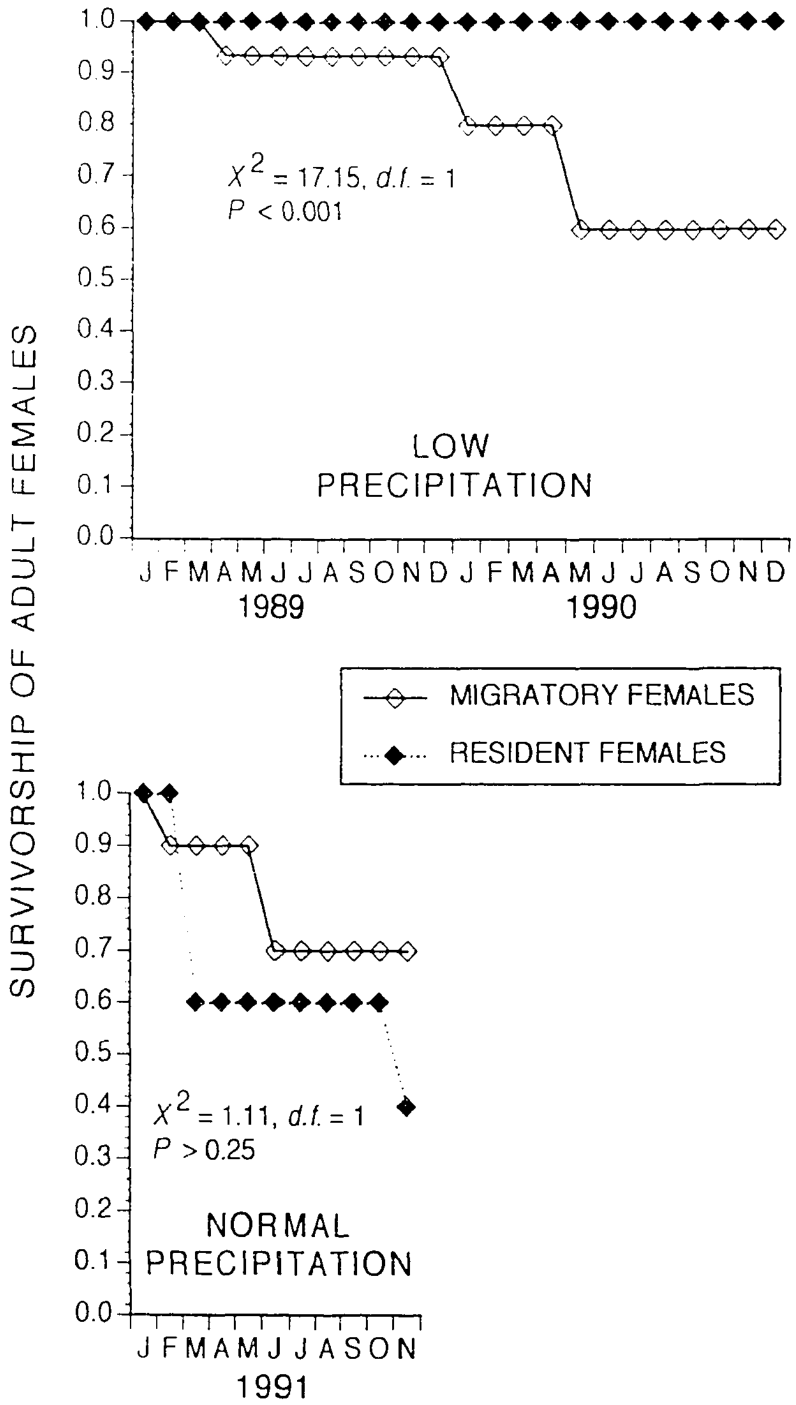

Fig. 10.--Survivorship of adult female mule deer during years of low precipitation (above) and normal precipitation (below), San Bernadino Co., California, 1989-1991. Number of telemetered females was 6 and 15 for resident and migratory deer, respectively.

were limited to winter. Annual survivorship in adult male deer was similar between low and normal years of precipitation. In 1989-1990, male survivorship was 0.83, and in 1991 survivorship was 0.80.

DISCUSSION

Both migratory and nonmigratory deer inhabit the upper basin of the Santa Ana River. The existence of both patterns in a single deer herd has been observed by others (Kufeld et al., 1989; Loft et al., 1984). Garrot et al. (1987) suggested that migration is obligatory for mountain-dwelling mule deer. Moreover, Gilbert et al. (1970) observed that snow depths >46 cm preclude deer use of some ranges. My study area encompassed the highest elevations in southern California; those deer occurring on north-facing slopes within the upper drainage of the Santa Ana River were migratory. Although Medin and Anderson (1979) suggested an elevational dividing line between summer and winter range of ca. 2,600 m for deer in Colorado, no such division appears to exist on south-facing slopes in my study area. Indeed, some deer were observed on south-facing slopes >3,000 m throughout winter. Deer are largely excluded from north-facing slopes >1,500 m, however, where snow accumulations of >4 m were observed during this study.

Several studies have addressed the factors that stimulate migration; these have implicated temperature, relative humidity, insect activity, photoperiod, and maturing vegetation as affecting the timing of migrations (Garrot et al., 1987; Leopold et al., 1951; McCullough, 1964; Russel, 1932). I observed that deer movements were associated with low temperatures and high precipitation. Weather alone, however, is unlikely to affect when deer migrate. During the 1st year of study, migration to winter range occurred largely after major snow storms, whereas in subsequent years, movements of deer were more gradual. Because the first deer to migrate in each year did so in October, before snow and low temperatures could force them from summer range, photoperiod and maturation of vegetation probably affect migration. Likewise, spring migration probably coincides with increasing temperatures, decreased precipitation, increased daylight, and senescence of vegetation on winter range. Effects of climate on quality and availability of forage probably help explain my large correlation coefficients for deer movements and climatic variables.

Migratory and resident females used range differently. In summer, when no overlap occurred in home ranges of migratory and resident females, migratory females used significantly more meadow and riparian habitats. Although many studies have noted the importance of these habitats to deer (Bowyer, 1986; Loft et al., 1984), resident deer in my study avoided these habitats in all seasons. This occurred because of the lack of meadows and riparian areas on south-facing slopes that resident deer inhabited. This also resulted in resident deer occurring closer to potential human disturbance and farther from water than did migratory females in summer; north-facing slopes had a greater proportion of available water and fewer human developments. Thus, deer in the study area migrated to locations containing the highest-quality habitats, which were only seasonally available.

According to Fretwell (1972), animals that are free to choose habitats and migration strategies should do so to maximize reproductive success. And, if the frequency distribution of individuals selecting each strategy stabilizes in a deme, then all individuals experience potentially equal reproductive success. Histøl and Hjeljord (1993) reported that migratory populations of moose (Alces alces) selected habitats differently in winter than did nonmigratory ones, presumably an innate or learned behavior by these cervids. Migratory deer appear to select a strategy that allows them access to the highest-quality habitats; why then do any deer remain resident on south-facing slopes in summer? During migration an animal leaves an area with which it is familiar and moves through areas where it may not be as knowledgeable of the current distribution of escape terrain, hiding cover, or predators. Thus, when deer migrate they may be at greater risk to predation. Indeed, O'Bryan and McCullough (1985) observed a 0.85 rate of mortality in recently translocated deer compared with a rate of 0.28 for resident deer in the area of translocation. Of seven mortalities that occurred from predation in my study, four were migratory deer during the short periods of migration. Conversely, predators often occur at greatest densities where prey is regularly available. Therefore, while deer move between winter and summer ranges, they may be at decreased risk of predation because predators would be left behind (Baker, 1978). This point is unlikely to hold for my study because migratory deer moved through the ranges of residents on their way to and from summer range where predation occurred. Thus, predators have available prey year round in these areas, and predators also are likely to occur on transition ranges. These deer probably are at increased risk of predation while migrating.

If migratory deer are at greater risk of predation than resident deer, a tradeoff may exist in whether to migrate. If deer migrate, they have access to high-quality habitats and may be able to produce more or healthier young, thereby increasing their reproductive success. Increased nutrition is a well-documented factor affecting reproductive performance in Odocoileus (McCullough, 1979). Nonetheless, migratory deer also may have an increased risk of predation, thereby reducing lifetime reproductive success.

Rates of survival and reproduction need not be similar in all years for a mixed strategy of migration to be maintained in a population. Indeed, I observed higher rates of mortality in migratory deer than in resident deer for years with below normal precipitation; however, in the year of normal precipitation, mortality was slightly higher for resident deer. Further, mortality in migratory females occurred exclusively around migration, whereas mortality in resident deer was limited to winter. Additionally, several authors have noted the effects of deep snow on ungulates, including decreased access to forage

(Gilbert et al., 1970), and increased costs of locomotion (Fancy and White, 1987; Parker et al., 1984), both of which can contribute to increased rates of mortality (Klein and Olson, 1960; Robinette et al., 1952), or affect subsequent maternal care of young (Langenau and Lerg, 1976; White and Luick, 1984). In areas of deep accumulations of snow in winter, deer may be forced to migrate as I noted for movements away from north slopes; however, where winter snows are transitory and snow depths are extremely variable, some deer may remain on winter range. Thus, in montane southern California, where annual precipitation (and snow cover) was extremely variable, some mule deer were facultative migrators. Variation in timing of migration among years (Table 1) and some females altering whether they migrated between years supports this hypothesis. Additionally, migratory behavior among deer in this population probably was not fixed genetically. The shift of several females from migratory to resident status, and most males (all those collared) being migratory yet having ranges that overlapped both migratory and nonmigratory females during rut, indicate a degree of behavioral plasticity.

The mating season for mule deer in central California lasts from late October to January (Dixon, 1934; Leopold et al., 1951), whereas mating occurs earlier in populations at more southerly latitudes and lower altitudes (Bischoff, 1957; Bowyer, 1991). Rut peaks in mid-November for deer inhabiting the San Bernardino Mountains (J. Davis, pers. comm.). The estrous cycle in female mule deer lasts 22-28 days, however, they are only in estrus from 24 to 36 h (Mackie et al., 1982). Thus, males must actively search for females over broad areas during that time. That male deer moved more between sequential radio-telemetry locations than did females in my study is not surprising. Many authors have observed increased movements and activity by male cervids during rut (Bowyer, 1981; Cederlund and Sand, in press; Miquelle, 1990; Taber and Dasmann, 1958).

Although rut may continue into December, males continued to move more than did females even during winter. One explanation for this may be that male cervids expend tremendous amounts of energy during rut while fighting with male competitors, and searching for mates. These dominant males also reduce the amount of forage they consume (Bowyer, 1981; Espmark, 1964; Miquelle, 1990; Taber and Dasmann, 1958). Thus, males enter winter with considerably less energy reserves than they possessed prior to rut. Males often do not survive winter because of malnutrition or increased susceptability to predation resulting from their depleted condition (Klein, 1965). That males I studied moved significantly more than females during winter also may be explained by increased foraging by males to compensate for the energy expended during rut. Likewise, overall increases in movements by deer during winter may be due, in part, to reduced availability of high-quality forage. Thus, in an attempt to maintain nutrient intake, deer must spend more time foraging in winter. These arguments assume that increased movement by deer equates to increased foraging, something not tested in this study.

Investigators widely report that mule deer have high fidelity to seasonal home ranges (Gruell and Papez, 1963; Kufeld et al., 1989; Leopold et al., 1951). Indeed, deer in this study routinely returned to approximately the same seasonal home ranges. Only 25% of the tests conducted for home-range fidelity showed significant differences in home ranges of individuals between years. Most other studies have not used the techniques presented herein, however, and meaningful comparisons cannot be made.

Home ranges of deer reported in the literature are extremely variable. Although the home ranges reported in this study are large, they are by no means exceptional. Eberhardt et al. (1984) noted home-range sizes for mule deer inhabiting sagebrush habitat as much as five times larger than those reported here. Even within my study, home-ranges varied from 87 to 3,001 ha. This variability provided the opportunity to examine which factors were associated with home-range size in mule deer. According to optimal foraging theory and bioenergetic models, home-range size should be inversely related to maximum density of resources (Ford, 1983; McNab, 1963). More simply stated, as the amount of high-quality resources increases in a home range, its size should decrease. In this study, home-range size was not related to the amount of selected habitats in that home range. Rather, home ranges of deer were positively related to the amount of avoided habitats. And, if avoided habitats can be equated to lower-quality resources, home-range size is affected more by the amount of poor-quality resources than the amount of high-quality ones. If selected habitats were widely distributed into small patches, however, this might increase home-range size and result in more avoided habitats in large home ranges.

The positive relationship between the abundance of avoided features and home-range size may explain why no differences were observed in the size of home ranges between subsets of the population. Several authors have observed sexual differences in home-range size, with male deer having larger home ranges (Gompper and Gittleman, 1991; Pac et al., 1988). No such trend was observed in this study. Further, because migratory females used the highest-quality resources (i.e., meadow and riparian habitats) more than did resident females, optimal-foraging theory would predict that migratory females should have smaller home ranges. Although, my data tended to support this hypothesis, I observed no significant trend. The extreme variability of home ranges and the abundance of avoided landscape features and habitat types throughout the study area may have contributed to rejection of predictions from optimal-foraging theory.

