Ecology and Population Dynamics of Mule Deer in the Eastern Sierra Nevada, California

By

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DISSERTATION

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Chair Date
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Abstract

Migratory behavior of Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) wintering on the east side of the Sierra Nevada, Inyo and Mono counties, was studied from January 1984 to November 1987. Radio-telemetry indicated no differences between years in timing of migration from the winter range, although on average females preceeded males. Upon leaving the winter range, deer moved to spring holding areas on the east slope at higher elevations. There were no year or sex differences in leaving spring holding areas for summer ranges. Summer ranges occurred mainly on the western slope and extended over 2500 sq km. Summer home ranges of males were at higher elevations, nearer water, and on steeper slopes than those of females. Other physical and floristic habitat characteristics showed no differences by sex. Timing of fall migration was influenced by snowstorms, especially in males.

Precipitation and forage growth on the winter range varied, and this was reflected in diet, condition, and reproduction. Fecal analysis showed that *Purshia* was most frequent in late fall and early spring diets, and *Artemisia* was most common in mid-winter in 1984 through 1988. Fecal nitrogen and diaminopimelic acid varied seasonally in relation to plant phenology, and were not closely correlated with animal condition or reproduction.

Deer numbers declined by half between 1985 and 1988. Pregnancy rates, fetal rates, fetal sizes, and adult weights and kidney fat varied with precipitation and forage growth on the winter range. The effects of an antlerless hunt, decreasing density of one of the two herds studied, reduced drought effects relative to the unhunted control.

Overall fetal sex ratio was unity. Females were more frequent among twins, and males were more frequent among singletons, than would be expected by chance. Percent male offspring was associated with increasing maternal body weight and kidney fat, and not with average annual fecundity or age. These results supported the fractional offspring hypothesis of sex ratio allocation.

Few opportunities for habitat improvement exist on either summer or winter range. Antlerless harvests of deer during periods of population growth can dampen fluctuations in animal numbers caused by variable rainfall.

Dale R. McCullough

Approved: Dr. Dale R. McCullough

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Deer are capital mountaineers, making their way into the heart of the roughest mountains; seeking not only pasturage, but a cool climate, and safe hidden places in which to bring forth their young...the deer climbs all the peaks save the lofty summits above the glaciers, crossing piles of angular boulders, roaring swollen streams, and sheer-walled cañons by fords and passes that would try the nerves of the hardiest mountaineers,--climbing with graceful ease and reserve of strength that cannot fail to arouse admiration...Standing, lying down, walking, feeding, running even for its life, it is always invincibly graceful, and adds beauty and animation to every landscape,--a charming animal, and a great credit to nature.

John Muir 1901

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AKCNOWLEGDGEMENTS

As with most dissertation projects, this one could not have been conducted without the help in many ways of many people and organizations. Terry Russi, wildlife biologist with the Bishop Resource Area of the Bureau of Land Management (BLM), initially suggested that I work in the area, and pledged his and his agency's support. Neither wavered throughout the course of the study. Jim Morrison, Resource Area Manager, cooperated thoroughly with the project, and even donating some skin on his knuckles in capture efforts.

Many people with the California Department of Fish and Game (CDFG) were essential to this work. Vern Koontz was a strong supporter from the beginning, as were Ron Thomas and Tom Blankinship. All assisted in myriad ways, administratively, politically, and in the field, and their efforts are appreciated enormously, as is the support of Vern Bleich. Telemetry equipment was provided by CDFG and BLM. All telemetry flights were provided by CDFG, and performed by their eminently skillful pilots. CDFG also provided the capture equipment and many personnel hours, especially for captures and collections, as well as helicopter time for captures and census.

A large cast of assistants provided much hard work and many long hours in exchange for little financial reward.

Tim Taylor was instrumental in many aspects of the work, including capture, radio-telemetry, and collections. Sylva Raker, Cathy Young, and Paul Meeker were excellent at the summer fieldwork they conducted. Dennis and Jeanne Oakeshott helped in many ways, not the least of which was bettering my ability to get along gracefully in the backcountry. Deb Lawhon assisted with data automation and organization. Dozens of local volunteers and employees of the BLM, CDFG, Los Angeles Department of Water and Power, U. S. Forest Service, and White Mountain Research Station assisted in various aspects of the project.

Financial assistance was provided by several sources. Inyo and Mono counties, through their Fish and Game Fine Funds, were essential to the conduct of this study. I am especially grateful to both Boards of Supervisors and to the counties' Fish and Game Advisory Commission for their support and interest. I hope the present effort aids in maintaining the natural values of that unique and valuable part of the world. The Sacramento Safari Club also was generous in its continuing support (assisted by the able mediation of Bill Clark of CDFG). Additional welcome and generous support was provided by the National Rifle Association, the Mzuri Wildlife Foundation, the Boone and Crockett Club, and the Theodore Roosevelt Memorial Fund of the American Museum of Natural History.

Much of my graduate work has been supervised by Dr. Dale McCullough, whose insights into large mammal ecology were of great value. Drs. Reginald Barrett and James Patton completed my thesis committee and provided helpful comments. Their cooperation in allowing me to meet a tight deadline is acknowledged and appreciated. Dr. John Wehausen provided additional helpful comments on the manuscript.

CHAPTER I. BACKGROUND

In his review of McCullough (1979), Caughley (1980:1339) wrote that "white-tailed deer and Drosophila were the most studied and least understood of animals". A similar description could apply to mule deer (Odocoileus hemionus). Although widely distributed and the focus of much research (see reviews in Wallmo 1981a), many aspects of the ecology, behavior, and management of these deer remain obscure. Some of the larger topics yet to be fully understood include details, and even general conceptual models, of population regulation, the role of predators in fluctuations of deer numbers, patterns of social structure and dispersal, and appropriate tactics to achieve management goals. Aside from these issues of a general nature, aspects of the local ecology of deer in many areas frequently are poorly known. Knowledge of factors such as the locations and distributions of seasonal ranges and travel routes, the proximate causes of migration, and the importance of climate and other factors on population are all important to understanding, and managing, deer in a local area. Such knowledge also can provide insight into more general questions.

The present work was an attempt to fill both types of knowledge gaps, general and local. It was initiated at the suggestion of federal and state land and wildlife managers, interested primarily in descriptive aspects of local deer ecology for managment purposes. Within this context, I sought to design research activities to address more general issues of population regulation and ecological differences between the sexes. Specific objectives were (1) to describe the extent and quality of summer and winter ranges, patterns of habitat use within them and migratory routes between them, emphasizing differences between the sexes; (2) to describe and evaluate seasonal diets of deer; (3) to investigate parameters of reproduction and condition, and relate these to other ecological factors; and (4) to evaluate the effects of an experimental density reduction effected by an antlerless hunt held in the winter of 1984-85.

II. STUDY AREA AND GENERAL METHODS

Mule deer (*Odocoileus hemionus*) occur in western North America from southeastern Alaska to north central Mexico (Wallmo 1981*b*). Cowan (1956) recognized 11 subspecies; the validity of 3 have been questioned (Wallmo 1981*b*; Anderson and Wallmo 1984). Two of these questionable forms occur on islands off Mexico. The type locality of the third, *O. h. inyoensis*, is approximately 20 km from the present study area. However, I will follow Wallmo (1981*b*) and refer to deer in this study as *O. h. hemionus*, the Rocky Mountain mule deer. This subspecies is the most widely distributed, and occurs from the crest of the Sierra Nevada-Cascade Mountains east to Iowa and Missouri (Wallmo 1981*b*).

STUDY AREA

The Sierra Nevada is a massive granite block, oriented in a generally northwest-southeast direction, and tilted toward the west. It extends nearly 600 km from Mt. Lassen in the north to Walker Pass, east of Bakersfield, in the south (Storer and Usinger 1968). The west side of the mountain range slopes gradually for 75 to 100 km, from the foothills near sea level to a crest that generally increases in elevation from north to south and sharply demarcates the east and west sides.

Winter storms from the Pacific Ocean deposit moisture as they rise up the western slope, leaving the east side much more arid. It is here that the Great Basin desert begins. As well as being drier, the eastern Sierra is much more narrow and steep than the west side, and is occasionally precipitous. In the Owens Valley area, which extends from the Sherwin Grade just north of the town of Bishop south for about 120 km, elevation changes from 4200 m at the mountain peaks to 1220 m on the valley floor occur over horizontal distances of <10 km.

An extensive area above about 2500 m, extending from the Yosemite region south for several hundred km to beyond Mt. Whitney, is known as the High Sierra. Extensive glaciation, deep winter snows, mild summers, and hundreds of peaks above 4000 m characterize this area. Routes of travel over the High Sierra are provided by a series of passes of generally increasing altitude from north to south. From Tioga Pass (3030 m) at Yosemite south for 320 km, only 1 road crosses the crest. This road, over Minaret Summit (2796 m) near the town of Mammoth Lakes, terminates nearby at Devil's Postpile National Monument. All other passes over the High Sierra remain accessible to humans traveling only by foot or horseback.

The present research focused on Rocky Mountain mule deer wintering in an area known as Round Valley, some 15 km west of the town of Bishop, Inyo and Mono counties, California (Figures 2-1 and 2-2). Round Valley is bounded on the north by the gently sloping Sherwin Grade and Sherwin Summit (2134 m), on the west and southwest by Wheeler Ridge (3640 m) and Mt. Tom (4161 m), and on the south by the gentle slope up to Buttermilk Country and by the Tungsten Hills. The eastern boundary is not as well defined topographically, and for the present purposes will be noted as U. S. Highway 395, the main north-south vehicular route from Reno, Nevada to southern California. Total area used by deer in the winter is about 90 sq. km. Elevation on this winter range varies from about 1450 to about 2000 m, the upper end of deer use varying with snow and season.

Soils in Round Valley are mainly sandy-skeletal, mixed mesic and thermic Xeric Torriorthents (Vaughn, no date), found in alluvium from granitic rock sources. These are deep, excessively well-drained, and contain boulders up to 2 m in diameter. All are young, with little horizon development. Slopes range from nearly flat at the lowest elevations to nearly vertical on Wheeler Ridge. The soil surface can be >50% boulders, stones, cobbles, and fine gravels.

Water occurs in several permanent streams and springs. Rock Creek drains from the north, Pine Creek runs between Wheeler Ridge and Mt. Tom, and Horton Creek drains the

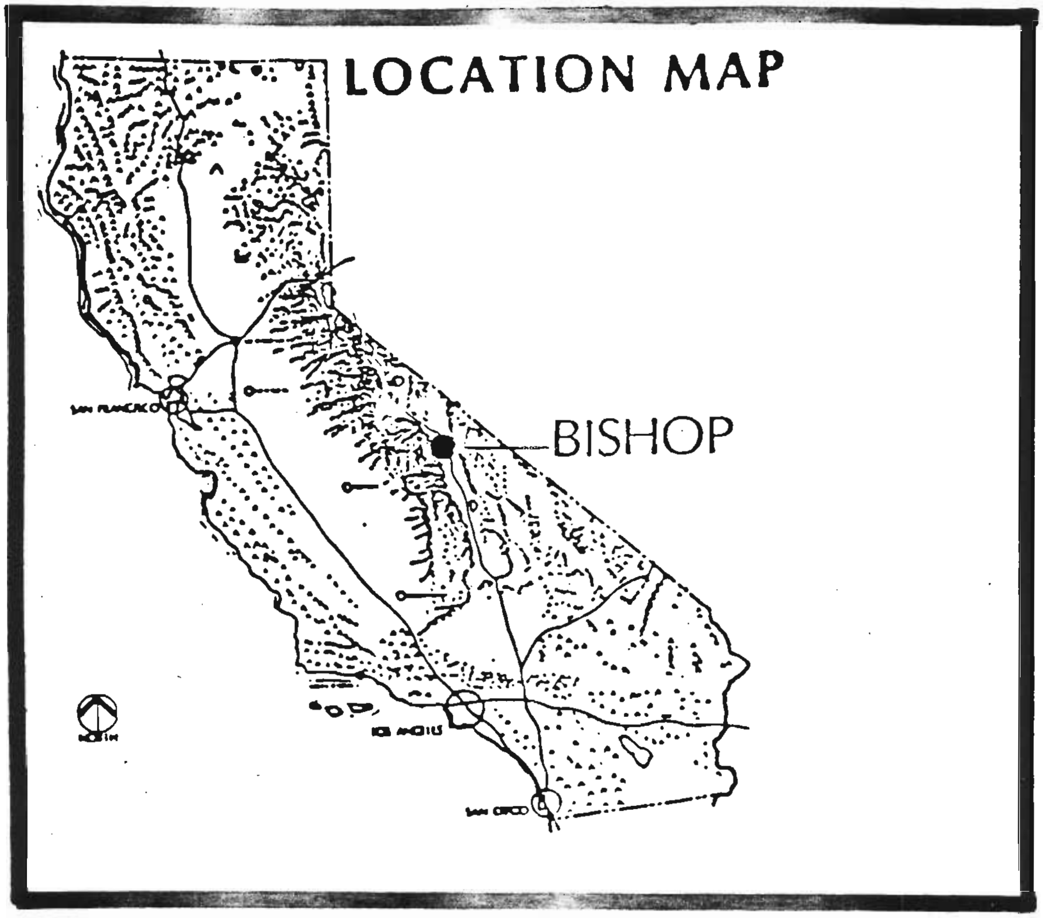

Figure 2-1. General location of the present study area in California. The mule deer winter range in Round Valley is about 15 km west of the town of Bishop.

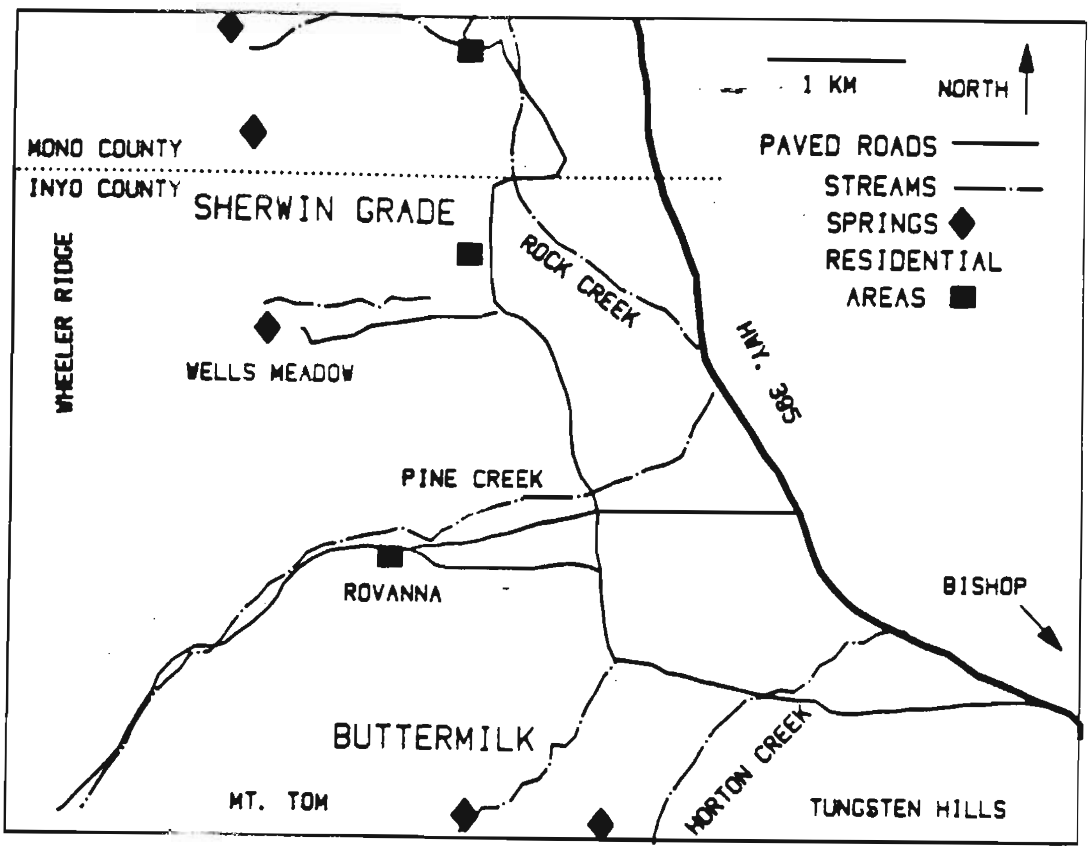

Figure 2-2. Prominent features in the mule deer winter range in Round Valley, Inyo and Mono Counties, Calif.

south side of Mt. Tom. Springs at the base of Wheeler Ridge and Mt. Tom form small creeks that usually continue to flow through the winter. Pine Creek forms the dividing line between the Sherwin Grade (SG) deer herd to the north and the Buttermilk (BM) herd to the south. One paved road bisects the winter range along Pine Creek; other paved roads follow the eastern edge of the deer use areas. Several 4-wheel drive roads provide access to the interior portions of the winter range.

Precipitation in the area varies with altitude, from an annual mean of 14.5 cm at the Bishop airport at 1240 m to 40.6 cm at 2860 m in Pine Creek Canyon (Natl. Oceanic and Atmos. Adm. 1987; Vaughn, no date). The annual total precipitation is quite variable, and has ranged from 3.8 to 45.8 cm since 1951 (Figure 2-3). The coefficient of variation (CV) of annual precipitation during this period was 61%. Within this annual variation, precipitation is strongly seasonal, with about 75% of the total precipitation occurring between November and March (Figure 2-4). The remaining precipitation occurs as scattered summer thundershowers. Precipitation in any month is extremely variable over years; since 1951, the CV's of monthly precipitation varied from 115% in November to 189% in October. Summers are hot, with daytime temperatures in July often exceeding 37 degrees C. January is the coldest month, with

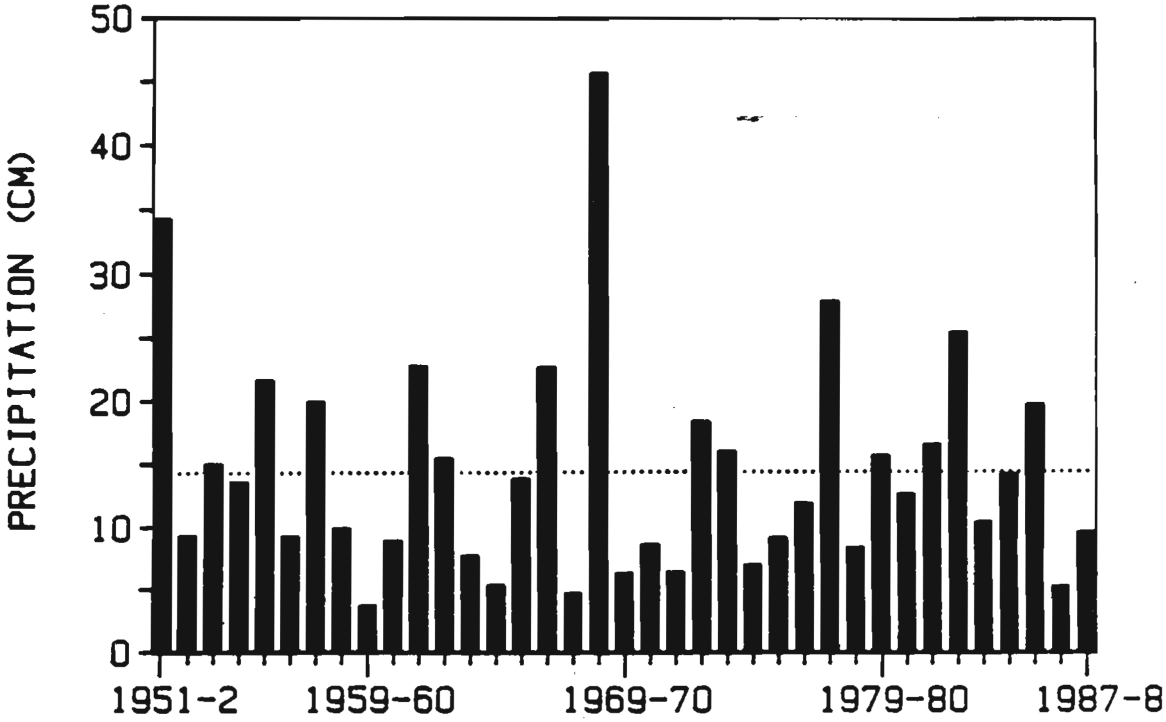

Figure 2-3. Annual (July through June) precipitation totals at the Bishop airport (1250 m), Inyo County, Calif., 1951 through 1988. The dotted line indicates the mean.