Human disturbance is a significant factor affecting deer in the Santa Ana River drainage. Indeed, all classes of deer were observed farther than random from human developments. Cornett et al. (1979) observed that deer use of a meadow near cabins was 40% of that in a similar undisturbed site. They also noted a 70% decrease in deer use of areas within 46 m of hiking trails. Further, Rost and Bailey (1979) observed that deer in Colorado avoided habitats adjacent to roads. Clearly, human disturbance reduced the value of habitat for mule deer. Although Bowyer (1984, 1986) noted that 77% of all mule deer observed were <500 m from water in summer, male deer and resident female deer in my study were observed farther than random from available water. One explanation for this discrepancy is the location of human developments in the study area. The Santa Ana River is paralleled by Highway 38 and several dirt roads for most of its length. Thus, by avoiding human disturbance, many deer also have avoided water. This interpretation is supported by the strong partial regression coefficient for distance to human developments and the weak one for distance to water in the home-range model for summer. Migratory females, however, by seasonally moving to areas further from human developments, are able to exploit important resources with less chance for human harassment.

I observed significant differences in use of habitat between migratory and resident deer, and between the sexes. Patterns of spatial use by deer in my study suggest that these cervids primarily avoided negative features of the environment, often avoiding potentially valuable resources as well. As Taylor and Taylor noted (1977), migration is a basic response to adversity. For deer in the Santa Ana River drainage, migration allows animals to avoid human disturbance, and guarantees access to high-quality habitats that are virtually absent from the ranges of resident deer. This probably translates into increased annual reproduction. Nonetheless, a mixed strategy of migration is selected for in this area because during migration, deer are at increased risk of predation. Further, during years of low precipitation (and snow), migratory females had higher rates of mortality than did their nonmigratory counterparts, although this relationship was reversed in years of normal precipitation. Such differences may be further exacerbated in years with deep snow. This tradeoff between lowered survival and use of higher-quality resources by migratory deer than for residents appears to be an important factor maintaining a mixed strategy of migration in this highly variable environment.

With the exception of Bowyer (1984, 1986, 1991) and Bowyer and Bleich (1984), few data on habitat use are available for deer populations in southern California. Research on California deer has focused primarily on populations in central and northern California (Dixon, 1934; Leopold et al., 1951; Linsdale and Tomich, 1953; Loft and Menke, 1984; Loft et al., 1991; Taber and Dasmann, 1958), and broader treatments (Longhurst et al., 1952, 1976) often lacked quantitative assessments of habitat requirements.

Bowyer (1986) noted that a better understanding of variables characterizing habitat and how mule deer distributed themselves with respect to these parameters was requisite for the conservation of this important resource. Three categories of deer in my study area were monitored for habitat and range use; each exhibited unique patterns. Therefore, biologists must address the needs of migratory and resident deer, as well as consider the needs of both sexes.

Chaparral communities in this study were largely avoided with a few notable exceptions. Males and migratory females selected chamise habitats in winter. Additionally, migratory females selected mixed chaparral, and resident deer avoided or used mixed chaparral as available in winter. This can be explained by the fire history of the area. Manzanita Flats, the wintering area for most migratory females and several migratory males, was burned in the Bear fire of 1970, whereas the remaining chaparral east of this area has largely been unburned during this century. Old-growth chaparral is nearly impenetrable and fire can open these areas for deer (Bowyer, 1986; Taber and Dasmann, 1958). Addionally, several authors (Dasmann and Dasmann, 1963; Taber and Dasmann, 1958) have noted marked increase in the availability of forbs and the dietary quality of chaparral after fire; these effects are only temporary, however. Fire is a natural part of chaparral ecosystems. Because of past fire-supression, many parts of the study area dominated by chaparral were allowed to age well beyond the 20-year (for soft chaparral) and 50-year (for hard chaparral) fire frequency set forth in the forest management plan (San Bernardino National Forest files.). If controlled burns are allowed in areas of old-growth chaparral, more higher-quality habitats may be made available to the migratory portion of this deer herd.

The importance of meadow and riparian habitats has been noted for other deer herds (Bowyer, 1986; Loft et al., 1984). In my study area, these habitats were exceedingly rare, and yet were selected by migrant females. Unfortunately, most meadow and riparian vegetation not occurring in the San Gorgonio Wilderness is located along the Santa Ana River, an area heavily affected by human developments and disturbance. Paved or dirt roads cross through the river in several locations. Addionally, several special-use cabins and campgrounds occur along the Santa Ana River; use of such areas by people is high year round. One reason why deer were further from water than from random locations was to avoid human disturbance, and such disturbance probably effected deer use of range both spatially and temporally.

High-elevation pine forests also were selected by deer in summer. Those forests in the San Gorgonio Wilderness are largely protected from human disturbance. Unfortunately, those pine forests most used by resident deer in the study area are affected adversely by human development, and as tourist use of the area around Big Bear Lake increases, human disturbance in this habitat is likely to grow.

As the pressures from an expanding human population limit space and habitat for local populations of mule deer, a clear understanding of the factors regulating deer use of habitat is paramount. Human development may not only limit the amount of habitat available to deer, it also may reduce the value of habitat. Even nonconsumptive uses of wildlife can have adverse effects on animal populations (Albert and Bowyer 1991, Boyle and Samson 1985, Snepenger and Bowyer 1990). Thus, efforts should be made to reduce or mitigate human disturbance in the upper drainage of the Santa Ana River whenever possible.

Identification and delineation of the timing and extent of movements by deer are essential for biologists to choose appropriate harvest strategies and to evaluate results of management (Brown, 1992). But without an understanding of how the migration strategy of individuals relates to use of habitat, management decisions intended to benefit deer may be counter productive. For deer in the San Bernardino Mountains, the choice to migrate is linked to availability of habitat and variable patterns of weather. Consequently, changes in habitat have consequences for movement patterns and rates of mortality in deer, and such outcomes may differ under various climatic conditions.

ACKNOWLEDGMENTS

This work was funded by grants from the California Department of Fish and Game, the National Rifle Association, and the San Bernadino County Fish and Game Commission. Additional support was provided by the U.S. Forest Service, the University of Alaska Fairbanks, and the University of Rhode Island. I thank R. T. Bowyer, F. Dean, E. Follmann, J. Fox and J. Kie for providing advice on all aspects of this project and for critically reviewing this manuscript. I thank D. Thomas for his ideas about how to measure habitat selection from locations with inherent telemetry errors. I also thank F. Chapin, J. Fox, and S. MacLean for suggestions during the development of this project. I am indebted to R. Anthes, P. August, V. Bleich, J. Maier, J. Davis, J. DeWald, S. Loe, M. Neel, J. Rechel, S. Sferra, A. Spina, and T. Paulek for assistance in the field or during analyses.

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CHAPTER II

FORAGE SELECTION BY MULE DEER: DOES NICHE BREADTH INCREASE WITH POPULATION DENSITY?

I investigated effects of population density of California mule deer (Odocoileus hemionus californicus) on forage selection by comparing diet characteristics of two subpopulations of deer that differed significantly in their density during winter. Quality of diet (as indexed by fecal nitrogen) for deer at the low-density site was higher than that of the high-density site in winter, when deer densities were most different. Diet quality was similar in summer when both areas had similar densities of deer. Contrary to predictions of the ideal-free distribution, diet quality was different between the two areas in autumn when population densities were similar; this may have been related to an elevated availability of graminoids on the high-density site. Niche breadth, as measured by diet diversity, differed in a manner opposite to the predictions of the ideal-free distribution. During winter, when differences in density between the two study sites were most evident, niche breadth along the dietary axis in the low-density area was twice the size on the high-density site. Generalist herbivores feeding primarily on low-quality browse in winter would be expected to increase diet breadth by feeding on high-quality forage, if high-quality forage was rare in the environment. Thus, deer could opportunistically improve the quality of their diets while broadening their dietary niches. Further, by rapidly eliminating high-quality forages from an area by heavy grazing, deer at higher densities would be expected to narrow their dietary niche. Theoretical models for changes in niche dimension need to consider such empirical outcomes.

Key words: California mule deer, Odocoileus hemionus californicus, density-dependent forage selection, ideal-free distribution, diet, niche dynamics.

In a heterogeneous environment, the resources available to a population can be viewed as continua along habitat gradients. Individuals spread out along such gradients according to how well they can utilize resources. According to Pianka (1988), populations of K-selected species at low densities would be expected to select near-optimal habitats or resources. As population density increases, however, intraspecific competition for these optimal resources also intensifies. This competition results in a reduction of optimal resources available per individual or total exclusion of some less-competitive individuals from the best resources. Consequently, some individuals that exploit sub-optimal but less-contested resources are favored. Therefore, the variety of resources or habitats utilized by a population should increase with increasing population density; that is, the breadth of the niche should increase (Fig. 12).

The concept of density-dependent resource selection depends on the assumptions that individuals in a population have: 1) ideal knowledge of resource distribution in their environments; and 2) free access to any resource. This ideal-free distribution, first conceived by Fretwell and Lucas (1970), has been reviewed by several authors (Morris, 1989; Sutherland, 1983; Rosenzweig, 1991). The basic tenet of the ideal-free distribution is that as intraspecific competition increases, use of sub-optimal resources becomes a more viable strategy. Thus, as populations increase, shifts should occur in resource selection. Many descriptions and tests of such density-dependent shifts exist, yet most published accounts involve small bodied, more r-selected species (canaries, Serinus canaria--Mayr, 1926; mallards, Anas platyrhynchos--Harper, 1982; voles, Microtus californicus--Ostfeld et al., 1985). Indeed, while the implications of the ideal-free distribution have been noted for large mammals (Berger, 1986; Fagen, 1988; Hobbs and Hanley, 1990), few critical tests of Fretwell's (1972) ideas using free-ranging, large mammals exist.

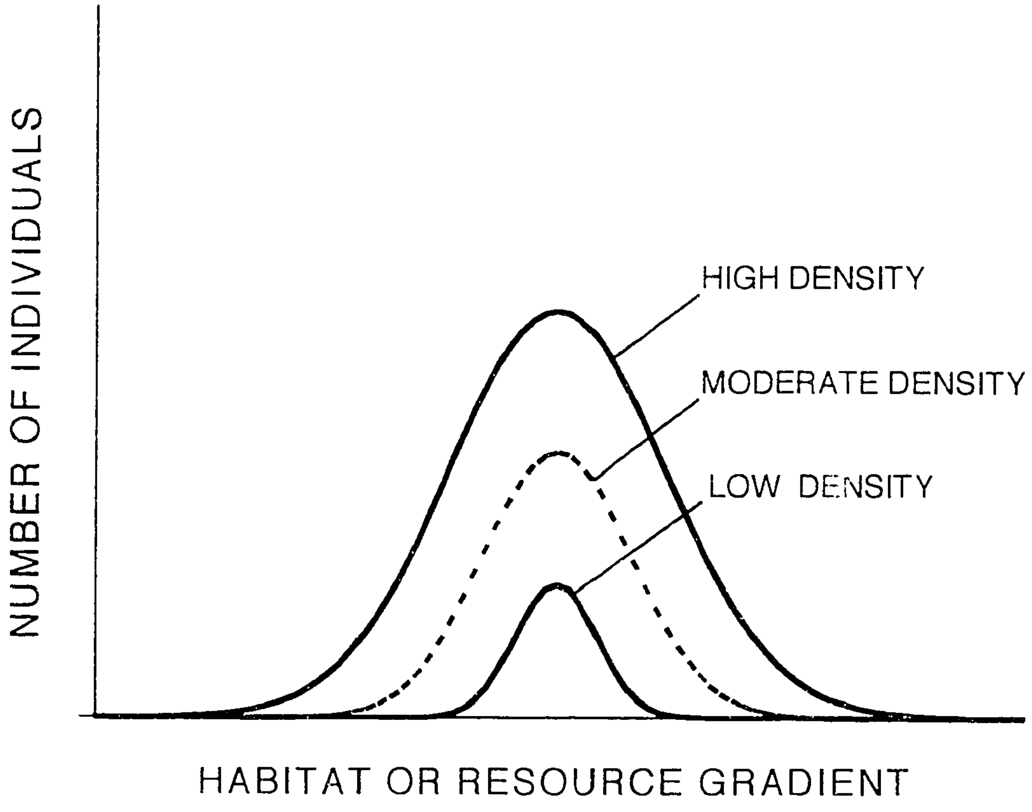

Fig. 11.--Diagram showing how habitat selection may broaden with increasing population density (adapted from Pianka, 1988).

Deer (Odocoileus) are comparatively large, long-lived mammals with a relatively low reproductive rate; females give extended care to young (McCullough, 1979). Deer inhabit somewhat stable environments at population densities that often are near carrying capacity (K). Hence, compared to other vertebrates, deer are a K-selected species (MacArthur and Wilson, 1967; Stubbs, 1977), and exhibit classic density-dependent population processes. For example, as deer populations approach K, ovulation and embryo rates decline (McCullough, 1979), mortality of young increases (Hungerford, 1970), and the physical condition of individuals becomes poor. This results in increased susceptibility to parasites, diseases, and predation (Eve and Kellogg, 1977; Kruuk, 1972; McCullough, 1979; Mech, 1970; Schaller, 1972). Nonetheless, how density of deer affects use of resources is poorly documented; our knowledge of this relationship is inchoate.

Quality of forage ingested is known to vary inversely with population density of deer (Hodgman and Bowyer, 1986; Kie et al., 1980; Nellis and Ross, 1969). Further, red deer (Cervus elaphus) altered their use of habitat in response to changing population size (Clutton-Brock et al., 1987). Nonetheless, data on how changes in population size affect habitat selection or use of forage are scant for most large mammals; yet, such information is vital if the consequences of density-dependence are to be completely understood. The goal of this study was to investigate further the effects of population density on forage selection by a large herbivore, the California mule deer (O. hemionus californicus). This research was designed to gain a broader theoretical framework and provide insights into the role of population density in forage selection by ungulates.

Within the drainage of the upper Santa Ana River there exist distinct subpopulations of California mule deer with markedly different densities, yet these subpopulations occur in approximately the same habitats (J. H. Davis, S. A. Holl, A. T.

Paulek, D. R. Yparraguirre, pers. comm.). In this study, I compared these subpopulations as a critical test of the ideal-free distribution for deer occurring at different densities. The null hypothesis is that with increasing density, no change occurs in the diet niche of mule deer. For the null hypothesis to be rejected and density-dependent forage selection to be invoked, at higher densities the niche breadth (on the forage axis) should be wider than for deer at lower densities. If no change occurs in the dietary niche or if their niche narrows with increasing density, the null hypothesis must be accepted and the concept of the ideal-free distribution rejected.

Because more individuals will be forced to feed on a sub-optimal diet, average quality of forage for higher-density populations should be lower than for populations at low or moderate density. This prediction is based on two possible foraging strategies by deer. First, if less high-quality forage is available per deer, these herbivores may be forced to feed on other plant species of lower quality. Nellis and Ross (1969) reported that use of forage species by mule deer was greatly affected by relative availability of forage; therefore, diet breadth should increase. Secondly, deer may not change the plant species in their diets, rather, they may continue feeding on the same species but feed on poorer-quality parts of plants. If this occurs the heavy browsing of these plants by deer should result . Because nutritive quality of browse decreases with increasing distance down the stem (Aldous 1944, Bailey 1967), as deer browse back stems, the quality of forage they obtain decreases. Thus, if deer keep the species composition in their diets constant the quality of their diet should decrease, and diet breadth should remain the same.

METHODS

Study area.--This study was conducted in the upper Santa Ana River drainage system. Nicholson (Chapter 1) described the general topography and vegetation of this area. Briefly, the Santa Ana River drainage is a 32,000 ha area that forms the major drainage system for the southwestern portion of the San Bernardino Mountains; ca. 145 km east of Los Angeles, California. Slopes associated with this drainage system generally are steep and topographically diverse. The vegetation of the study area primarily is Jeffrey pine (Pinus jeffreyi) forests on northern exposures, dense chaparral on southern slopes, and Canyon live oak (Quercus chrysolepis) in valley bottoms (Muntz 1974).

I chose two neighboring subdrainages within the upper Santa Ana complex for intensive study. I selected these sites because they appeared ecologically similar, and because rates of hunter success (J. DeWald, in litt.) suggested the two areas had markedly different densities of deer. Both Rattlesnake and Staircase canyons are located on the south-facing portion of the Santa Ana River drainage, between Sugarloaf Mountain and Snow Summit. Rattlesnake Canyon (ca. 695 ha) appeared to contain a lower density of deer than did Staircase Canyon (ca. 424 ha). Elevations within the two canyons were broadly overlapping, and similar vegetation occurred in each canyon. Although both drainages contained year-round populations of deer, Staircase Canyon served as a major winter range for migratory deer in the Santa Ana drainage. Migratory deer rarely used Rattlesnake Canyon in winter.

Vegetation composition.--A habitat map for each canyon was developed from LANDS-TM imagery using Terra Mar software (Terra Mar, Inc., Garden Grove, CA; Chapter 1); eight classes of vegetation were distinguished with this methodology. These classes included: montane hardwood, montane conifer, mixed hardwood-conifer, manzanita chaparral, Ceanothus chaparral, sagebrush-mixed chaparral, grassland, and areas of bare ground and tallus slopes. The final habitat map was transferred to a Geographic Information System (GIS; ARC/INFO, Environmental Systems Research Institute, Redlands, CA), where total area of each habitat in the study areas was determined.

Herbaceous and shrub-dominated habitats were sampled using a modification of the step-point method (Evens and Love, 1957) proposed by Bowyer and Bleich (1984). Percent cover and percent relative frequency of plant species were sampled along 53 randomly located transects. Step-points occurred approximately 2 m apart (4 strides), and transects were located at least 20 m apart. A thin line (<1 mm in width) was drawn on the toe of a boot; percent of herbaceous plants and shrub cover (woody plants) were calculated from any portion of the plant hit by the vertical projection of this thin line, whereas relative frequency was determined only for hits that struck the base of plants. Each transect consisted of 100 points. Percent cover of the overstory canopy in tree-dominated habitats was estimated using a spherical densiometer (Lemmon, 1957). At each step-point, percent cover was calculated from any portion of a tree hit by a standard intersection of the spherical densiometer. Additionally, relative frequency was determined from step-points that struck the base of trees or shrubs.

Measures of forage quality.--A subset of forage species was clipped and dried for laboratory analysis and to determine dry biomass at 3-month intervals. For trees and shrubs, this included only current annual growth from at least three composited samples from individual plants within each study area. Measures of forage quality included in vitro dry matter digestability (IVDMD; Tilly and Terry, 1963), and percent crude protein determined by Kjeldhal analysis (Horwitz, 1975).

Diet quality and composition.--The canyons were sampled at monthly intervals for fecal pellets of deer using permanent circular plots of 2-m radius placed 20 m apart along randomly located transects. Each 1 km-long transect consisted of 50 circular plots, and each canyon had three transects for a total of 150 plots per canyon. Crude protein in feces (FCP) was used as an index to dietary quality. Fecal groups were oven-dried at 50° C for

24 h, ground with an all-purpose mill, and sifted through a screen with a 0.425-mm mesh prior to standard Kjeldhal analysis Horwitz (1975).

Crude protein in feces (FCP) has been shown to be positively correlated with dietary nitrogen for cervids feeding on diets high in browse (Leslie and Starkey, 1985; 1987; Mubanga et al., 1985). FCP has also been shown to be useful for indexing seasonal differences in diet quality for deer (Beier, 1987; Pletscher, 1987). Further, Hodgman and Bowyer (1986) and Wehausen (1980) demonstrated that FCP may provide a useful index to range quality. Use of FCP as a measure of diet quality may give questionable results when diets are composed mainly of species high in protein-complexing phenolics (Robbins et al., 1987); however, the effects of these secondary compounds may be negated by deer feeding on a diverse, natural diet (Leslie and Starkey, 1985).

Food habits of deer were determined to the species level from microhistological examination of plant fragments recovered from feces of deer. Anthony and Smith (1974) reported that 15 fecal groups were sufficient to describe the within-season diets of deer. Thus, whenever possible, 15 fresh groups of deer feces were composited monthly for analysis of food habits. Problems with microhistological analysis of plant epidermis have arisen in comparing forages with differential digestibilities (Gill et al., 1983, McInnis et al., 1983). I assumed, however, that this technique provided a valid index to diets of deer in the two areas because such biases would not be expected to vary between areas.

Statistical analyses.--Differences in deer densities were inferred by using analysis of variance (ANOVA, PROC ANOVA; SAS Institute, 1988) to test for differences in the number of pellet groups collected in permanent plots during each season. Although the use of pellet groups as an index to population density has been questioned (Fuller, 1991), Riney (1957) reported that pellet-group counts could be used to detect major changes in population size, and Loft and Kie (1988) observed that they could be used to rank relative use of habitats. Further, because I used pellet-group counts to compare differences between nearby canyons of similar habitat composition within seasons, biases from differential rates of defecation associated with changes in habitats, age of animals, or season (Neff, 1968), probably did not affect my results.

Because the total number of plant species occurring in the study areas and in the diets of deer was large (Appendix A and B), I used a reduced set of 23 plant species that represented the most common species in the environment or in the diets of deer. Any plant species that composed $\geq$10% of a habitat or $\geq$5% of a seasonal diet were included in analyses. Likewise, I reduced forage to classes (shrubs, trees, graminoids and rushes, forbs, and other) for some analyses. I used a multivariate analysis of variance (MANOVA) to test for differences in the vegetative composition of habitats between areas. MANOVA was used to test whether similar habitats in the two study areas differed in forage class or species composition. Data were arcsin-square root transformed to meet the distributional assumptions of this procedure.

Differences in diets between Rattlesnake and Staircase canyons were evaluated using several techniques. The multi-response permutation procedure (MRPP) of BLOSSOM (Mielke, 1991; Slauson et al., 1991) was used to test for differences in diet quality as indexed by FCP. I used MRPP to test the null hypothesis that no differences occurred in FCP between study areas within season. Principal component analysis (PCA) and MANOVA were used to detect differences in diet composition (forage classes) between the two study areas. Using PCA, I combined the proportion of each forage class and other nonclassified food items (such as mistletoe; Phorodendron villosum) into two principal components. Further, I used MANOVA to detect differences between the two canyons in principal component 1 and principal component 2. When significant differences occurred along these axes I inferred that diets differed between areas.

Differences in diets of deer were also inferred by calculating indices of niche overlap for each seasonal diet in each area (Ricklefs, 1973). Further, niche breadth was estimated using the Shannon-Wiener formula for diversity (H'-- Ricklefs, 1973), rescaled such that H' was related to the number of species (Ricklefs, 1973). Niche breadth and niche overlap were estimated using the common species of plants occurring in the diets of deer.

RESULTS

Population density, as indexed by the number of pellet groups collected on permanent plots in Staircase and Rattlesnake canyons, differed markedly between the two study areas in winter (Fig. 13). No difference, however, was observed between areas in pellet-group counts in either summer or autumn. Further, densities of pellet groups were significantly different among seasons in both study areas, with the highest densities occurring in winter ($F = 32.03$, $d.f. = 5, 17$, $P < 0.001$).

To determine if both study areas were equitable in availability of forage, I analyzed the composition of the seven vegetated habitat types and compared species composition of habitats between areas (Appendix A and B). I observed no significant differences in the species composition of habitats between Rattlesnake and Staircase canyons. Species and forage-class composition within habitats likewise were similar between areas ($F = 2.713$, $d.f. = 20, 5$, $P > 0.05$; $F = 2.731$, $d.f. = 4,21$, $P > 0.05$, respectively); although species and forage-class composition differed among habitats (Rattlesnake, $F = 3.847$, $d.f. = 60, 11$, $P < 0.01$; Staircase, $F = 19.07$, $d.f. = 12,59$, $P > 0.001$).

Habitat maps of each study area revealed that relative availability of habitat types in the two study areas was similar but not identical. Rattlesnake Canyon was composed of more montane conifer habitat (36% vs 20%), *Ceanothus* chaparral (7% vs 3%), and manzanita chaparral (7% vs 2%), whereas Staircase Canyon was composed of more montane hardwood (22% vs 15%), sagebrush (17% vs 5%), and grassland (11% vs 1%).

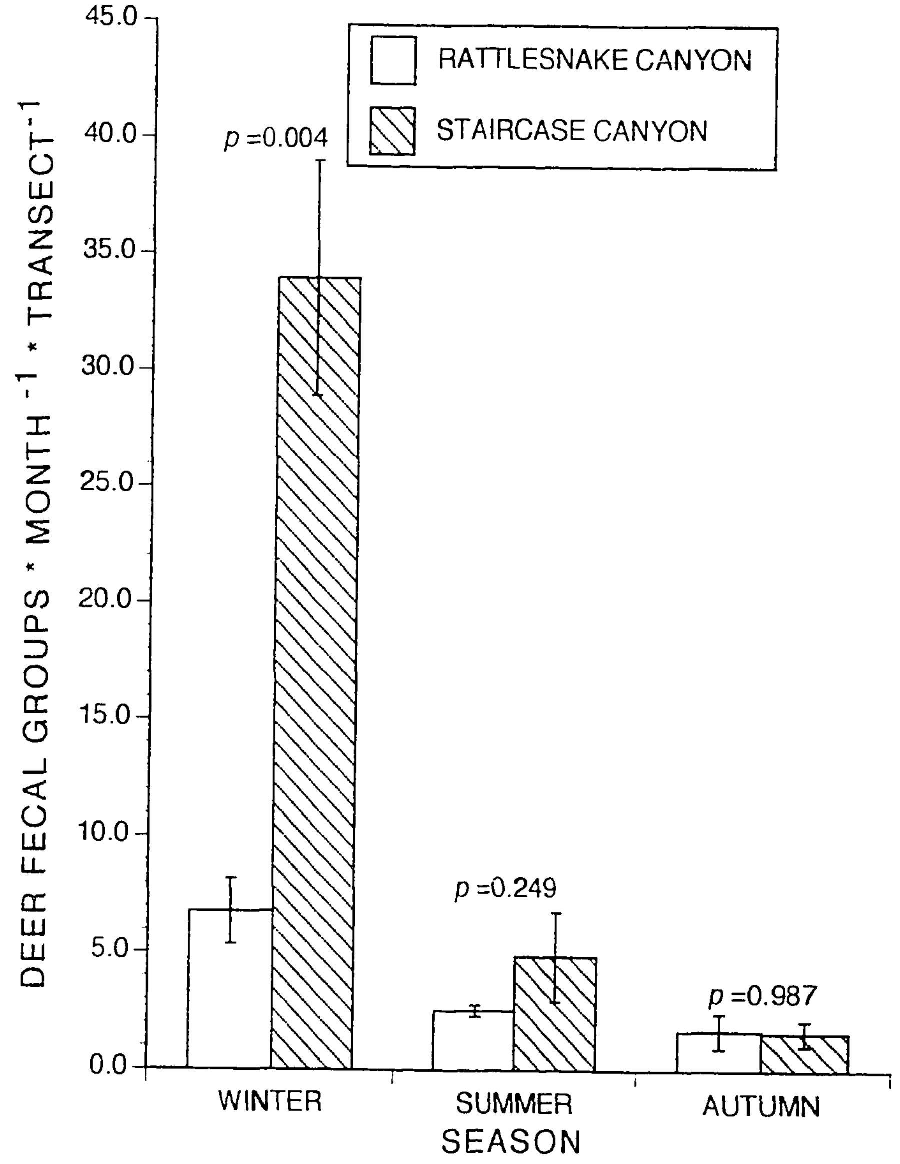

Fig. 12.--Mean (± SE) fecal groups of deer collected seasonally on transects in Rattlesnake and Staircase canyons, San Bernardino Co., California, 1991. Probability values are a result of ANOVA comparisons of densities of fecal group between areas within seasons.