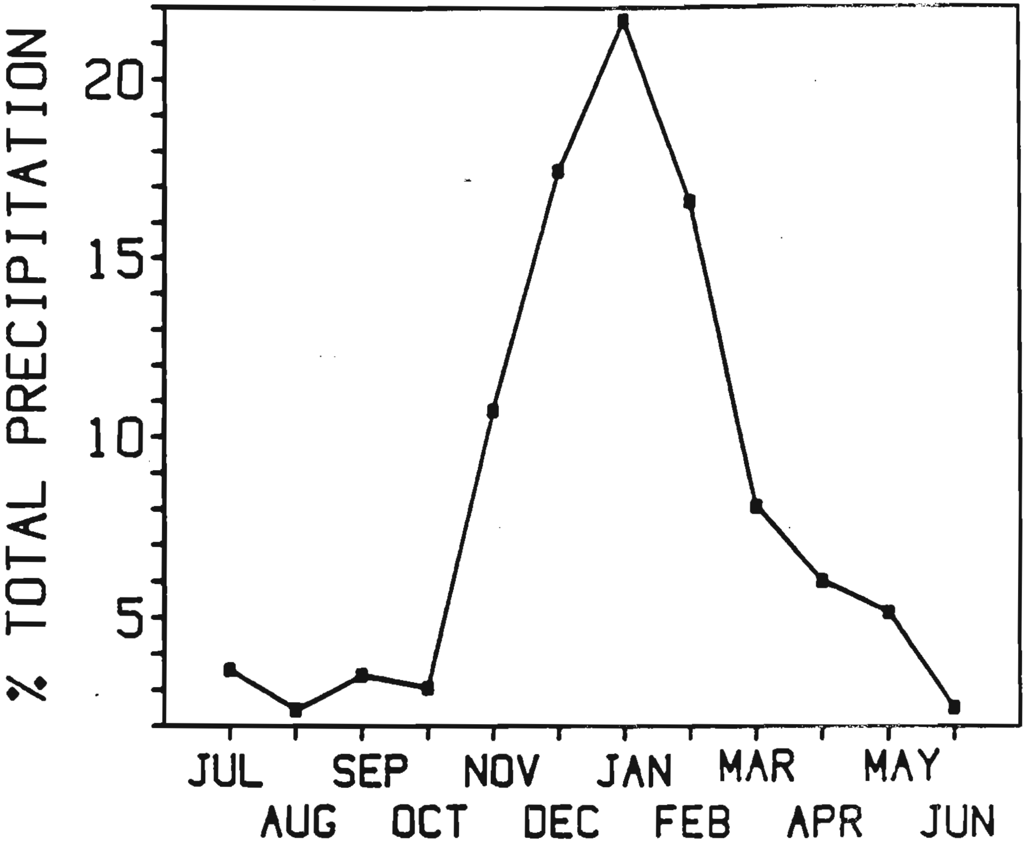

Figure 2-4. Average monthly precipitation totals at the Bishop airport (1250 m), Inyo County, Calif., 1951-1987.

an average temperature of 4 degrees C, and frequent nighttime lows of <-15 degrees C. Potential evapotranspiration is 66.8 cm, or nearly 5 times the mean precipitation.

Vegetation in Round Valley is typical of the Great Basin Desert, and conforms to the Sagebrush Scrub of Munz and Keck (1959). Total vegetative cover is about 20 to 40% (U. S. Bur. Land Manage. files, Bishop, Calif.). Shrubs are dominant, with blackbrush (*Coleogyne ramosissima*), rabbitbrush (*Chrysothamnus nauseosus*, *C. viscidiflorus*, and *C. teretifolius*), big sagebrush (*Artemisia tridentata*), and antelope bitterbrush (*Purshia tridentata*) most common. *Coleogyne* is most frequent at the lower elevations, comprising >80% species composition in some areas. At slightly higher elevations and on more mesic sites, *Purshia* and *Artemisia* become more frequent. Other shrub species present are *Ceanothus greggii* and *Prunus andersoni*. Grasses include *Stipa speciosa*, *Oryzopsis hymenoides*, *Sitanion jubatum* and *S. histrix*, and *Bromus tectorum*. Pinyon pines (*Pinus monticola*) and Utah junipers (*Juniperus osteosperma*) are present at the higher elevations. Forbs are few, especially in winter, and include *Eriogonum kennedyi* and *Lomatum* sp. *Salix* sp., *Rosa* sp., and *Betula occidentalis* occur in some riparian areas.

Summer ranges of deer occurred on both sides of the crest (Chapter 4), and included the Sagebrush, Jeffery

Pine, Lodgepole Pine-Red Fir, and Subalpine Belts of Storer and Usinger (1968). Migration routes and some summer ranges also included the Alpine Belt. Most of the soils at these higher elevations are of granitic and volcanic origin, and most of the area was subjected to several periods of glaciation. Most precipitation falls as snow in winter; summers are mild with occasional afternoon thundershowers. As on the winter range, total annual precipitation on the summer range is quite variable. For example, at about 3200 m on Mammoth Mountain, total snowfall for the winter of 1982-83 was 1440 cm; for 1986-87 it was 238 cm (U. S. For. Serv., Mammoth Lakes Ranger District, Mammoth Lakes, Calif.). Total average precipitation at the Lake Mary Store (2722 m) near Mammoth Lakes from 1947 to 1986 was 74.9 cm, and ranged from 43.9 to 142 cm (City of Los Angeles, Department of Water and Power, unpubl. data).

Most of the winter range is administered by the U. S. Bureau of Land Management, Bakersfield District, Bishop Resource Area. Some of the lower areas are owned by the City of Los Angeles, and much of this is leased for use as irrigated pasture for cattle. Above about 1700 to 2000 m, most of the land is managed by the U. S. Forest Service, Inyo National Forest, White Mountain Ranger District. The [redacted] deer-proof fence in 1985. Additional private lands used for residences occur on the edges of the Sherwin Grade range. Summer range on the east side of the crest is largely managed by the Inyo National Forest, White Mountain and Mammoth Lakes Ranger Districts, although some includes lands owned by the City of Los Angeles and other private owners. Summer range west of the crest is mainly on the Sierra National Forest, Minarets, Pineridge, and Kings River Ranger Districts, and in Kings Canyon National Park, Madera and Fresno counties.

Livestock use of the winter range at present is light, and is confined to the SG range during winter. The U.S. Forest Service pastures some horses near Wells Meadow, and some cattle graze the area just to the south as part of the private alfalfa ranch operation. Livestock use of summer areas, including cattle and sheep, varies from very heavy to none.

METHODS

Fieldwork began in January 1984 and continued intensively through May of 1987. Additional dietary data were collected by BLM personnel in the winter of 1987-88.

Deer were captured on the winter range during January through March 1984 and January and February 1985 with Clover traps (Clover 1956) baited with alfalfa, drive nets using a helicopter, remotely-triggered drop-nets, net guns fired from a helicopter, and tranquilizer darts. Deer captured in 1984 in Clover traps were chemically immobilized with Rompon (xylazine hydrochloride), the effects of which were reversed with yohimbine after handling (Jessup et al. 1985). Capture efforts were distributed throughout accessible areas of the winter range to minimize biases in the marked sample.

On the winter range, 121 deer were captured on the BM range (44 males, 77 females), and 108 on the SG range (49 males and 59 females). An additional ten females also were captured during May of 1984 and 1985 with tranquilizer darts on a spring range near Mammoth Lakes. Eight males and 9 females from the BM range, 7 males and 10 females from the SG range, and all 10 females from the spring range were fitted with radio collars (Telonics Inc., Mesa, Ariz.). Males were chosen for telemetry on the basis of large size and probable relatively old age; females were selected with no known bias.

Specific methods appropriate to the various components of the study are presented in the relevant chapter.

CHAPTER III. MIGRATION

That there are no aseasonal habitats (Sinclair 1983:240) is especially evident in temperate, montane ecosystems. The eastern Sierra Nevada, temperate and montane, with vertical extremes in relative horizontal proximity, presents animals with climatic and ecological extremes. The deep snow and low temperatures which characterize its high altitudes in winter contrast strongly with the hot, dry conditions of nearby lower areas in summer. This situation changes seasonally, allowing favorable ecological conditions at high elevations in summer, and mild winters in lower areas. One tactic allowing animals to live in such areas of predictable fluctuations is seasonal movement, or migration.

Observations of radioed and otherwise marked animals provide detailed information on seasonal movements. These movements can be related to factors external to the animal, such as weather and topography, to provide understanding of how animals make a living in a seasonally variable environment. Comparisons of patterns and timing of seasonal movements between years can provide insight into the proximal causes of such movements. Ultimately, of course, these movements are related to individual reproductive success (Baker 1978).

The concept of migration to enhance reproductive success by avoiding resource bottlenecks was sharpened by Sinclair (1983:242), who hypothesized that "...migration is an adaptation to find greater food resources for breeding". Although many studies have described aspects of mule deer migration (Russell 1932, Leopold et al. 1951, Ashcraft 1961, Gruell and Papez 1963, McCullough 1964, Zalunardo 1965, Bertram and Rempel 1977, Garrott et al. 1987), questions remain as to the proximate causes of the timing of migrations, and the influence of sex and weather on migration patterns.

The objective of this study was to examine the migration of mule deer in the eastern Sierra Nevada, California, and to relate it to other aspects of the ecology of these animals.

METHODS

Deer were captured and fitted with radio collars (Chapter 2). While animals were on the winter range, approximate locations of these telemetered deer were determined $\geq$ 1 times per week. The direction of each radio signal was determined from at least 2 standard locations on each of the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, and approximate locations were then established by triangulation. The standard locations to determine the direction were chosen to allow the determination of which winter range, BM or SG, the animal was on. These data were supplemented by additional radio locations as I moved through the areas, and by visual sightings.

During the spring and fall migrations, and during summer, locations of radioed deer were determined from a fixed-wing airplane; 44 telemetry flights were taken between 1984 and 1986. Airspeed was approximately 160 km/hr, and elevation varied with safety considerations, but generally was between 75 and 200 m above the terrain. These aerial locations were supplemented with radio locations determined on the ground from a vehicle or on foot and with visual observations during daily fieldwork. In the case of animals summering in backcountry areas, observers on backpack trips visited 38 of the 42 deer that reached summer ranges and plotted their locations on U.S.G.S. 7.5 or 15 minute maps.

I expressed summer range site fidelity as the greatest linear map distance between locations in consecutive summers (1 July - 7 September) for the 22 deer that were radioed for >1 summer. Twenty-one of these deer were located on the ground during at least 1 summer; 1 was located only from the air. Of these 22 deer, 10 (45%; 1 male, 9 females) were located in 2 consecutive summers, 9 (41%; 3 males, 6 females) in 3 consecutive summers, and 3 (14%; 1 male, 2 females) in 4 consecutive summers.

Each year from 1984 to 1987, I determined the dates each radioed animal left the winter range, defined as the area below the 2135 m elevation contour, for both the BM and SG winter ranges. For those deer summering on the west side of the Sierra crest, I determined the dates they crossed the crest in both spring and fall of 1984 through 1986. The steep eastern slope of the Sierra Nevada provided the opportunity to determine the presence or absence of a radioed animal on the east side with little error, even if precise location could not be determined. In situations in which I could not determine an exact date of crossing, I estimated the date as the mid-point of the interval in which I did and did not receive a signal. Julian date was the dependent variable in analysis of variance, with years and sex as factors. Of the 22 deer in the 1985 sample, 12 were also radioed in 1984; all 19 deer in 1986 and 4 in 1987 were used in 1985. The fact that I included the same individuals in this analysis for several years appears to violate the assumption of independence. However, a lack of independence would tend to promote uniformity among years, since the same individuals might tend to do the same thing across years. Any differences I found would emphasize that real differences did occur between years, despite the fact that I used the same individuals for >1 year.