The amount of mixed hardwood-conifer habitat was similar in the two canyons (Rattlesnake = 23%, Staircase = 24%). When I estimated the amount of each forage class available in each canyon I noted similar amounts of forage. Staircase Canyon was composed of 6% forbs, 8% graminoids, 15% shrubs and 44% trees, whereas Rattlesnake Canyon was composed of 4% forbs, 4% graminoids, 15% shrubs and 44% trees. The remainder of each area was bare ground. Thus, although the amount of habitats in the two areas differed slightly, relative availability of forage was similar with one important exception: Staircase Canyon had twice as much graminoid vegetation available to deer than did Rattlesnake Canyon. Comparisons of common forage species between study areas revealed similar trends.

I compared values of fecal crude protein (FCP) from both study areas as an index to diet quality. Significant differences in diet quality occurred between areas and among seasons; FCP was higher for Rattlesnake Canyon than for Staircase Canyon during winter, when Rattlesnake Canyon was at lower population density (Fig. 14). Further, deer feces from Staircase Canyon had significantly higher FCP than did Rattlesnake Canyon in autumn, when the two areas did not differ in density. There was no difference between the two canyons in FCP during summer, however. Both study areas exhibited a significant difference in FCP interseasonally with a peak in FCP occurring in summer for both areas Fig. 14).

There was a high correspondence between FCP and measures of forage quality; FCP was highest in summer and autumn as were crude protein content and in vitro dry matter digestability; IVDMD) for most forages (Fig. 15, 16). Trees showed no annual trend in crude protein content and IVDMD; for those species examined quality was highest in winter (probably owing to inclusion of seeds and nuts in analyses of available annual growth). Deer consumed large amounts of shrubs, and secondary compounds of

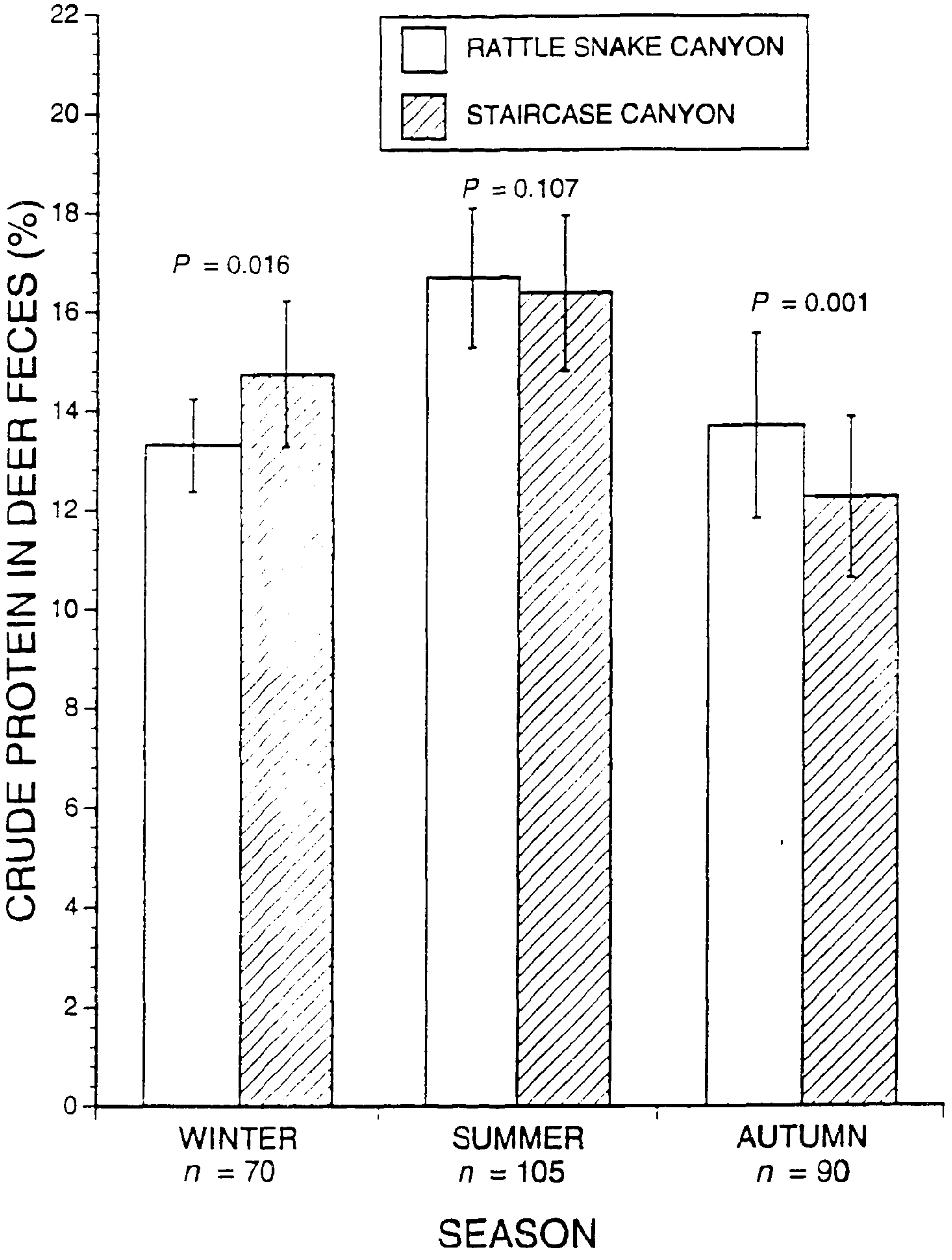

Fig 13.--Median levels of fecal crude protein (FCP) of mule deer, San Bernardino Co., California, 1991. Error bars indicate one-half the interquartile distance. Probability values are the result of a multiresponse permutation procedure analysis (MRPP) testing the null hypothesis of no difference in FCP between study areas within seasons.

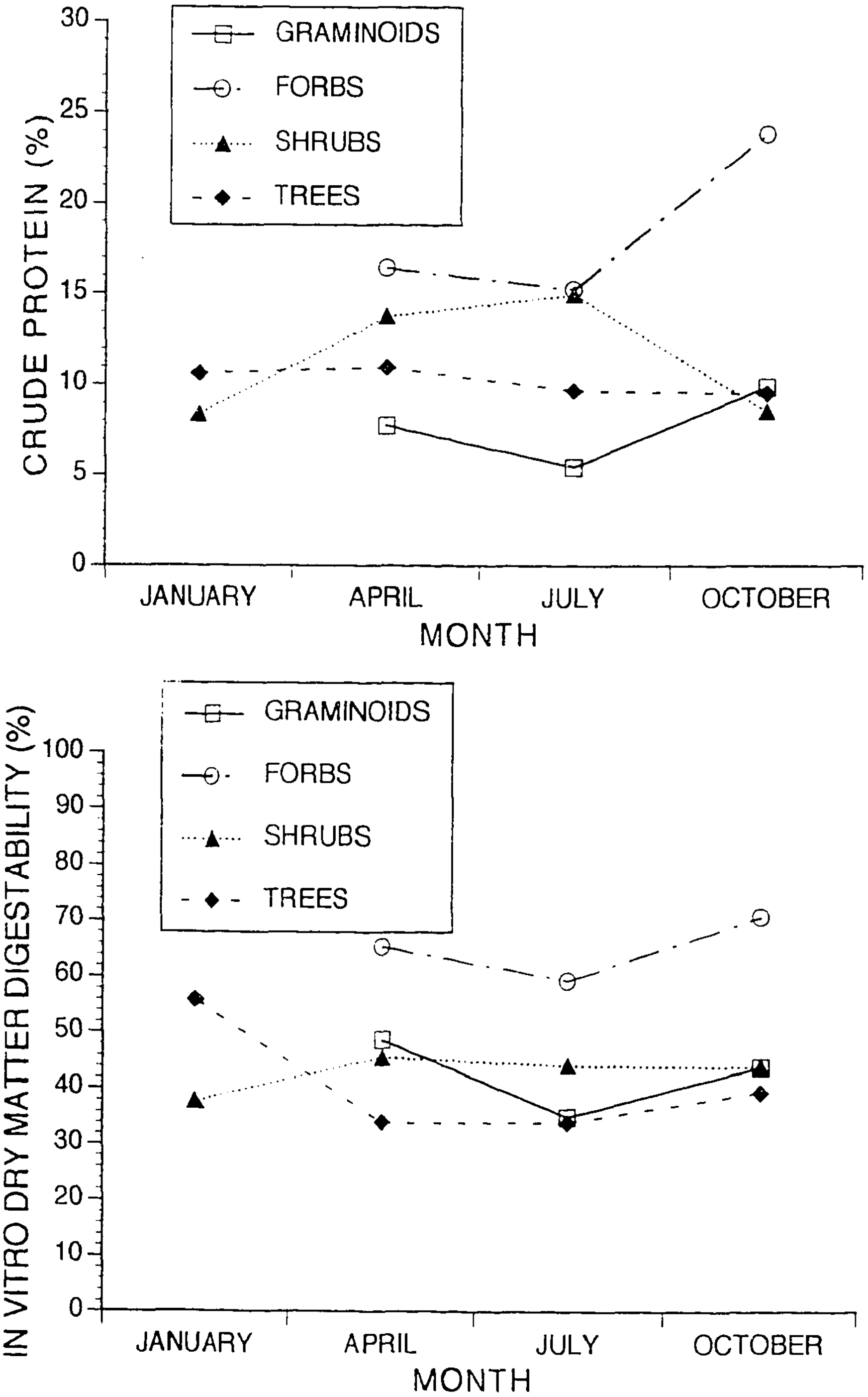

Fig 14.--Crude protein (above) and in vitro dry matter digestability (below) of forage classes eaten by mule deer in San Bernardino Co., California, 1991.

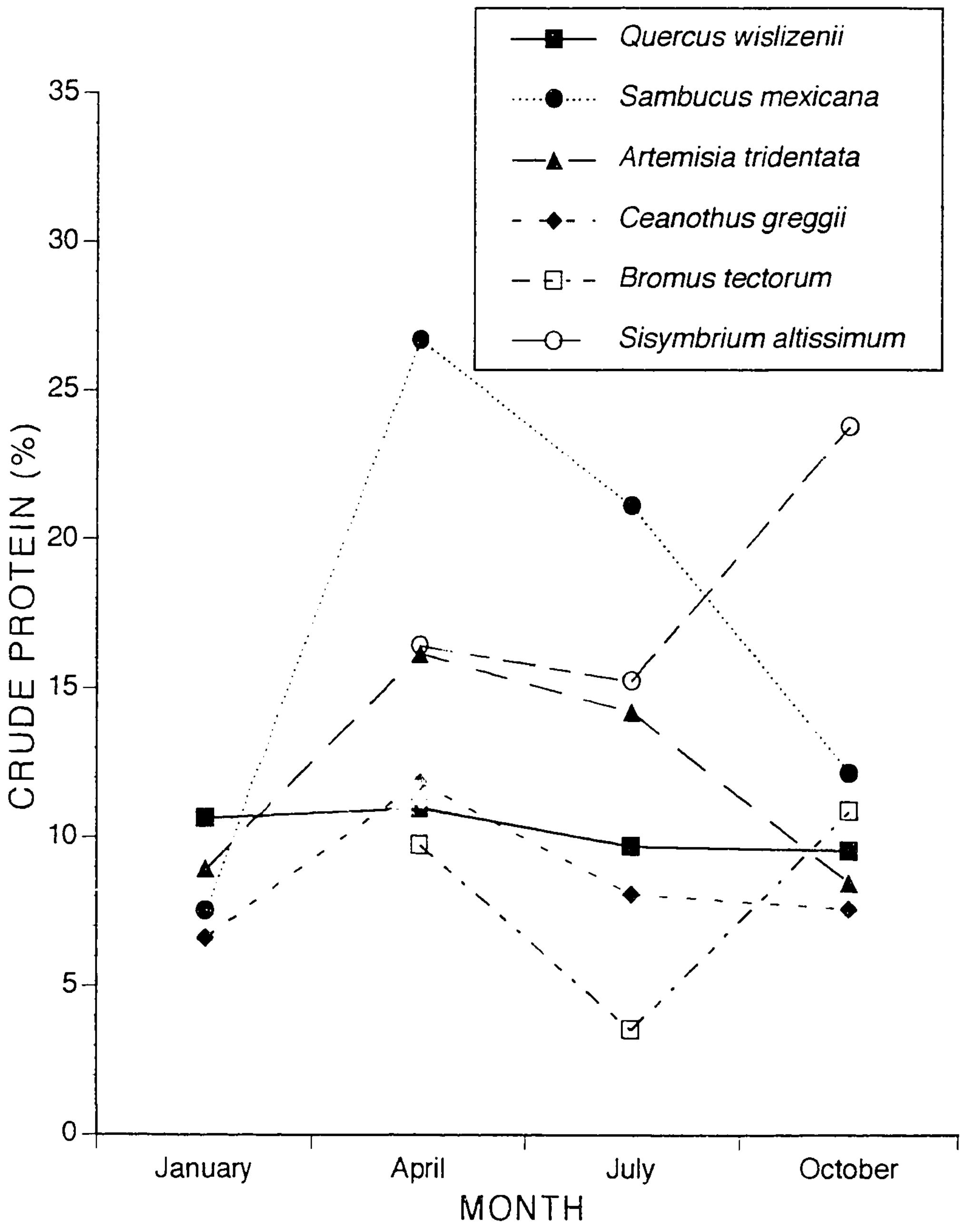

Fig 15.--Crude protein content of selected forage species eaten by mule deer in San Bernardino Co., California, 1991.

these species may have caused increases in FCP. Nonetheless, I observed no correlation between the percent of shrubs in the diet and FCP ($r^2 = 0.007$, $P = 0.155$, $n = 265$), suggesting that secondary compounds were not markedly biasing this index to forage quality.

As a measure of niche breadth, I examined the percent composition of plant species and forage classes in the diets of deer. Based on principal component analysis, clear differences in the diets of deer (using forage classes in the diets) on the two study areas were evident (Fig. 17); the first two principal components explained 84% of the variation. Principal component one was significantly different between Staircase and Rattlesnake canyons in both winter and autumn, but not in summer ($F = 13.40$, *d.f.* 1,6, $P < 0.05$; $F = 50.69$, *d.f.* 1,5, $P < 0.01$; $F = 1.09$, *d.f.* 1,6, $P > 0.3$, respectively). Eigenvalues for principal component one were highly positive for graminoids (0.517) and forbs (0.496) in the diet of deer, whereas eigenvalues were negative for shrubs (-0.693) and slightly positive for trees (0.077). Principal component one is largely a grazing-browsing axis with positive values associated with diets rich in forbs and graminoids. This interpretation is evident when diets of deer in the two areas are compared (Fig. 18, 19). Diets of deer in Rattlesnake Canyon were composed of nearly 40% forbs and grasses in winter, whereas those in Staircase Canyon were >70% shrub. This occurred even though Staircase Canyon contained nearly twice as much graminoid forage as did Rattlesnake Canyon.

The interpretation of principal component two was less clear, with positive eigenvalues for trees (0.754) and graminoids (0.364) and negative eigenvalues for forbs (-0.546) and shrubs (-0.036). This axis may represent habitat types, with forb-rich sagebrush habitats occurring at the negative end and grass-rich oak woodlands occurring on the positive end. Unclassified diet items (i.e., mistletoe, nuts) probably occur near oaks because this category was composed mostly of mistletoe that grows on *Quercus*.

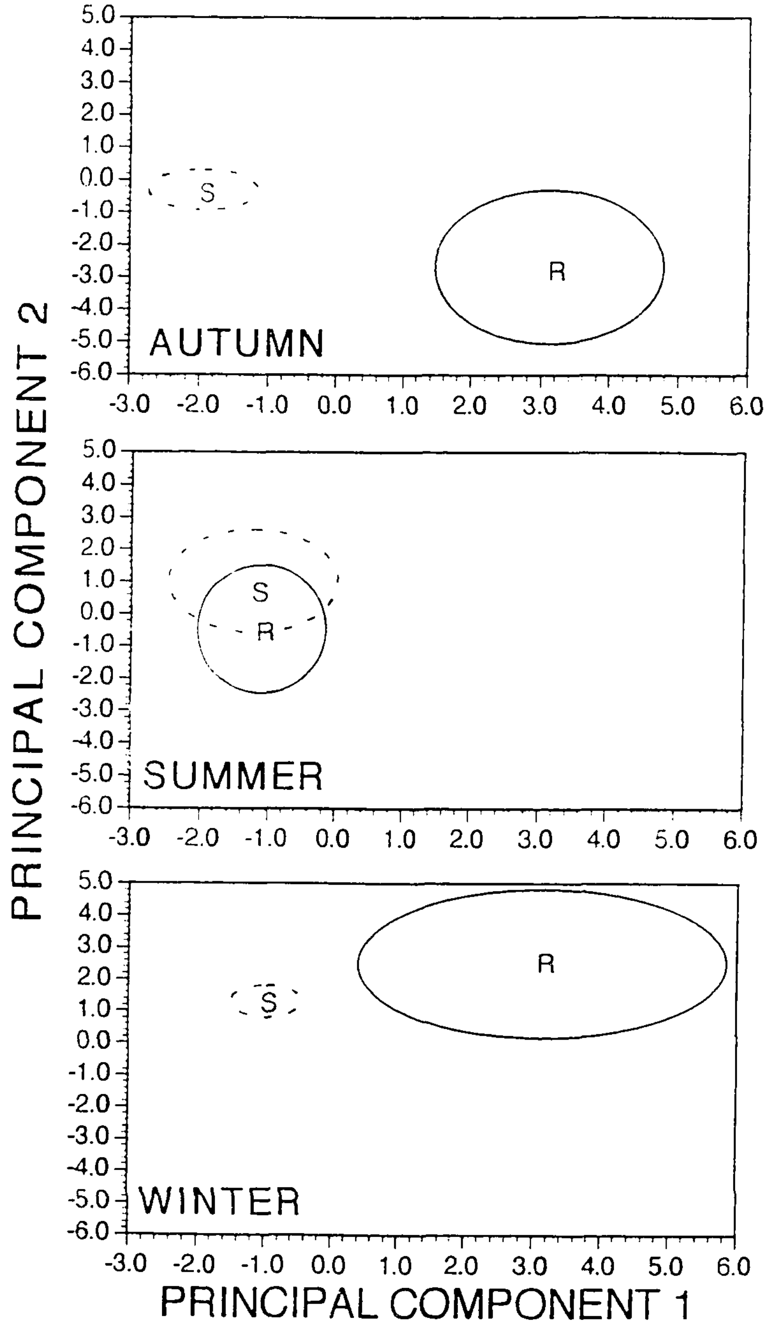

Fig 16.--Diets of deer in Rattlesnake Canyon (R) and Staircase Canyon (S), San Bernardino Co., California, 1991. Diets are plotted against the first two principal components of a principal component analysis for the forage classes present in deer diets. Ninety-five percent confidence ellipses for mean seasonal diets are presented for each area.

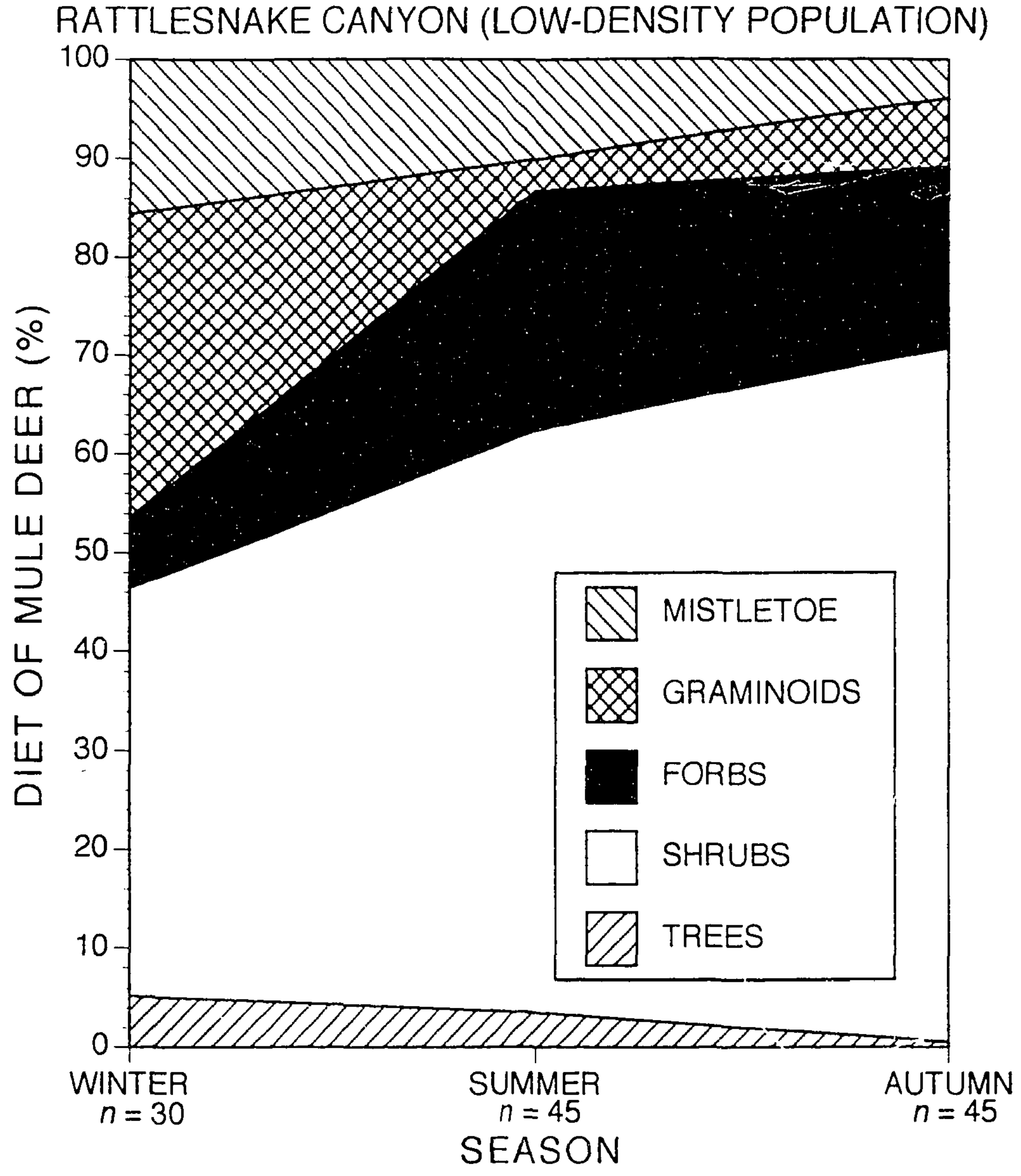

Fig 17.--Percent of forage classes in the diets of deer in Rattlesnake Canyon, San Bernardino Co., California, 1991.

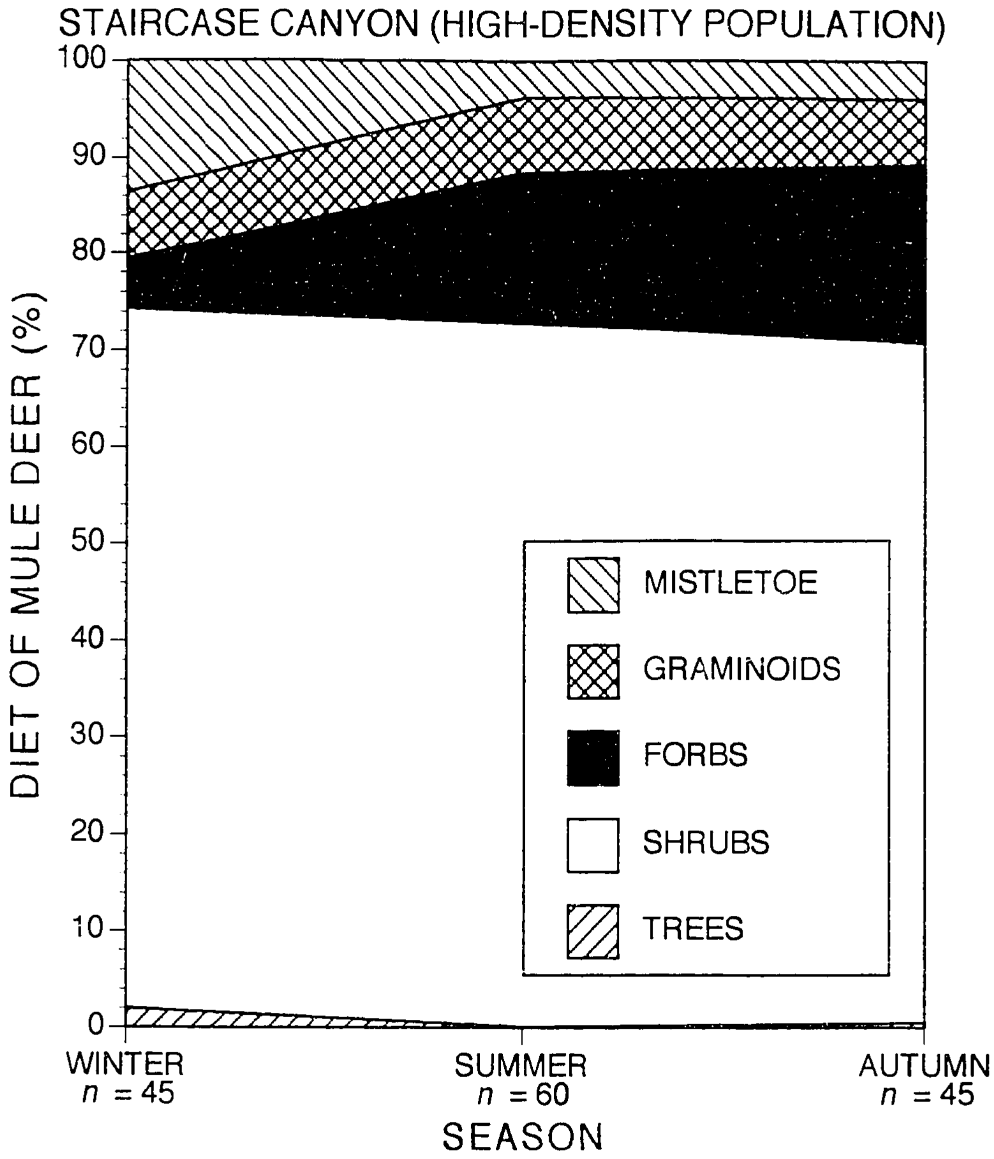

Fig 18.--Percent of forages classes in the diets of deer in Staircase Canyon, San Bernardino Co., California, 1991.

Principal component two did not differ between the two study areas in any season, but did differ among seasons ($\underline{F} = 8.65$, $\underline{d.f.} = 5,17$, $\underline{P} < 0.01$).

As further evidence of diet differences between Staircase and Rattlesnake canyons, niche overlap, based on similarity of diets at the species level of composition, was extremely low (Fig. 20); diets of deer showed the greatest overlap (ca. 55%) between areas in summer. Further, niche overlap was lowest in autumn when it decreased to ca. 22%. Diet diversity ($\underline{e}^{H'}$) also differed between study areas (Fig. 20). In winter, diets of deer in Rattlesnake Canyon were twice as diverse as those in Staircase Canyon. In summer and autumn, however, deer diets were more diverse in Staircase Canyon, although these differences were not as large as during winter.