To compare the temporal patterns of migration, I calculated the rates of these 3 types of movement: (1) leaving the winter range; (2) crossing the Sierra crest in spring; and (3) crossing the Sierra crest in the fall. I did this by dividing the percent of radioed deer moving on a certain day by the days since the last movement of a radioed deer, for each type of movement. I thus had a rate measure, the "percent of radioed deer moving per day", for each type of movement in each year. This allowed the comparison, for example, of a migration in which most animals moved in a few days from one protracted over weeks. I began with a somewhat arbitrary date for each type of movement: 31 March for leaving winter range, 15 May for crossing the crest in spring, and 10 September for crossing in the fall. Sample sizes ranged from 8 to 26 for any year/movement type combination.

To determine if individual deer tended to move at the same time each year relative to each other, I ranked the Julian date that telemetered deer present in 2 consecutive year's samples moved in each of the years, for each of the 3 types of movement. I examined differences between years with a Spearman rank correlation, correcting for ties.

From April through June of 1985, 1986, and 1987, commencing as soon as snow conditions permitted, an observer counted deer weekly from a vehicle along an 11 km standardized route through a major spring holding area located from about 1 to 8 km south of the town of Mammoth Lakes. Surveys began 30 minutes before official sunrise, and the direction was alternated on consecutive surveys.

Fall precipitation was measured at the U. S. Forest Service (USFS) weather station at the Mammoth Lakes Ranger District, Inyo National Forest, Mammoth Lakes, Calif., at an elevation of about 2400 m. Winter snowfall totals were from the USFS weather station on Mammoth Mountain, at about 2940 m.

RESULTS

April 11 – May 1

Spring Migration

From 1984 to 1987, the **first radioed deer left** the winter range on 1, **1, 9, and 11 April**, respectively; in the same years, the **last radioed deer left on 24, 24,** 17 and 11 **May (Figure 3-1).** The mean dates did not differ significantly by year (F = 0.34; 3, 70 df; P = 0.76); differences by sex approached statistical significance (F = 2.83; 1, 70 df; P = 0.09), with males leaving the winter range an average of 6.9 days later than females.

The temporal pattern of movement off the winter range was similar among years (Figure 3-2). The apparent peaks in 1984 and 1985 are largely artifacts of the need to estimate movement dates because of absence from the study area.

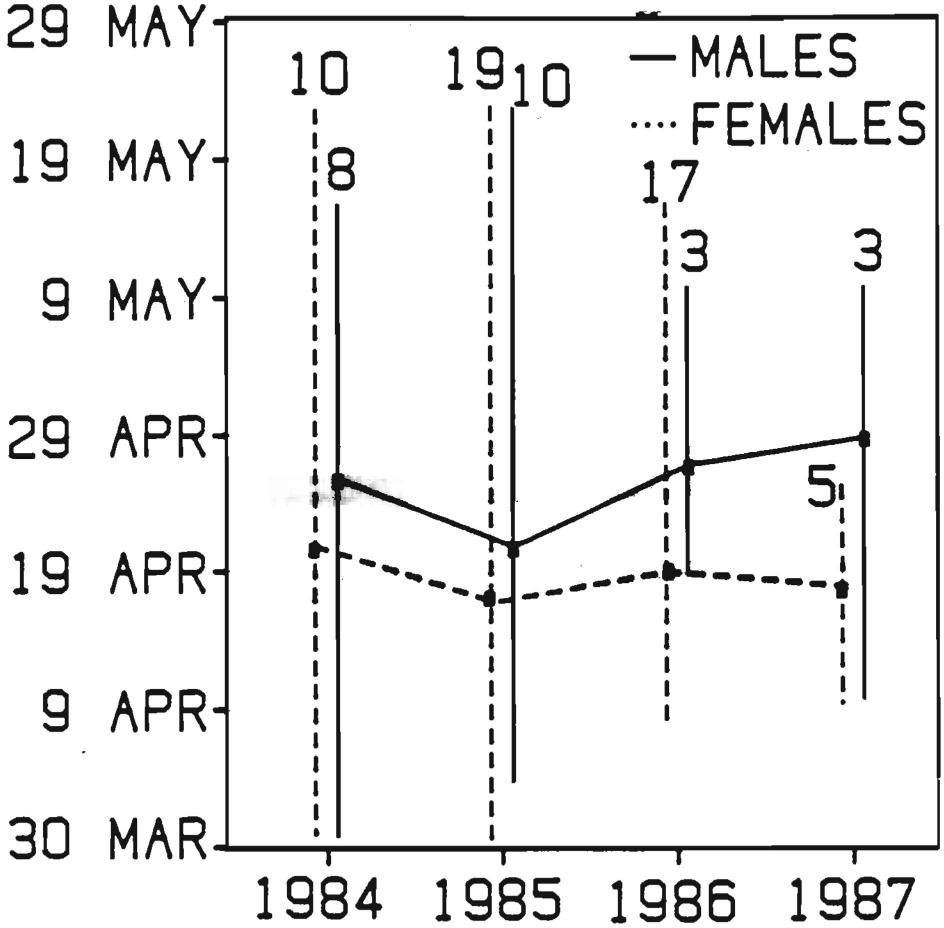

Figure 3-1. Timing of migration of radioed mule deer off the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono Counties, Calif., in spring of 1984 through 1987. Vertical lines indicate the earliest, mean, and latest date that radioed deer left the winter range in each year, by sex. Numbers of radioed deer in each sample is indicated above the vertical lines.

Deer telemetered in successive years tended to leave the winter range in the same relative sequence between 1984 and 1985 ($\underline{r}_s = 0.841$, $\underline{n} = 9$, $\underline{P} < 0.01$) and 1985 and 1986 ($\underline{r}_s = 0.97$, $\underline{n} = 16$, $\underline{P} < 0.01$), but not between 1986 and 1987 ($\underline{r}_s = 0.62$, $\underline{n} = 8$, $\underline{P} > 0.10$). There were many individual differences in the timing of movements, however. For example, in 1985, individuals left the winter range as many as 12 days earlier, or 9 days later, than in the previous year (Table 3-1). In 1987, these differences are even greater, ranging from 20 days earlier to 17 days later than the same individual moved the previous year. These differences are to an extent masked by the rankings.

Because of the north-south orientation of cliffs and mountains immediately west of Round Valley, with the exception of Pine Creek Canyon, deer could move only north or south to leave the winter range. No radioed deer used Pine Creek Canyon. Of the 17 radioed deer from the BM range, 10 (3 of 8 males, 7 of 9 females) migrated north, through the SG range, to reach their summer range; 5 males and 2 females moved south. Of the 17 deer radioed on the SG range, 15 (5 of 7 males, 10 of 10 females) migrated to the north; 2 males went south. Thus, more radioed deer moved north than south ($\underline{G} = 3.985$; $\underline{P} < 0.05$). Small sample sizes preclude analysis by sex or herd. Of the 10 females captured on the spring range, 4 wintered on the BM range, 5

BM 59% North
SG 88% North

Table 3-1. Differences in number of days in the timing of migration by individually radioed mule deer off the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono Counties, Calif., in consecutive years, 1985-87. Positive numbers indicate that movement was later than the previous year; negative numbers mean that movement was earlier. A blank indicates that the animal was not radioed that or the previous year.

Sex	Animal Number	Year		
		1985	1986	1987
Male	121	9		
	71	8		
	139	2	10	-9
	402		-9	17
	51		9	0
Female	238	9	3	
	11	0		
	100	-5		
	311	-7		
	245	-7	7	
	330	-12	12	
	285		16	-20
	424		15	
	341		10	3
	411		8	-2
	465		4	
	31		3	
	472		3	
	270		-6	
	375		-10	
	350		-18	
	391			-9
	91			16

wintered on the SG range, and one died before fall migration.

After leaving the winter range, deer moved to higher elevation "holding areas" (Bertram and Rempel 1977) at 2100 to 2400 m on the east side of the Sierra Nevada, and remained there from 4 to 6 weeks. Deer already were present in the hundreds on the first road surveys of the spring near Mammoth Lakes (Figure 3-3). The pattern of deer counted in this holding area was similar in all 3 years: maximum numbers were counted in late April and early May, with numbers dropping off to a minimum by mid-June, as the deer continued on to summer ranges. During early spring, a portion of the wintering animals also used the irrigated meadows immediately adjacent to the winter range in Round Valley for feeding.

In areas used by deer in the spring, vegetation was largely Sagebrush Scrub (Munz and Keck 1959), characterized by stands of *Artemisia tridentata*, *Purshia tridentata*, *Ceanothus velutinus*, and scattered *Pinus Jeffreyi*, *Abies concolor*, or both, frequently with meadows along watercourses. This is a common vegetation type in the eastern Sierra, and thus spring holding areas were not particularly circumscribed or in unusual or rare habitats. South of the winter range, extensive areas of this vegetation occur along the eastern bases of Mt. Tom and Basin Mountain and

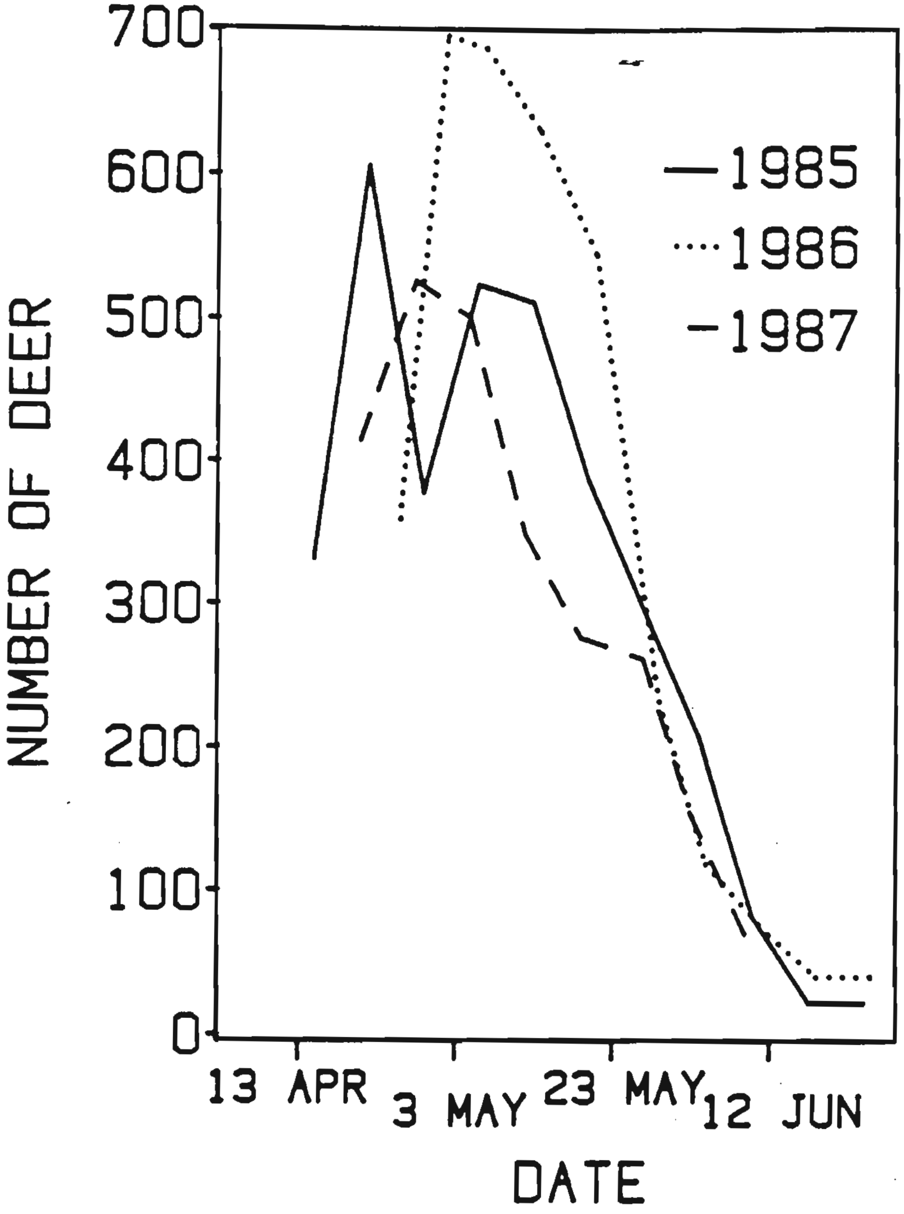

Figure 3-3. Number of mule deer counted from a vehicle on standardized weekly dawn surveys through a spring holding area near the town of Mammoth Lakes, Mono County, Calif., 1985 through 1987.