DISCUSSION

According to Fretwell (1972), populations that conform to an ideal-free distribution should have broader niches at higher densities than at lower ones. Further, because of increased competition and decreased availability of high-quality forage, as population density increases diet quality should decrease.

Deer densities in the two areas studied were significantly different in winter and similar in summer and autumn. Thus, theory would predict a wider diet breadth for deer in Staircase Canyon than for deer in Rattlesnake Canyon during winter. Moreover, no differences should have occurred in niche breadth in summer or autumn. Contrary to predictions, deer in the low-density population (Rattlesnake Canyon) had a significantly different diet with a niche breadth that was double that of the high-density population. Additionally, deer in the two canyons had substantially different diets in autumn, although niche breadth for the two sets of deer was similar. Predictions for summer were as expected--no difference in breadth of diet occurred.

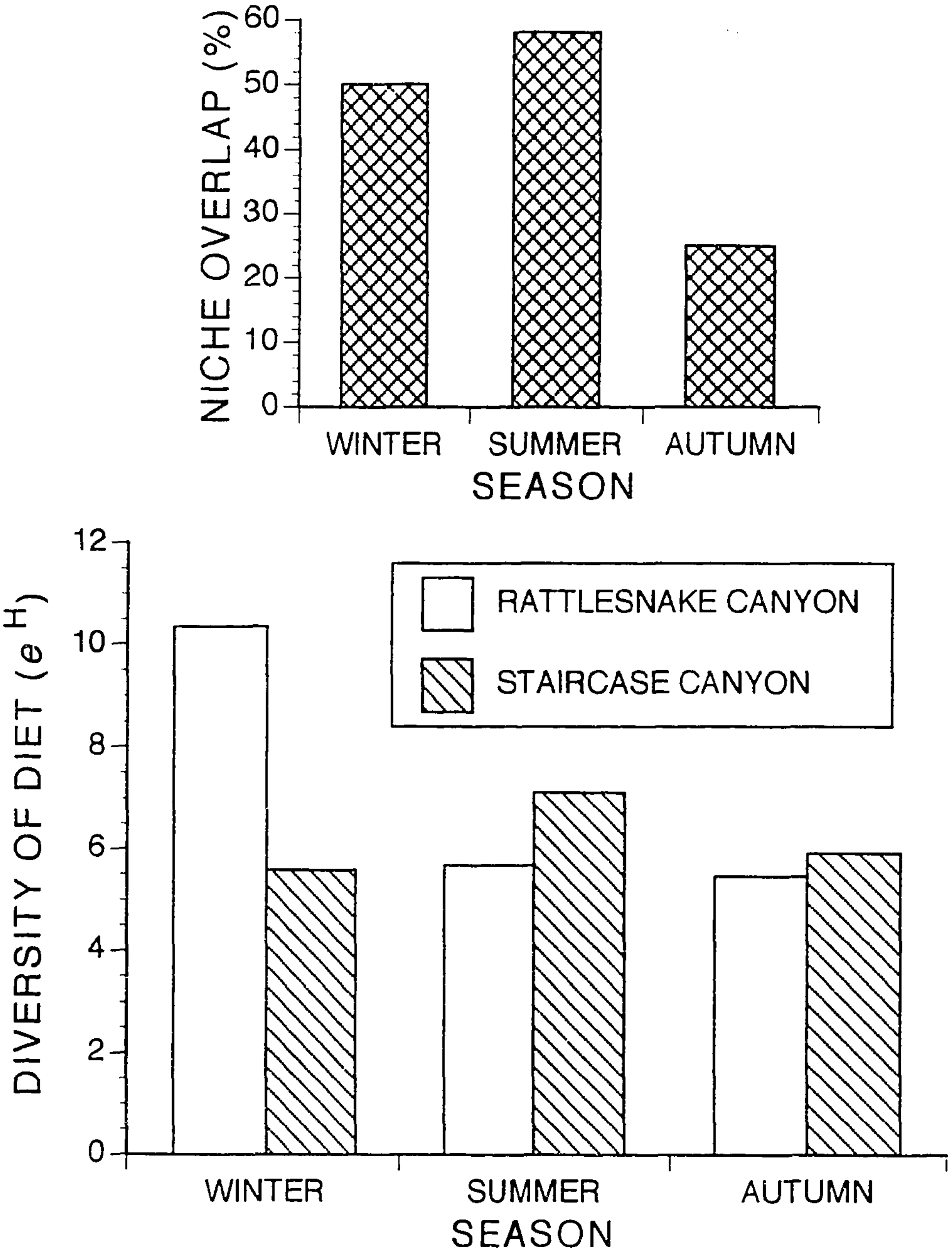

Fig. 19.--Niche breadth (diet diversity) and niche overlap between deer in Rattlesnake and Staircase canyons, San Bernardino Co., California, 1991.

Jenkins (1982) noted that, for generalist herbivores like mule deer, if the quality of food items is not equal, a greater variety of food types may be needed to satisfy all nutritional needs. Forage quality varied widely across forage species and between seasons for the forage species I sampled. Further, shrubs that were relatively low in digestibility were the bulk of deer diets in both areas; high-quality forbs and grasses were only seasonally available. When forbs and newly emerging grasses are available to browsing deer, they would be expected to broaden their dietary niches to include forbs and thereby improve diet quality. If Jenkins (1982) is correct, predictions about density-dependent foraging should be reversed for generalist herbivores feeding primarily on browse. My observations support this view. Another interpretation is that deer on the high-density area reduced the per capita availability of forbs so that availability of this highly sought forage was reduced over winter. If that occurred, the operative niche breadth would be reduced to the extent that foods became unavailable.

I did not directly measure habitat use on these two localized areas. Indeed, most discussions of the ideal-free distribution involve habitat selection (Messier et al., 1990; Rosenzweig, 1985; Rosenzweig and Abramsky, 1985). While I can never know if diet content directly related to habitat selection in this population of deer, other studies have observed changes in deer diets with changes in habitat (Leopold and Krausman, 1987). Because different habitats had different species and forage-class composition, deer had to use several habitats to maintain the diverse diets observed in this study. Thus it appears that diet breadth is an important axis of total niche breadth.

Although predictions concerning niche breadth were not met, predictions on diet quality were realized. During winter, deer in Rattlesnake Canyon (the low-density area) had significantly higher quality diets than deer in Staircase Canyon (the high-density area). Also, no difference was observed in diet quality during summer when the two canyons did not differ in deer density. Contrary to predictions, differences in forage quality reversed in autumn with FCP levels in Staircase Canyon significantly higher than those in Rattlesnake Canyon, although no difference was observed in deer density during this season. Significant differences could have occurred in diet quality for the two areas because of the difference in availability of graminoids on those sites. Staircase Canyon had nearly two times as much graminoid habitat available to deer as did Rattlesnake Canyon. This difference in forage availability probably did not affect observed differences in diet composition during winter because population sizes were so different. Further, with high intraspecific competition for graminoids and forbs in Staircase Canyon during winter, the effective amount of graminoids per deer in the drainage was probably lower than in Rattlesnake Canyon. Indeed, the amount of graminoids in the diets of deer in Staircase Canyon increased as deer density in the canyon decreased.

Differences in diet quality tracked differences in diet composition. Similar to FCP levels, deer diets were significantly different between the areas in summer and in winter. This suggests that diet quality for this herd is, in part, related to diet composition. Indeed, forage quality generally tracked the amount of forbs present in the diets of deer.

Although the specific predictions of the ideal-free distribution were not met in this study, diet quality, diet composition, and diet breadth all changed with the density of deer. Density-dependent effects were observed for the diet of mule deer, but not in the manner predicted by the ideal-free distribution. As several authors have noted, changes in habitat or diet selection with changes in population density can have profound implications for models of habitat suitability (Hobbs and Hanley, 1990). One outcome of the ideal-free distribution is that animals should distribute themselves within habitats (or along resource gradients) at densities that reflect the quality of those resources. In other words, more animals should be observed in those habitats (or consume those forages) that are most valuable to individuals. As a result, habitat-evaluation models are often created that assume animal density and resource density or value are equivalent. Nevertheless, Rosenzweig (1985) warned that optimal habitats will necessarily be used according to their resource density only when populations are at low levels. Although Rosenzweig's (1985) observation is true if the ideal-free distribution holds, as I have observed in this study, an ideal-free distribution does not necessarily occur along all niche axes or in all populations. Clearly, no simple relationship exists between the quality of habitats (or other resources) and the number of large mammals that use that resource. Thus, habitat models that do not account for effects of population density on habitat use are of suspect value--the same holds for studies of diet composition.

Warner (1990) noted that patterns of resource use may be affected by tradition, and that such behavior may complicate measures of resource selection. Thus, strong traditional patterns might affect my test of the ideal-free distribution for diet selection by mule deer. Indeed, many mammals exhibit philopatry (Greenwood, 1980) and this likewise can affect how animals use resources. For Odocoileus, however, males are the principal dispersers and females are less vagile (Kammermeyer and Marchinton, 1976; Robinette, 1966); consequently, philopatry would only be expected to have a strong effect on resource selection by female deer. Mule deer in southern California tend to be in mixed-sex groups during winter (Bowyer, 1984), and some of my fecal samples undoubtedly were from male deer that were not likely to be philopatric. Moreover, some adult females exhibited a facultative pattern with respect to whether they migrated (Chapter 1) -- this argues against a strong bias from traditional use of a particular area and its associated resources.

Berger (1986) noted that feral horses (Equus caballus) also failed to follow an ideal-free distribution. This occurred primarily because horses occurred in year-round harems where adult males exhibited despotic behavior (Berger, 1986). The explanation for mule deer is unlikely because winter samples were collected at a time in which rutting activities should have been waning (Bowyer 1986, 1991). Thus, neither philopatry nor despotic behavior offers likely explanations for the departure from the predictions of the ideal-free distribution I observed for mule deer during winter.

Use of habitats and the forages they contain by mule deer is highly variable and depends upon local habitat quality as well as the condition of the animals themselves. Kufeld et al. (1973) reported that Rocky Mountain mule deer (O. h. hemionus) consumed at least 788 species of plants, including 202 species of trees and shrubs, 484 species of forbs, and 84 species of grasses, rushes, and sedges. Deer apparently have the ability to select plant parts and plants from certain soil types that are high in nutritional content. Therefore, deer may choose forage not only by what species are present, but also by the quality of those species at a particular site. Understanding why particular species are consumed requires a tremendous amount of information about the characteristics of the forage and needs of the individual animal. My research documents that such assessments cannot be made without also considering the density of the population. Our understanding of niche dynamics has been advanced tremendously by the concept of the ideal-free distribution. Nonetheless, my empirical study suggests that more thought needs to be given to theoretical outcomes where there is not free access to resources. A reduction in forage availability with increasing population density is probably common among large herbivores. In this study, such an outcome produced a narrowing of niche breadth on one niche axis. How the overall niche of large herbivores varies with population density clearly warrants further study, and is necessary if our understanding of niche dynamics is to progress.

ACKNOWLEDGMENTS

This work was funded by grants from the California Department of Fish and Game, the National Rifle Association, and the San Bernadino County Fish and Game Commission. Additional support was provided by the U.S. Forest Service, the University of Alaska Fairbanks, and the University of Rhode Island. Diet and forage analyses were performed at the Habitat Laboratory of Washington State University by B. Davitt. I thank R. T. Bowyer, F. Dean, E. Follmann, J. Fox and J. Kie for providing advice on all aspects of this project and for critically reviewing this manuscript. I also thank F. Chapin, J. Fox, and S. MacLean for suggestions during the development of this project. I am indebted to R. Anthes, P. August, V. Bleich, J. Maier, J. Davis, J. DeWald, S. Loe, M. Neel, J. Rechel, S. Sferra, A. Spina, and T. Paulek for assistance in the field or during analyses.

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Appendix A. Plant species encountered during vegetation sampling in Rattlesnake and Staircase canyons, San Bernardino National Forest, San Bernardino Co., California.

Family	Species
AMARYLLIDACEAE	Muilla maritima
ANACARDIACEAE	Rhus trilobata
APIACEAE	Osmorhiza chilensis
	Tauschia parishii
ASCLEPIADACEAE	Asclepias eriocarpa var. microcarpa
ASTERACEAE	Achillea millefolium
	Agoseris retrorsa
	Artemisia dracunculus
	Artemisia ludoviciana
	Artemisia tridentata
	Brickellia californica
	Chaenactis glabriuscula
	Chaenactis sanolinoides
	Chrysothamnus nauseosus
	Chrysothamnus nauseosus bernardinus
	Cirsium californicum
	Conyza canadensis
	Corethrogyne filagnifolia var. glomerata
	Erigeron breweri porphyreticus
	Eriophyllum confertiflorum
	Gnaphalium thermale
	Helianthus gracilentus
	Hieracium horridus
	Hymenopappus filifolia var. lugens
	Hypochoeris
	Machaeranthera canescens
	Madia elegans
	Solidago californicus

Family	Species
	Sonchus oleraceus
	Stephanomeria virgata
	Taraxacum officinale
	Tetradymia canescens
	Tragopogon porrifolius
BETULACEAE	Alnus rhombifolia
BORAGINACEAE	Cryptantha barbigera
	Cryptantha echinella
	Cryptantha intermedia
	Cryptantha macrantha
BRASSICACEAE	Arabis
	Arabis glabra
	Arabis hirsuta
	Arabis holboelii
	Arabis pulchra
	Caulanthus amplexicaulis
	Descurainia pinnata
	Erysimum capitatum
	Lepidium virginicum
	Rorippa nasturtium-aquaticum
	Sisymbrium altissimum
CACTACEAE	Opuntia littoralis var. piercei
	Opuntia parryi
CAPRIFOLIACEAE	Sambucus mexicana
	Symphoricarpos parishii
CARYOPHYLLACEAE	Cerastium vulgatum
	Silene lemmonii
CHENOPODIACEAE	Chenopodium fremontii
CONVOLVULACEAE	Calystegia fulcrata
CUPRESSACEAE	Calocedrus decurrens

Family	Species
	Juniperus occidentalis australis
	Juniperus occidentalis austromontanus
CYPERACEAE	*Carex aurea*
	Carex brevipes
	Carex multicaulus
	Scirpus microcarpus
ERICACEAE	*Arctostaphylos glandulosa*
	Arctostaphylos patula
	Arctostaphylos pringlei
	Arctostaphylos pungens
EQUISETACEAE	*Equisetum laevigatum*
EUPHORBIACEAE	*Euphorbia palmeri*
FABACEAE	*Amorpha californica*
	Astragalus douglasii
	Astragalus lentiginosus var. *sierrieae*
	Astragalus leucolobis
	Lathyrus laetiflorus
	Lotus nevadensis
	Lotus oblongifolius
	Lotus strigosus
	Lupinus andersonii
	Lupinus concinnus
	Lupinus excubitus austromontanus
	Medicago lupulina
	Psoralea rigida
FAGACEAE	*Quercus chrysolepis*
FUMARIACEAE	*Dicentra chrysantha*
GARRYACEAE	*Garrya flavescens*
GERANIACEAE	*Erodium cicutarium*
GROSSULARIACEAE	*Ribes cereum*
	Ribes malvaceum

Family	Species
HYDROPHYLLACEAE	
	Eriodyction trichocalyx
	Phacelia curvipes
	Phacelia davidsonii
	Phacelia imbricata
IRIDACEAE	
	Sisyrhinchium bellum
JUNCACEAE	
	Juncus balticus
LAMIACEAE	
	Marrubium vulgare
	Monardella lanceolata
	Monardella odoratissima australis
	Salvia columbarieae
	Scutellaria austinae
	Stachys albens
	Trichostemma parishii
LEMNACEAE	
	Lemna
LILIACEAE	
	Calochortus invenstus
	Smilacena stellata
LINACEAE	
	Linum lewisii
LOASACEAE	
	Mentzelia
MALVACEAE	
	Malacothamnus fasciculatus
	Sphaeralcea ambigua
NYCTAGINACEAE	
	Mirabilis bigelovii
ONAGRACEAE	
	Camissonia
	Epilobium ciliatum
	Gayophytum diffusum parviflorum
	Oenothera caespitosa
	Zauschneria californica latifolia
PAPAVERACEAE	
	Argemone munita
PELLEACEAE	
	Pellea mucronata

Family	Species
PINACEAE	
	Abies concolor
	Pinus coulteri
	Pinus jeffreyi
	Pinus lambertiana
	Pinus monophylla (minor component)
POACEAE	
	Agropyron cristatum
	Agropyron parishii
	Agropyron trachycaulum
	Agrostis exarata
	Agrostis tenuis
	Bromus carinatus
	Bromus tectorum
	Dactylis glomerata
	Festuca rubra
	Hordeum murinum
	Melica imperfecta
	Melica stricta
	Muehlenbergia rigens
	Poa fendleriana
	Poa pratensis
	Poa scabrella
	Poa secunda
	Sitanion hystrix
	Stipa comata
	Stipa coronata
	Stipa occidentalis
	Stipa speciosa
POLEMONIACEAE	
	Allophyllum violaceum
	Eriastrum densifolium austromontanum
	Gilia austrooccidentalis
	Leptodactylon pungens hallii
	Linanthus breviculus
	Phacelia davidsonii
	Phlox dolicantha
POLYGONACEAE	
	Eriogonum davidsonii
	Eriogonum elongatum
	Eriogonum fasciculatum

Family	Species
	Eriogonum wrightii subscaposum
	Polygonum douglasii
PORTULACACEAE	
	Calyptridium monandrum
	Claytonia perfoliata
PTERIDACEAE	
	Pteridium aquilinum
RANUNCULACEAE	
	Aquilegia formosa var. pauciflora
	Clematis lasiantha
	Delphinium parishii
RHAMNACEAE	
	Ceanothus cordulatus
	Ceanothus greggii
	Ceanothus integerrimus
	Ceanothus leucodermis
	Rhamnus californicus
ROSACEAE	
	Amelanchier utahensis
	Cercocarpus betuloides
	Potentilla glandulosa
	Prunus emarginata
	Rosa californica
RUBIACEAE	
	Galium angustifolium angustifolium
	Galium aparine
	Galium nuttallii
	Kelloggia galioides
SALICACEAE	
	Salix lasiolepis var. bracelinae
SAXIFRAGACEAE	
	Lithophragma
	Ribes cereum
	Ribes nevadense
SCROPHULARIACEAE	
	Antirrhinum coulterianum
	Castilleja martinii var. martinii
	Cordylanthus rigidus
	Keckiella ternata
	Mimulus guttatus
	Pedicularis semibarbata

Family	Species
	Penstemon labrosus
	Penstemon spectabilis
	Verbascum thapsus
STERCULIACEAE	
	Fremontodendron californicum
URTICACEAE	
	Urtica holosericea
VIOLACEAE	
	Viola purpurea
	Viola pedunculata

Appendix B. Percent of forage species in the diets of mule deer based on microhistological examination of deer feces, San Bernardino Co., California, 1990-1991.

Table 6. Percent of forage species in the diets of mule deer in Staircase Canyon, the high density area of this study, San Bernardino Co., California, 1990-1991.

	Percent of Monthly Diets				
Forage Species	Dec-Jan	Feb-Mar	Apr	May	Jun
TREES					
Abies concolor	3.3	0.0	0.0	0.0	0.0
Calocedrus decurrens	0.0	0.0	0.0	0.0	0.0
Juniperus occidentalis	0.0	0.0	0.0	0.0	0.0
Pinus	2.6	0.0	0.0	0.0	0.0
Other Trees	0.0	0.0	0.0	0.0	0.0
Total Trees	5.9	0.0	0.0	0.0	0.0
SHRUBS					
Adenostoma fasciculatum	0.9	0.5	0.0	0.0	0.0
Amorpha californica	3.3	0.0	0.0	0.0	0.0
Arctostaphylos	1.7	2.9	0.0	7.9	5.3
Artemisia tridentata	4.0	27.7	43.4	29.4	20.7
Baccharis glutinosa	2.4	0.0	0.0	0.0	0.0
Ceanothus crassifolius	1.4	0.0	0.8	0.0	4.7
Ceanothus greggii	17.0	6.2	9.4	7.7	6.3
Ceanothus integerrimus	2.6	0.9	4.2	3.1	1.3
Ceanothus leucodermis	0.5	2.3	0.5	0.0	1.7
Ceanothus	0.0	0.0	0.0	0.0	0.0
Cercocarpus	9.8	2.0	0.5	5.6	5.7
Chrysothamnus nauseosus	3.1	0.5	1.6	1.5	1.0
Eriodictyon trichocalyx	0.3	0.0	0.0	0.0	0.0
Eriogonum fasciculatum	0.0	0.9	0.0	0.5	0.2
Garrya flavescens	0.0	0.0	0.0	0.0	1.7
Malacothamnus fasciculatus	0.9	0.0	0.0	0.0	0.0
Populus trichocampa	0.0	0.7	0.5	0.0	2.3
Prunus	0.0	0.5	4.4	1.5	0.7
Quercus chrysolepis	0.0	0.0	0.0	0.0	0.0
Quercus dumosa	0.2	0.0	0.0	0.0	0.0
Quercus kelloggii	1.0	0.0	0.0	0.0	0.0
Quercus	2.7	3.9	1.0	0.8	2.8

Table 6. Continued

	Percent of Monthly Diets				
Forage Species	Dec-Jan	Feb-Mar	Apr	May	Jun
Quercus wislizenii	0.0	0.0	0.0	0.0	0.0
Rhamnus	1.9	0.0	0.0	0.0	1.0
Rhamnus californicus	0.0	0.0	0.0	0.0	0.0
Rhus	0.0	0.0	0.8	0.0	0.0
Ribes	0.0	0.0	0.8	0.3	0.0
Salix	5.7	17.5	3.1	2.0	0.7
Sambucus mexicana	0.0	0.0	0.0	0.0	0.0
Symphoricarpos albus	0.0	5.5	4.2	0.5	0.0
Symphoricarpos	1.4	0.0	0.0	0.0	0.0
Other shrubs	0.7	5.3	3.1	4.6	6.0
Total Shrubs	61.5	77.3	78.3	65.4	62.1
FORBS					
Achillea millefolium	0.0	0.0	0.0	0.0	0.0
Astragalus	0.0	0.0	0.0	0.0	0.0
Eqisetum	0.0	0.0	0.0	0.0	0.0
Eriogonum	0.0	0.0	0.5	0.0	0.0
Linanthus breviculus	0.0	0.0	0.0	0.0	0.0
Lotus	0.0	0.0	0.0	0.0	0.3
Lupinus	0.0	0.0	0.0	0.0	0.7
Medicago	0.0	0.0	0.0	0.0	0.0
Mentzelia	0.3	0.2	4.3	5.9	13.9
Mimulus	0.0	0.0	0.0	0.0	0.0
Mirabilis bigelovii	2.2	0.0	0.3	0.0	0.0
Monardella	0.0	0.0	0.0	0.0	0.0
Mustards	0.0	0.0	1.0	1.8	1.5
Onagracea	0.0	0.0	0.0	0.0	0.0
Phacelia	0.0	0.0	0.0	0.0	1.0
Sphaeralcea	0.0	0.0	0.0	0.0	0.0
Vicia	0.0	0.0	0.0	0.0	0.0
flowers	0.0	0.0	0.0	0.0	0.0
pods	0.0	0.0	0.0	0.0	0.0
Other forbs	4.3	1.5	0.9	1.7	4.8
Total Forbs	6.8	1.7	7.0	9.4	22.2
SEDGE					
Carex	0.0	0.0	0.0	0.0	0.0

Table 6. Continued

Forage Species	Percent of Monthly Diets Dec-Jan	Feb-Mar	Apr	May	Jun
RUSH					
Juncus	0.0	0.0	0.0	0.0	2.0
GRASSES					
Agropyron	0.0	0.0	0.0	2.3	1.0
Agrostis	0.0	0.0	0.0	0.0	0.0
Bromus	0.0	0.0	6.2	4.4	8.4
Festuca	0.0	0.0	0.0	0.0	0.0
Hordeum	0.0	0.0	0.0	0.0	0.0
Muhlenbergia	0.0	0.0	0.0	0.0	0.0
Poa	0.0	0.0	0.0	2.6	0.0
Stipa	0.0	0.0	0.0	0.0	0.0
Other grasses	5.9	6.6	2.3	4.4	3.3
Total grasses	5.9	6.6	8.5	13.7	12.7
OTHER DIET ITEMS					
Phorodendron villosum	18.9	14.4	6.2	11.5	0.0
Ferns	0.0	0.0	0.0	0.0	0.0
Insects	0.0	0.0	0.0	0.0	0.0
Seeds/Nuts	1.0	0.0	0.0	0.0	0.0
Compositae	0.0	0.0	0.0	0.0	1.0
GRAND TOTAL	100	100	100	100	100.0

Table 6. Continued

	Percent of Monthly Diets				
Forage Species	Jul	Aug	Sep	Oct	Nov
TREES					
Abies concolor	0.0	0.0	0.0	0.0	0.0
Calocedrus decurrens	0.0	0.0	0.0	0.0	0.0
Juniperus occidentalis	0.0	0.0	1.5	0.0	0.0
Pinus	0.0	0.3	0.0	0.0	0.0
Other Trees	0.0	0.0	0.0	0.0	0.0
Total Trees	0.0	0.3	1.5	0.0	0.0
SHRUBS					
Adenostoma fasciculatum	0.0	0.0	0.0	0.0	0.0
Amorpha californica	1.6	2.2	1.7	0.9	0.0
Arctostaphylos	0.0	0.0	0.5	0.9	2.6
Artemisia tridentata	1.6	0.0	0.6	1.6	1.3
Baccharis glutinosa	0.0	0.0	0.0	0.0	0.0
Ceanothus crassifolius	2.1	0.0	0.5	0.0	0.0
Ceanothus greggii	29.4	29.2	22.8	13.9	25.5
Ceanothus integerrimus	3.0	3.3	3.4	0.0	4.1
Ceanothus leucodermis	15.1	10.1	13.4	3.7	0.0
Ceanothus	1.4	0.0	0.0	0.0	0.0
Cercocarpus	5.2	4.1	4.2	12.7	6.1
Chrysothamnus nauseosus	0.0	0.0	0.0	0.0	0.0
Eriodictyon trichocalyx	0.0	0.0	0.5	0.0	0.0
Eriogonum fasciculatum	0.0	0.0	0.7	0.0	3.5
Garrya flavescens	1.8	0.8	0.7	0.0	0.6
Malacothamnus fasciculatus	0.0	0.5	1.2	1.7	0.9
Populus trichocampa	0.9	0.0	0.0	0.0	0.0
Prunus	2.7	0.3	0.0	0.0	0.0
Quercus chrysolepis	0.0	0.0	0.0	0.0	0.0
Quercus dumosa	2.4	8.5	0.5	0.8	1.6
Quercus kelloggii	0.9	0.6	0.0	0.0	0.0
Quercus	2.3	6.0	3.6	3.2	2.3
Quercus wislizenii	8.3	2.2	2.5	2.5	4.0
Rhamnus	0.0	0.6	0.0	0.0	0.9
Rhamnus californicus	0.0	0.0	0.0	0.0	0.0
Rhus	0.6	1.4	0.0	0.0	0.6
Ribes	0.0	0.0	1.0	15.3	0.0
Salix	4.6	0.0	4.4	7.1	6.1
Sambucus mexicana	0.0	0.0	1.0	0.0	0.0
Symphoricarpos albus	0.0	0.0	0.7	0.9	0.0