g8continue south along the migration route toward Bishop and Piute Passes. To the north, similar vegetation exists along the base and extending several hundred meters up the escarpment of the Sierra Nevada, and continues into and past the town of Mammoth Lakes.

The diminution of deer counted in the holding area during the spring was reflected by an increase of deer crossing the crest to summer ranges. Of the radioed deer that summered west of the crest, the first crossed the crest on 18, 16, and 25 May in 1984 to 1986, respectively (Figure 3-4). The last deer crossed on 29, 20, and 18 June. There were no significant differences in mean spring crossing dates by year (F = 0.88; 2, 59 df; P = 0.51) or sex (F = 2.19; 1, 59 df; P = 0.14). Rates of crossing show that this activity was centered around the beginning of June (Figure 3-5). Rank correlations between timing of crossing the crest were significant between 1984 and 1985 (r_s = 0.63, n = 10, $P < 0.05$) and 1985 and 1986 (r_s = 0.69, n = 18, $P < 0.0$), but not between 1986 and 1987 (r_s = 0.06, n = 5, $P < 0.5$).

The temporal uniformity over years in leaving the spring holding area for summer ranges occurred despite greatly different snow conditions between years. In the winters of 1983-4, 1984-5, and 1985-6, the USFS recorded total snowfalls of 671, 767, and 1021 cm on Mammoth Moun-

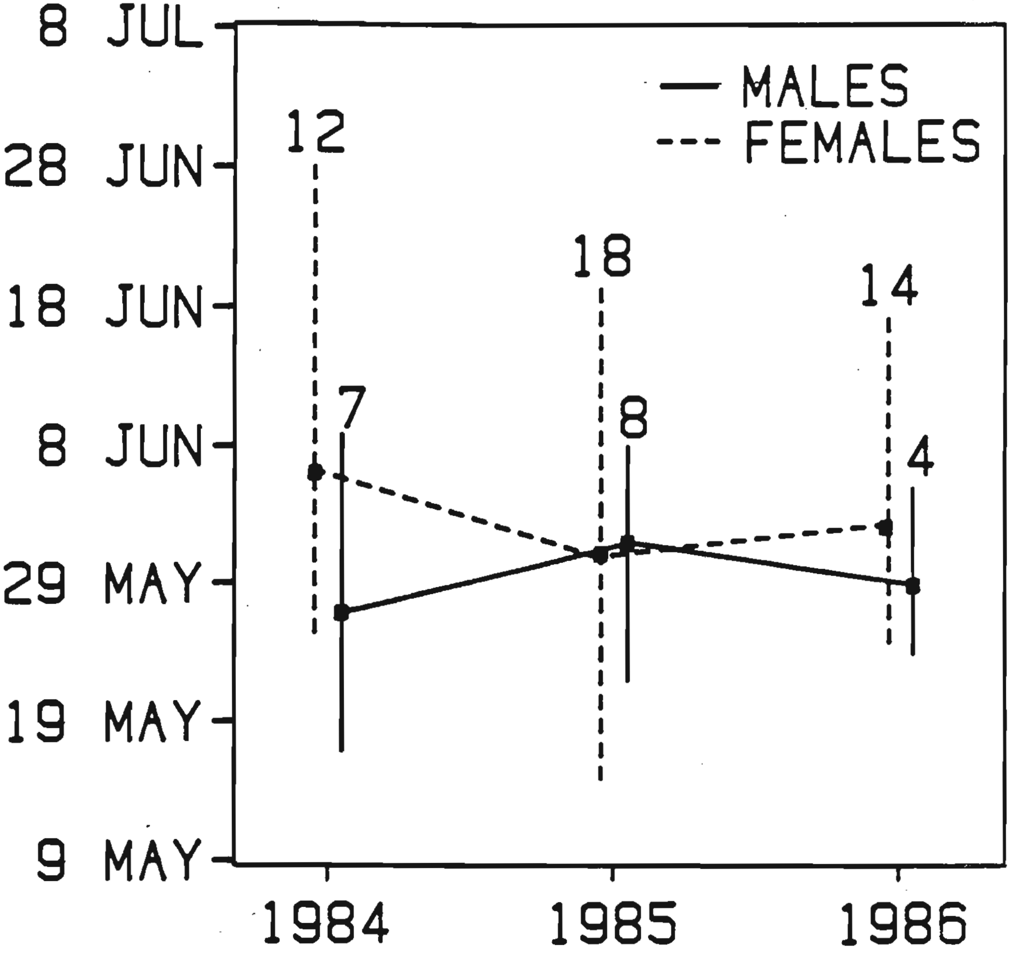

Figure 3-4. Timing of migration of radioed mule deer over the crest of the Sierra Nevada in spring of 1984 through 1988, Inyo and Mono Counties, Calif. Vertical lines indicate the earliest, mean, and latest dates that radioed deer crossed the crest in each year, by sex. Numbers of radioed deer in each sample are shown above the vertical lines.

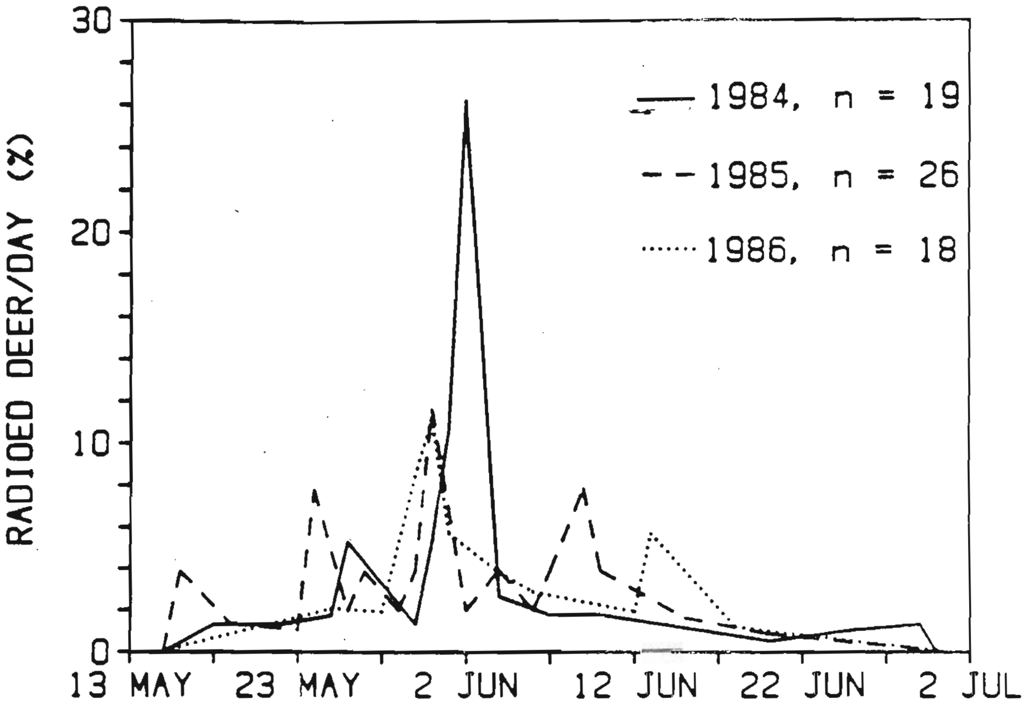

Figure 3-5. Proportion of radioed deer per day crossing the Sierra crest on spring migration, beginning 15 May of each year, 1984 through 1986, Inyo and Mono Counties, Calif.

tain. Despite these differences in snowfall and consequent snowpack at higher elevations, no differences in the timing of spring migration were evident. The winter of 1986-7 had snowfall of only 246 cm, one-fourth of that of the previous year. Although the sample size is small, the mean date that 3 radioed males and 2 radioed females crossed the crest in the spring of 1987 was the same as the previous year, 2 June. Thus, the amount of snow on the ground did not influence the timing of the migration over the Sierra crest in the spring.

As with the timing of leaving the winter range, the temporal uniformity over years in crossing the Sierra crest in the spring masked the behavior of individuals. From 1985 to 1987, individually telemetered deer varied crossing date by as much as 3 weeks later, and 2 weeks earlier, than in the previous year (Table 3-2).

The passes over the Sierra crest used by 27 of the 29 deer captured on the winter range and summering west of the crest were determined (Table 3-3). The passes used by 2 deer were unknown. I excluded animals captured on spring ranges near Mammoth Lakes in this analysis, because they constituted a sample already biased toward use of the more northerly routes. The most frequently used routes, accounting for half of the radioed sample, were Piute and Solitude/Duck passes. The latter route traverses 2 passes:

Table 3-2. Differences in number of days in the timing of migration by radioed mule deer over the crest of the Sierra Nevada, Inyo and Mono Counties, Calif., during spring in consecutive years, 1985-87. Positive numbers mean that movement was later than the previous year; negative numbers mean that the movement was earlier. A blank means that the animal was not radioed that or the previous year.

		Year		
Sex	Animal Number	1985	1986	1987
Male	71	3	2	
	121	-1		
	139	6	7	-7
	51		1	
	402		2	10
Female	11	8		
	129	0	4	
	341	-3	8	-9
	238	-5	-2	
	245	-14	-3	
	424	-14	9	
	330	-16	14	
	350		1	
	375		-3	
	391		1	6
	31		4	7
	211		8	
	392		1	
	270		-6	
	462		-1	
	472		21	

Table 3-3. Passes used by radio-collared mule deer from the Buttermilk and Sherwin Grade winter ranges to cross the Sierra Nevada, Inyo and Mono Counties, Calif., the number of radioed deer using them, and the major drainages used by the deer in summer.