Table 6 Continued

Forage Species	Percent of Monthly Diets				
	Jul	Aug	Sep	Oct	Nov
Symphoricarpos	0.0	0.0	0.0	6.9	0.0
Other shrubs	2.5	7.4	8.3	3.9	2.9
Total Shrubs	86.4	77.2	72.2	76.0	63.0
FORBS					
Achillea millefolium	0.0	0.0	1.2	0.0	0.0
Astragalus	0.0	0.0	0.0	0.0	0.0
Eqisetum	0.0	0.0	0.0	0.0	0.0
Eriogonum	0.0	0.0	2.2	0.7	0.0
Linanthus breviculus	0.0	3.3	0.7	0.0	0.0
Lotus	0.0	2.2	0.0	0.4	1.2
Lupinus	0.0	0.0	0.0	3.0	0.6
Medicago	0.0	0.0	0.0	0.0	0.0
Mentzelia	0.9	0.0	0.0	0.0	0.0
Mimulus	0.0	0.0	0.0	0.0	0.0
Mirabilis bigelovii	0.7	0.0	1.7	1.3	0.6
Monardella	2.1	0.0	0.0	0.0	0.0
Mustards	0.0	1.1	1.6	3.2	8.1
Onagracea	0.0	0.8	0.0	0.0	0.0
Phacelia	0.0	0.0	0.0	0.0	0.0
Sphaeralcea	0.0	0.0	0.0	2.6	2.0
Vicia	0.0	0.0	0.0	0.3	0.0
flowers	0.0	0.0	0.0	0.0	0.0
pods	0.0	0.0	5.6	0.0	0.0
Other forbs	6.0	13.4	6.9	6.3	4.9
Total Forbs	9.7	20.8	19.9	17.8	17.4
SEDGE					
Carex	0.0	0.0	0.0	0.0	0.0
RUSH					
Juncus	0.0	0.0	0.0	0.0	0.0
GRASSES					
Agropyron	0.0	0.0	0.0	0.6	0.0
Agrostis	0.0	0.0	0.0	0.0	0.0
Bromus	1.6	0.0	0.0	3.0	9.0
Festuca	0.0	0.0	0.0	0.0	0.0
Hordeum	0.0	0.0	0.0	0.0	0.0
Muhlenbergia	0.0	0.0	0.0	0.0	0.0

Table 6. Continued

Forage Species	Percent of Monthly Diets Jul	Aug	Sep	Oct	Nov
Poa	0.9	0.0	0.0	0.7	0.0
Stipa	0.0	0.0	0.0	0.0	3.2
Other grasses	0.0	0.3	0.0	0.4	3.6
Total grasses	2.5	0.3	0.0	4.7	15.8
OTHER DIET ITEMS					
Phorodendron villosum	1.4	0.0	4.9	1.5	3.8
Ferns	0.0	0.0	0.0	0.0	0.0
Insects	0.0	0.0	0.0	0.0	0.0
Seeds/Nuts	0.0	0.0	0.0	0.0	0.0
Compositae	0.0	1.4	1.5	0.0	0.0
GRAND TOTAL	100.0	100.0	100.0	100.0	100.0

Table 7. Percent of forage species in the diets of mule deer in Rattlesnake Canyon, the low density area of this study, San Bernardino Co., California, 1990-1991.

	Percent of Monthly Diets			
Forage Species	Dec-Feb	Mar-May	Jun	Jul
TREES				
Abies concolor	0.0	0.0	4.5	0.0
Calocedrus decurrens	1.2	0.5	0.0	0.0
Juniperus occidentalis	1.5	1.7	1.1	0.0
Pinus	1.0	4.5	5.1	0.0
Other Trees	0.0	0.0	0.0	0.0
Total Trees	3.7	6.7	10.7	0.0
SHRUBS				
Adenostoma fasciculatum	0.0	0.0	0.0	0.0
Amorpha californica	0.0	0.0	0.9	0.3
Arctostaphylos	8.7	4.2	0.0	1.0
Artemisia tridentata	2.7	4.8	3.1	0.7
Baccharis glutinosa	0.0	0.0	0.0	0.0
Ceanothus crassifolius	0.0	0.0	0.0	0.0
Ceanothus greggii	11.1	2.4	7.3	18.1
Ceanothus integerrimus	1.8	0.0	0.0	8.2
Ceanothus leucodermis	14.0	2.1	1.5	2.1
Ceanothus	0.0	0.0	0.0	0.0
Cercocarpus	0.1	0.0	0.6	12.1
Chrysothamnus nauseosus	0.0	3.0	0.2	0.0
Eriodictyon trichocalyx	0.0	0.0	0.0	0.0
Eriogonum fasciculatum	0.0	0.0	0.2	0.0
Garrya flavescens	0.0	1.5	0.0	0.0
Malacothamnus fasciculatus	0.0	0.0	0.0	1.3
Populus trichocampa	0.0	0.0	0.0	2.1
Prunus	0.0	0.5	0.0	0.5
Quercus chrysolepis	0.0	0.0	0.0	0.0
Quercus dumosa	0.8	0.0	0.2	1.4
Quercus kelloggii	0.0	0.0	0.0	0.0
Quercus	7.5	1.0	2.1	0.3
Quercus wislizenii	0.8	0.0	22.5	6.2
Rhamnus	0.0	0.0	0.0	0.0
Rhamnus californicus	0.0	0.0	0.0	0.0
Rhus	0.3	0.5	1.3	1.0

Table 7. Continued

	Percent of Monthly Diets			
Forage Species	Dec-Feb	Mar-May	Jun	Jul
Ribes	0.0	0.0	0.0	0.8
Salix	5.3	4.3	3.9	3.9
Sambucus mexicana	0.0	0.0	0.0	0.0
Symphoricarpos albus	0.0	0.0	0.0	0.0
Symphoricarpos	0.0	0.5	0.0	3.2
Other shrubs	1.6	2.9	4.3	7.1
Total Shrubs	54.7	27.8	48.1	70.3
FORBS				
Achillea millefolium	0.0	0.0	0.0	0.0
Astragalus	0.0	0.0	0.0	0.0
Eqisetum	0.0	0.0	0.0	0.0
Eriogonum	1.8	0.0	0.0	1.6
Linanthus breviculus	0.0	0.0	0.0	0.0
Lotus	0.0	0.0	0.0	1.8
Lupinus	1.0	0.0	0.0	0.0
Medicago	0.0	0.0	0.0	0.0
Mentzelia	0.0	2.1	1.9	0.4
Mimulus	0.0	0.0	0.0	0.0
Mirabilis bigelovii	0.8	0.0	0.0	0.3
Monardella	0.0	0.0	0.0	0.0
Mustards	1.6	2.5	1.8	0.8
Onagracea	0.0	0.0	0.0	1.0
Phacelia	0.0	0.0	1.1	0.0
Sphaeralcea	0.0	0.0	0.0	0.0
Vicia	0.0	0.0	0.0	0.0
flowers	0.0	0.0	0.0	0.0
pods	0.0	0.0	0.0	0.0
Other forbs	1.7	2.8	6.9	17.0
Total Forbs	6.9	7.4	11.7	22.9
SEDGE				
Carex	0.0	0.7	0.0	0.5
RUSH				
Juncus	0.0	2.1	1.3	0.0

Table 7. Continued

	Percent of Monthly Diets			
Forage Species	Dec-Feb	Mar-May	Jun	Jul
GRASSES				
Agropyron	2.0	1.2	0.6	0.0
Agrostis	0.0	3.6	0.0	0.0
Bromus	0.3	2.1	1.1	0.0
Festuca	9.7	8.5	0.9	0.0
Hordeum	1.0	0.0	0.0	0.0
Muhlenbergia	0.0	0.9	0.0	0.0
Poa	4.8	8.3	0.6	0.0
Stipa	5.5	6.4	2.1	0.0
Other grasses	2.0	2.6	1.9	0.0
Total grasses	25.3	33.6	7.2	0.0
OTHER DIET ITEMS				
Phorodendron villosum	9.4	21.7	20.8	5.8
Ferns	0.0	0.0	0.0	0.0
Insects	0.0	0.0	0.2	0.0
Seeds/Nuts	0.0	0.0	0.0	0.0
Compositae	0.0	0.0	0.0	0.5
GRAND TOTAL	100.0	100.0	100.0	100.0

Table 7. Continued

	Percent of Monthly Diets			
Forage Species	Aug	Sep	Oct	Nov
TREES				
Abies concolor	0.0	0.0	0.0	0.0
Calocedrus decurrens	0.0	0.0	0.0	0.0
Juniperus occidentalis	0.0	0.0	0.0	0.0
Pinus	0.0	0.0	0.0	0.0
Other Trees	0.0	0.0	0.0	0.0
Total Trees	0.0	0.0	0.0	0.0
SHRUBS				
Adenostoma fasciculatum	0.0	0.0	0.0	0.0
Amorpha californica	3.1	0.3	0.0	0.0
Arctostaphylos	0.9	0.0	0.7	0.0
Artemisia tridentata	0.0	0.0	0.0	0.4
Baccharis glutinosa	0.0	0.0	0.0	0.0
Ceanothus crassifolius	0.0	0.0	0.0	0.0
Ceanothus greggii	15.6	0.9	5.4	3.2
Ceanothus integerrimus	0.3	0.0	0.0	0.0
Ceanothus leucodermis	4.1	0.0	0.0	0.0
Ceanothus	0.0	0.0	0.0	0.0
Cercocarpus	0.6	0.0	0.0	0.0
Chrysothamnus nauseosus	0.0	1.6	0.0	6.7
Eriodictyon trichocalyx	0.0	0.0	0.0	0.0
Eriogonum fasciculatum	0.0	0.0	0.0	0.0
Garrya flavescens	0.0	0.0	0.0	0.0
Malacothamnus fasciculatus	2.8	0.0	0.0	3.2
Populus trichocampa	0.0	0.0	0.0	1.3
Prunus	0.0	0.0	0.0	0.0
Quercus chrysolepis	0.0	0.0	0.0	0.0
Quercus dumosa	6.1	0.0	0.0	0.0
Quercus kelloggii	0.0	0.0	0.0	0.0
Quercus	0.0	0.0	3.9	6.2
Quercus wislizenii	11.6	0.0	0.0	0.0
Rhamnus	0.0	0.0	0.0	0.0
Rhamnus californicus	0.0	0.0	0.0	0.0
Rhus	0.0	0.0	0.0	0.0
Ribes	3.1	0.0	1.5	4.0
Salix	2.8	0.9	0.2	2.2
Sambucus mexicana	0.0	0.0	0.0	0.0
Symphoricarpos albus	0.0	0.0	0.0	0.0
Symphoricarpos	0.0	0.0	0.0	2.4

Table 7. Continued

Forage Species	Percent of Monthly Diets			
	Aug	Sep	Oct	Nov
Other shrubs	7.2	1.6	0.5	1.9
Total Shrubs	58.2	5.3	12.2	31.5
FORBS				
Achillea millefolium	0.0	0.0	0.0	0.0
Astragalus	0.0	0.0	2.0	0.4
Eqisetum	0.3	0.0	0.0	0.0
Eriogonum	0.0	0.0	0.0	0.0
Linanthus breviculus	0.6	0.0	0.0	0.0
Lotus	9.1	10.0	3.7	0.0
Lupinus	5.5	41.0	29.7	16.8
Medicago	0.5	0.6	0.0	0.0
Mentzelia	0.0	0.0	0.0	0.0
Mimulus	0.6	0.0	0.0	0.0
Mirabilis bigelovii	0.0	1.2	0.0	0.0
Monardella	0.0	0.0	0.0	0.0
Mustards	5.0	13.1	3.5	3.6
Onagracea	0.6	2.8	3.2	0.0
Phacelia	0.0	0.0	0.0	0.0
Sphaeralcea	3.1	0.0	0.0	0.0
Vicia	0.0	0.0	0.0	0.0
flowers	0.0	0.0	5.7	0.0
pods	0.0	0.0	0.0	0.0
Other forbs	12.8	6.7	9.1	7.5
Total Forbs	38.1	75.4	56.9	28.3
SEDGE				
Carex	0.0	0.0	0.0	0.0
RUSH				
Juncus	0.0	0.0	0.0	0.0
GRASSES				
Agropyron	0.0	0.0	2.2	3.5
Agrostis	0.0	0.0	2.0	0.0
Bromus	0.0	1.9	1.7	2.7
Festuca	0.0	1.6	1.2	9.7
Hordeum	0.0	0.0	0.0	0.0
Muhlenbergia	0.0	0.0	0.0	0.0
Poa	0.0	1.6	1.7	6.4

Table 7. Continued

Forage Species	Percent of Monthly Diets Aug	Sep	Oct	Nov
Stipa	0.0	6.8	11.1	9.4
Other grasses	0.6	3.4	2.0	1.3
Total grasses	0.6	15.3	21.9	33.0
OTHER DIET ITEMS				
Phorodendron villosum	2.8	0.0	0.0	0.0
Ferns	0.0	0.0	3.7	0.0
Insects	0.3	0.0	0.7	0.0
Seeds/Nuts	0.0	4.0	4.1	7.2
Compositae	0.0	0.0	0.0	0.0
GRAND TOTAL	100.0	100.0	99.5	100.0