Pass	Number of radioed deer	Summer range drainages
Bishop	1	Middle Fork Kings River
Lamarck	1	North Fork Kings River
Piute	7	South Fork San Joaquin River
Hopkins	4	Mono Creek
Solitude/ Duck	7 26%	Fish Creek, Mono Creek, S. Fk. San Joaquin, N. Fk. Kings
Mammoth	2 7%	Middle Fork San Joaquin
San Joaquin	5 19%	Middle Fork San Joaquin
Total	27	

[illegible] 3500

1450 North
305 Mont
1645 San Joaquin

26
7
19
52%

59% BM North 3000
88% SG North 2500

1770
2200
3970

gSolitude Pass crosses a spur ridge of the Sierra Nevada at the southern boundary of the town of Mammoth Lakes, and provides access to Duck Pass at the Sierra crest some 5 km farther. Next in importance were Hopkins Pass and San Joaquin Ridge. Bishop and Mammoth Passes, and Lamarck Col, were used by the fewest radioed animals.

Major drainages used for summering by deer that crossed these passes are indicated in Table 3-3. The deer moving over Solitude/Duck Pass summered over a larger area of the western Sierra than did deer using any other of the passes. Some of the deer using this pass traveled as far as the South Fork of the Kings River, near Florence Lake, and the North Fork of the Kings River, northwest of Courtright Reservoir. As well as traveling up to 50 km airline distance from Duck Pass, these deer traversed 3 or 4 major drainages to reach summer ranges after crossing the Sierra crest. The most complex route recorded crossed Solitude and Duck Passes into the Fish Creek drainage, then probably crossed Silver Pass into the Mono Creek drainage, continued down Mono Creek south of Lake Thomas A. Edison, crossed the South Fork of the San Joaquin River, and continued over Kaiser Ridge into the North Fork of the Kings River.

Of the 9 does captured on the spring range that reached summer areas, 6 used Solitude and Duck Passes to reach west side summer ranges, 2 had summer ranges on the reach west side summer ranges, 2 had summer ranges on the east side, and 1 summered on Mammoth Pass.

Summer Locations

Of the 32 deer captured on the BM and SG winter ranges that reached summer ranges, 28 (87.5%) crossed the Sierra crest and summered on the west side. The summer range locations of these deer, plus those of deer captured on the spring range, extended from the headwaters of the Middle Fork of the San Joaquin River south throughout the upper San Joaquin drainage above about 2134 m into the North and Middle Forks of the Kings River (Figure 3-6). Two males and 4 females summered on the east side of the Sierra, from Mammoth Pass on the north to the North Fork of Bishop Creek on the south. Thus, an area nearly 100 km by 25 km, or about 2500 sq km, served as summer range for deer from the BM and SG herds.

Of the 26 deer that summered on the west side of the crest that were visited on the ground (Chapter 4), 21 (81%) migrated north and 5 (19%) migrated south from the winter range. The summer range elevations of those moving south averaged 437 m higher than that of those moving north (3201 m vs. 2764 m; $t = 2.48$, $P = 0.02$).

Summer Range Fidelity

The distances between the summer ranges of deer located in consecutive years averaged 0.74 km (range 0.16-4

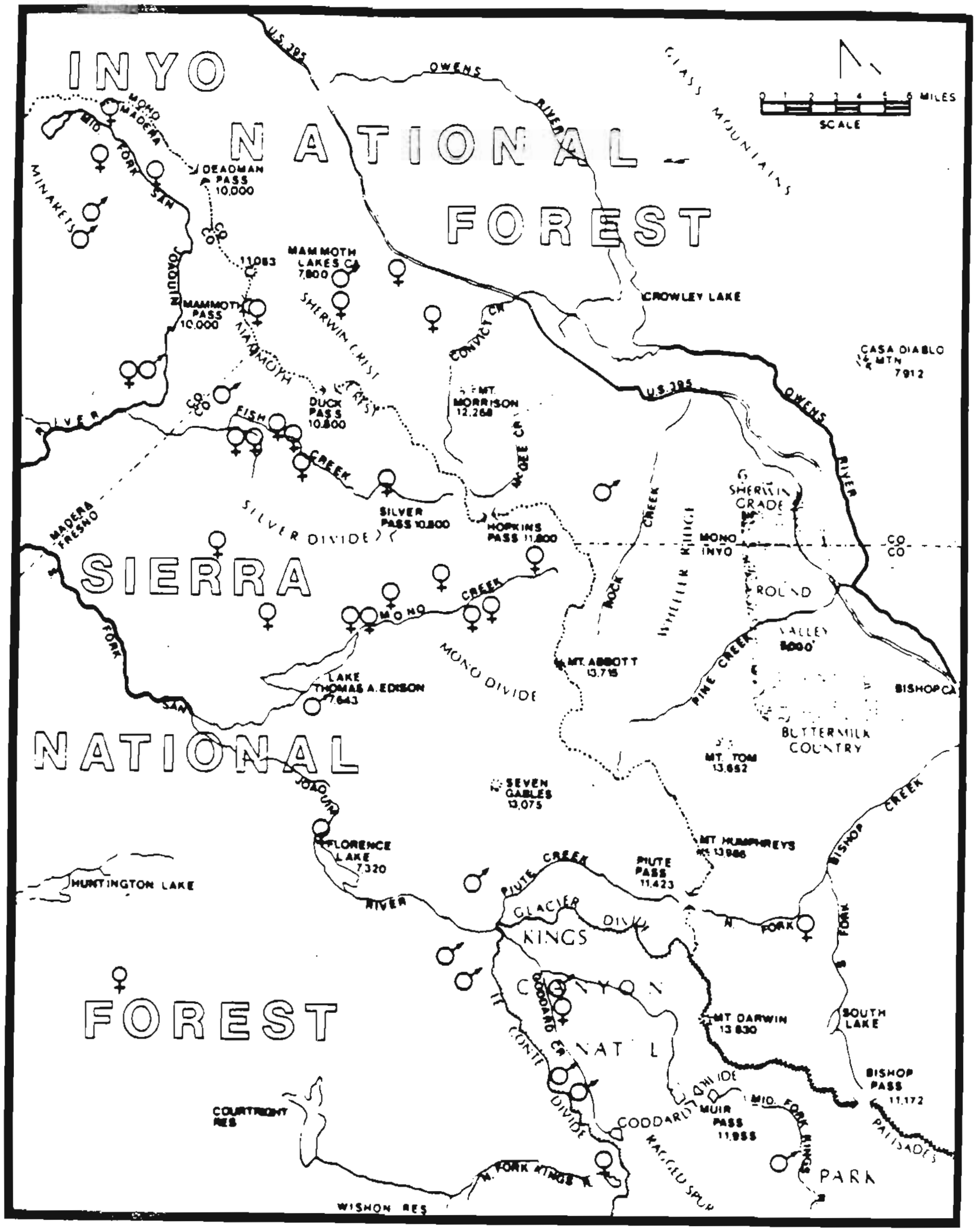

Figure 3-6. Summer range locations of radioed mule deer from the Buttermilk and Sherwin Grade winter ranges (shaded), Inyo, Mono, Fresno and Madera Counties, Calif., indicated by sex, 1984 through 1987. The Sierra crest is shown as a dotted line from upper left to lower right; major passes are indicated as breaks in the line. Elevations are in feet.

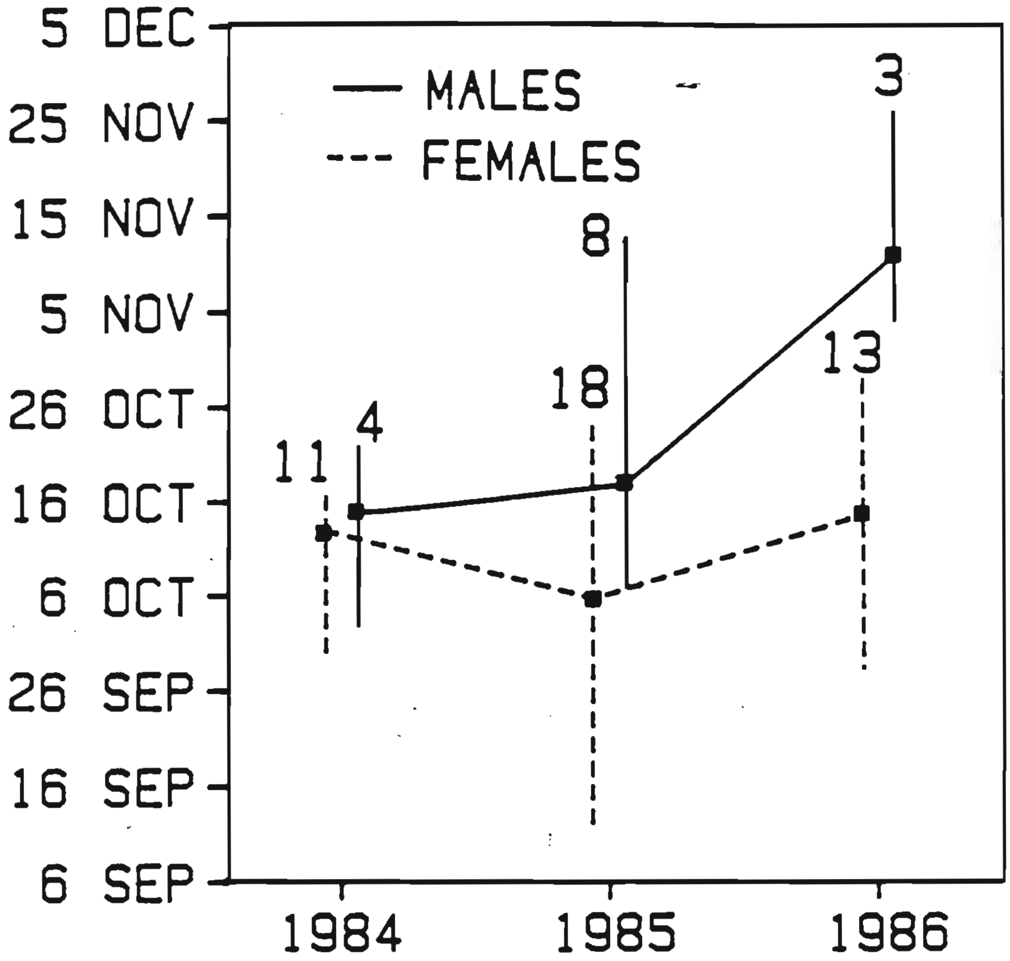

Figure 3-7. Timing of migration of radioed mule deer over the crest of the Sierra Nevada in fall of 1984 through 1986, Inyo and Mono Counties, Calif. Vertical lines indicate the earliest, mean, and latest dates that radioed deer crossed the crest in each year, by sex. Numbers of radioed deer in each sample are shown above the vertical lines.

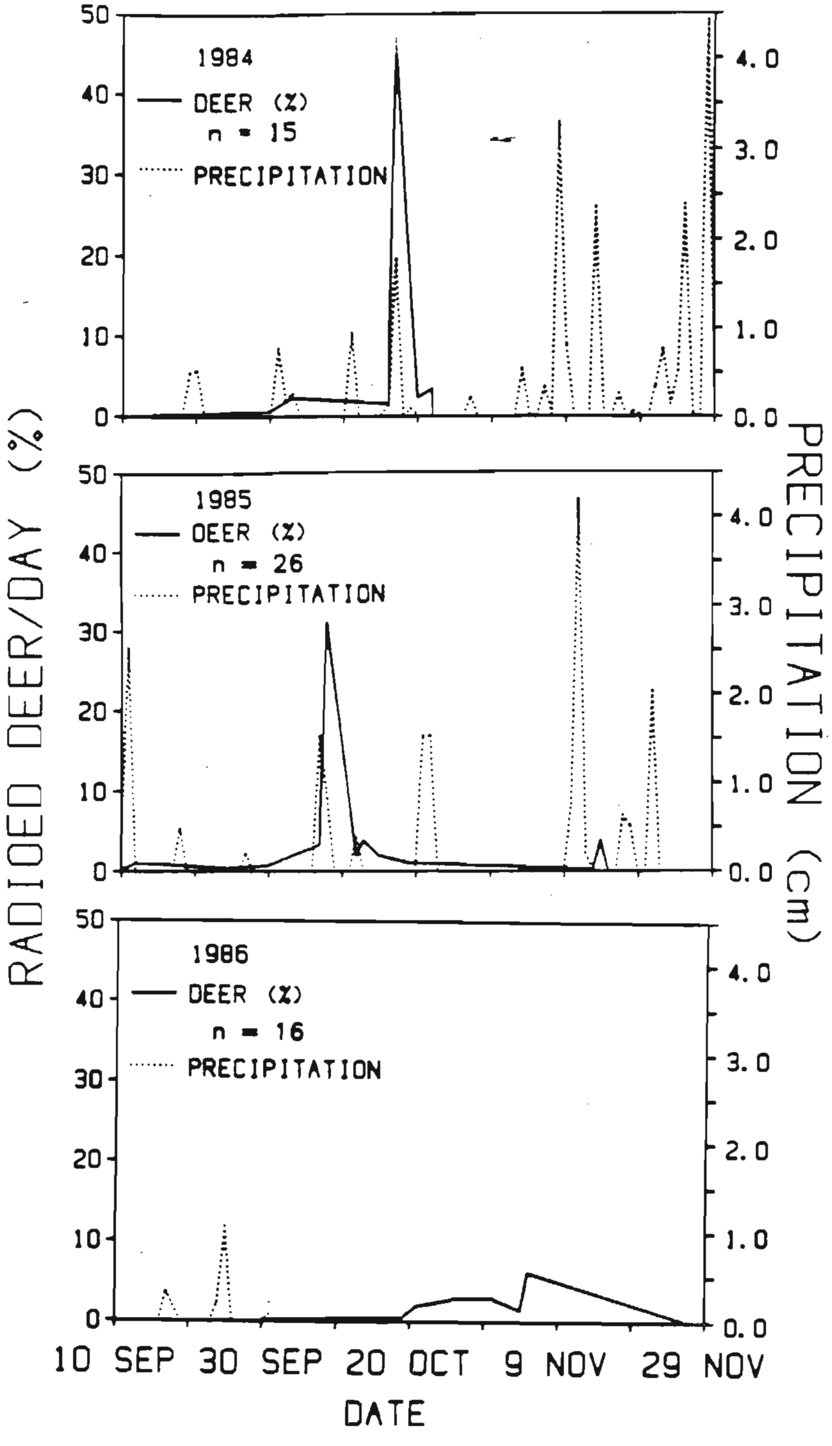

Figure 3-8. Percent of radioed mule deer per day crossing the Sierra crest, and daily precipitation, during the fall migration in 1984 (top), 1985 (middle), and 1986 (bottom), Mono and Inyo Counties, Calif.

tually no snow at the recording station did not trigger movement. In 1985, a storm on 11 September resulting in about 2.5 cm of precipitation and 35 cm of snow at 2400 m resulted in little movement. Following a storm on 7 October 1985, 14 of 26 (54%) radioed deer crossed the crest. The rest appeared gradually through 13 November, when the last radioed animal migrated over the crest subsequent to a major winter storm. In 1986 there were no major storms. The migration was gradual, unpunctuated by any rapid, mass movements, and occurred later than in previous years. In no case, however, did a living individual fail to return to the winter range.

In all years, the mean date for radioed males crossing the crest during fall migration was later than that for females, but the magnitude of the differences varied among years (Figures 3-7 and 3-8). With the storm on 17 October 1984, males migrated an average of 1 day later than females; in the absence of storms in 1986, males averaged 27 days later than females. Thus, the statistical interaction of sex and year in the timing of fall migration was in reality an interaction of sex and weather.

The rank correlations of the timing of the fall migration were not significant between 1984 and 1985 ($r_s = 0.14$, $n = 9$, $P > 0.5$) or between 1985 and 1986 ($r_s = 0.02$, $n = 16$, $P > 0.5$). As with the timing of migration off the winter range and over the crest in spring, the timing of crossing the crest in the fall varied among individuals over years (Table 3-4). No use of fall holding areas (Bertram and Rempel 1977) was observed. Deer typically moved directly to the winter range. An exception was one radioed male that, after crossing the crest back from his west side summer range in the fall of 1986, remained at about 3100 m on the slope of Basin Mountain, about 7 km south of and 1000 m above the winter range. He was on the winter range in early January the day after a snowstorm.

DISCUSSION

Garrott et al. (1987) found that a female mule deer in northwest Colorado varied the timing of spring migration by as much as 1 month in different years. They attributed these differences among years to severity of winters and consequent energetic demands on deer. They hypothesized that after a severe winter, deer are in poor condition and need more time to reverse their negative energy balance before initiating migration. After milder winters, condition is regained faster and migration occurs earlier. Bertram and Rempel (1977) reported that deer on the west side of the Sierra Nevada varied the timing of their spring migration by 2 weeks, and attributed this to differences in plant phenology.

Table 3-4 Differences in number of days in the timing of migration by radioed mule deer over the crest of the Sierra Nevada, Inyo and Mono Counties, Calif., during fall in consecutive years, 1985-86. Positive numbers mean that movement was later than the previous year; negative numbers mean that movement was earlier. A blank means that the animal was not radioed that or the previous year.

Sex	Animal Number	Year 1985	 1986
Males	71	-9	
	121	4	
	139	22	3
	51		17
	402		-8
Females	11	-10	
	129	-9	23
	341		-8
	238	15	12
	245	-9	13
	424	-9	22
	330	-22	9
	350		-2
	375		11
	391		1
	31		-3
	211		10
	392		1
	270		20
	462		17

In the present study, although individuals differed in the timing of their migratory movements over years, I found no evidence that the overall timing or pattern of mule deer migration from the winter range differed among years (Figures 3-1 and 3-2). Furthermore, deer tended to migrate in the same relative sequence in 2 of the 3 periods. This similarity occurred despite the differences in animal condition and vegetation growth measured in these years (Chapter 6). One [redacted] be that the deer in this study [redacted]. Even in 1986, after a winter of very heavy snowfall, deer were on the holding area in the hundreds as soon as road counts were begun (Figure 3-3). [redacted] As discussed in Chapter 5, the late winter/early spring diets expanded from largely *Artemisia* and *Purshia* to a mix including *Ceanothus* when deer reached the spring holding area. Another reason for this unvarying timing could be that deer [redacted]f. Average daytime high temperatures in Bishop in April are about 22 C, and in May are 27 C. Although mule deer can tolerate a wide range of ambient temperatures (Wallmo 1981*b*), patterns of preference among temperatures available to interns of preference among temperatures available to individuals are poorly known.

Adult males may leave the winter range somewhat later than females, an observation also made in western Colorado (Wright and Swift 1942). Given the nutritional demands of pregnancy, females may be under greater nutritional pressure than males for early dietary improvement and, thus, may tend to leave the winter range sooner for the better forage conditions of spring ranges.

Deer in this study made extensive use of holding areas in the spring (Figure 3-3), which may provide several benefits, including nutritional (Chapter 5) and thermal advantages, due to their higher elevation. Bertram and Rempel (1977) described a similar pattern of use of spring ranges in the western Sierra, and emphasized the importance of these holding areas in providing herbaceous forage. They also reported that spring holding areas typically occurred at the base of an abrupt elevation change, which was also true in this study.

This last point indicates that, especially in the eastern Sierra, spring holding areas may also provide a geographical benefit: they are among the last large areas of good habitat present in the spring before the deer cross the Sierra crest to reach their summer ranges. Crossing the crest in this part of the range involves travel of up to 10 km, over elevations of nearly 4000 m, before reaching more favorable habitat. Summer ranges of individual deer were as many as 40 km airline distance farther. The large aggregations of deer seen on the holding area near Mammoth Lakes (Figure 3-3) indicated that deer may "bunch up" in these last areas before continuing the migration. Extensive areas of similar habitat nearby are used only briefly as the deer travel through them on the way to the holding area. Garrott et al. (1987) did not mention use of holding areas by mule deer in Colorado, but did mention use of agricultural meadows in the spring. A relatively minor portion of the deer in this study used agricultural meadows. Another potentially important difference relates to the terrain. The Colorado situation did not present such extreme topography or sharply separated ecological conditions as were present in the eastern Sierra.

The timing and pattern of movement off the holding area and over the crest in spring were not different among years or between sexes (Figures 3-4 and 3-5), again suggesting that animal condition or vegetation did not greatly affect this movement. The passes animals used to reach summer ranges ranged from about 2800 m to 3960 m elevation. Snow was present on all passes in all years of study when the deer crossed, but the amounts differed greatly due to precipitation the previous winter. That these differences in snow depths did not affect the timing of migration was due largely to the fact that by spring the snow was consolidated, usually enabling deer to walk over the surface. They ultimately descended out of areas of snow to summer ranges.

In his early work on the BM deer, Jones (1954) stated that in 1951, deer began moving off the winter range about 1 April, and began crossing Piute Pass about 15 May. This agrees well with the present observations made more than 3 decades later. Hindered by the lack of marked or telemetered animals, however, he indicated that BM deer did not summer north of Pine Creek, and that about one-third of the population crossed to western Sierra summer ranges. My results indicate that most BM deer travel north of Pine Creek to summer ranges west of the Sierra crest. Jones (1954) mentioned the importance of Bishop Pass to migratory deer, and briefly referred to a minor migration route over Lamarck Col, but said nothing about Hopkins, Duck/Solitude, or Mammoth passes, or San Joaquin Ridge. All of these were important routes in this study. Archaeological evidence, including aboriginal ambush sites near Solitude Pass (U. S. For. Serv. Draft Environmental Impact Statement for the Sherwin Ski Area, Mono County, Calif. Inyo Natl. For., Bishop, Calif. 1988), and stories of long-time residents of the area support the conclusion that these patterns of the area support the conclusion that these patterns of migration were not recently established

That most (74%) of the radioed sample of deer migrated to the north from the winter range can be explained by the amount and accessibility of summer habitat in each direction. To the south, deer used Bishop (3633 m) and Piute (3482 m) passes, and Lamarck Col (3926 m), to reach summer ranges averaging 3201 m in elevation. The deer going north used the lower Hopkins (3463 m), Duck (3322 m) and Mammoth (2719 m) passes, as well as San Joaquin Ridge north of Mammoth Mountain (2774-3000 m), to reach summer ranges averaging 2764 m. The Middle Fork of the San Joaquin River and Fish and Mono creeks, those drainages used by most of the animals going north from the winter range, offer extensive areas at elevations appropriate for deer summer range. The South Fork of the San Joaquin River, Goddard Creek, and the North Fork of the Kings River, areas of summer ranges of those deer migrating south, are largely higher, rockier, and less vegetated than the areas to the north. Thus they support fewer deer.

The strong fidelity shown by individual deer to summer ranges is characteristic of mule deer (Ashcraft 1961, Robinette 1966, Gruell and Papez 1963, Jordan 1967, Bertram and Rempel 1977, Garrott et al. 1987). With few exceptions, both males and females returned to the same summer tions, both males and females returned to the same summer ranges for as many as 4 consecutive years.

Some of the summer range locations in this study overlapped those reported for *O. h. californicus* from the San Joaquin herd by Jordan (1967). This was particularly evident in the Fish Creek drainage, and in the Mono Creek drainage and around Lake Thomas A. Edison. Although there is some ecological overlap of the 2 subspecies on the summer range, they remain generally reproductively isolated because breeding occurs on the winter range, when they are separated by high mountains and usually by deep snow. The existence among deer in Round Valley of morphological characteristics such as tail pattern which overlap those of *O. h. californicus* (Kucera, unpubl. data), however, indicates that the reproductive isolation is not complete. Nellis et al. (1974) found evidence of interbreeding between *O. h. hemionus* and *O. h. columbianus* in northern Washington, based on tail and rump-patch morphology. These authors also related the distribution of the different morphologies to habitat characteristics. Habitat partitioning among eastern and western Sierra Nevada subspecies of deer on western Sierra summer ranges is unstudied.

The pattern of the fall migration is largely determined by fall weather, particularly snowstorms. Previous studies have discussed the importance of snow to fall migration (Russell 1932, Dixon 1934, Leopold et al. 1951, Richens 1967, Gilbert et al. 1970), but quantified documentation was often lacking. Bertram and Rempel (1977) stated that deer moved in anticipation of fall storms, but I found no evidence of this. Garrott et al. (1987) argued that in northwest Colorado, deer moved not because of snow, but to maximize the quality of their diets prior to winter. They did this in either of 2 ways: by migrating well ahead of snow to take advantage of agricultural areas, or by remaining on the summer range and taking advantage of the higher quality forage there until snow covered the vegetation, increased energetic costs of movement, or both.

Deer in this study did not make extensive use of fall holding areas, as Bertram and Rempel (1977) reported for western Sierra deer. This may be due largely to the fact that in this part of the Sierra Nevada, elevation changes are sufficiently extreme that appropriate areas are not available. In the presence of storms in 1984 and 1985, deer moved rapidly over the crest and directly back to the winter range in Round Valley. In the absence of a snowstorms in 1986, the movement was more protracted, yet no use of anything that could be called a holding area was observed, at least on the east side of the mountains. Because of the remote nature of most of the summer range west of the crest, no information is available regarding movements of animals just prior to crossing the crest. I could not tell if deer moved nearer the passes as fall progressed, or if they remained on their summer home ranges until migrating.

If, as Bertram and Rempel (1977) reported, fall holding areas occur immediately above a rapid drop in elevation and provide cover and forage, such combinations are not available for these deer. The only possibilities occur near the Sierra crest, where elevation restricts forage growth and assures severe weather, and immediately above the winter range at about 2130 m. The latter was not used; in years with storms, there was snow at this elevation, and in the open year, animals showed no delay in movement just above the winter range. Perhaps the proximity of the winter range made delay nearby unattractive.

The timing of the fall migration of females in the present study varied little among years (Figure 3-7), but did respond to snowfall (Figure 3-8). [redacted] tendency to move over the Sierra crest in early to mid-October, the specific timing influenced within narrow limits by snowfall. The pattern of fall migration was different in males; in the absence of significant snow, males delayed fall migration nearly 1 month (Figure 7). Granting that individuals of both sexes need to gain weight to survive the winter, why should there be differences in the timing of their fall movements? One reason is that females are likely to be in poorer condition than males, having been through pregnancy and lactation during the summer, and thus must return to the winter range sooner. This assumes that the vegetation on the summer range has deteriorated in quality below that available on the winter range. Additionally, females are with their fawns produced the previous summer. At 3 or 4 months of age, fawns are less able to negotiate the deep, loose snow produced by early storms. Males have had no such nutritional demands on them over the summer, and with larger body sizes and greater reserves, they may be less affected by lower diet quality.

Another important factor influencing sexual differences in the timing of fall migration is that males are hunted. There are at least 2 ways in which heavy hunting pressure on males could lead to later migration: they have learned to avoid the hunting season by delaying their migration, or only those males tending to migrate later survived, and those were the ones captured for this study. It is difficult to see how males could have learned to migrate later. I consider it more likely that selection for late migration probably has been more important than learning to delay migration. Most interactions with hunters are likely to be fatal, as evidenced by low buck ratios in these herds. As an illustration, 4 of the 5 radioed males that crossed the crest back to the east side in early October 1985 were killed by hunters, and the fifth was wounded. Only the 3 males that migrated after the regular hunting season survived unscathed. Therefore, males that tend to migrate later, for whatever reason, tended to survive. An investigation of sex differences in the timing of deer from an unhunted population would be necessary to test for the importance of hunting.

CHAPTER IV. SUMMER HABITATS

Little detail is known of the structural or floristic characteristics of summer habitats of mule deer (Odocoileus hemionus) in the Sierra Nevada. Early studies described summer habitats in general terms, and all were most concerned with the western Sierra subspecies, the California mule deer (O. h. californicus). Grinnell and Storer (1924:232) described the general altitudinal and seasonal distribution of deer in the Yosemite area, stating that during summer, most deer "were in the brush country of the higher mountains, in the Transition and Canadian life zones", and reported their highest record of deer as 3,230 m (10,600 ft). Russell (1932:19) described summer range of deer in Yosemite National Park as as the "Canadian and Hudsonian Zones (6200 feet to 10,500 feet"), and listed some of the more conspicuous plants of those areas. Dixon (1934) echoed these reports.

Leopold et al. (1951:48) also referred to life zones to describe summer ranges of California mule deer from the Jawbone/Clavey River area just north of Yosemite. These authors stated that the Transition and Lower Canadian zones ("6000 to 7500 feet") contained the highest summer deer densities. They also suggested that those Rocky Mountain mule deer (O. h. hemionus) from the east side of the

Sierra Nevada which summered on the west side did so generally at higher elevations than did the west side deer, although the summer ranges of the two did overlap. Jordan (1967) related relative deer densities on various sites in the San Joaquin River drainage to several physical characteristics such as elevation, slope, brush cover, etc., but in a qualitative manner.

More recent studies of deer in the Sierra Nevada (Schneegas and Franklin 1972, Bertram and Rempel 1977) have emphasized migration and movements rather than habitats _per se_. These studies also largely involved deer trapped on the summer range, thus precluding the possibility of making general statements about summer habitats, even if that had been the focus of the work.

None of these studies provided detailed, quantified data on summer range characteristics from a representative sample of deer. Doing this requires a sample of deer captured away from the summer range. In the only study which included individually marked deer captured on a winter range (Jordan 1967), the animals were marked with bells or other devices that did not allow certain relocation after capture. Recognizing this limitation, Jordan (1967:188) recommended the use of radio-telemetry to improve success in relocating marked deer on Sierra Nevada summer ranges.

Given the lack of specific data regarding summer range characteristics of deer in the Sierra Nevada, it is impossible to make conclusions regarding possible differences in summer habitats between the sexes. However, anecdotal reports of such differences exist in the literature. Both Russell (1932:19) and Dixon (1934:59) reported that males, particularly larger, older ones, typically summer at elevations higher than females, often near or above timberline. More recent studies using radio-telemetry have been hampered by the absence of males in the radioed sample. This often grew from the belief that collaring males was impossible due to the seasonal swelling of the necks (e. g., Garrott et al. 1987:635).

Spatial segregation or habitat differences between the sexes has been reported for mule deer in Utah (Robinette et. al 1977, King and Smith 1980), Montana (Mackie 1970), Arizona (Scarbrough 1985, Ordway and Krausman 1986), Oregon (Miller 1970) and elsewhere in California (Dasmann and Taber 1956, Bowyer 1984). Similar phenomena have been reported for white-tailed deer (O. virginianus) in Michigan (Hirth 1977, McCullough 1979), for red deer (Cervus elaphus) in Scotland (Clutton-Brock et al. 1982), and for moose (Alces alces) on Isle Royal, Michigan (Edwards 1983). These studies vary widely in the detail with which habitat differences were determined.

The objectives of the present study were to quantify the summer habitat characteristics of deer captured and radioed on a winter range on the east side of the Sierra Nevada, and to examine habitat characteristics for differences between the sexes.

METHODS

The summer ranges of deer were visited on the ground, after approximate locations were determined from the air (Chapter 3). An animal was observed over a period of up to 24 hours, and for the general area: (1) the percent slope was estimated; (2) the aspect was taken with a compass bearing or recorded from a topographic map; (3) distance to the nearest free water and human trail or road was estimated; and (4) the elevation was determined from a topographic map. A transect was run in a randomly chosen direction through what was judged to be the central or a representative part of the home range, beginning at a location determined by the investigator throwing a rock over his or her shoulder. Ground cover was assessed by 100 step-points (Evans and Love 1957) taken along the transect. At each point, the plant species hit was recorded. If no plant was hit, either bare ground (i.e., soil), rock, or litter was recorded, along with the closest plant. The number of hits on living plants, bare ground, rock, or litter per transect multiplied by 100 yielded the percent cover, bare ground, rock, or litter, respectively. At every 10th step-point: (1) the distance to nearest tree, shrub, and boulder ≥ 1 m^3 was measured; (2) the nearest species of tree and shrub were recorded; (3) the diameter at breast height (DBH) of the nearest tree was measured; and (4) percent canopy closure was estimated visually. Data were taken between 20 June and 7 September, 1984 and 1985.

Univariate *F* tests and linear discriminant function analysis (DFA) with stepwise inclusion of variables (Norusis 1988) were used to examine differences in habitat components between the sexes. Normal plots of untransformed variables were examined visually for departures from normality. Those that did not appear to meet the assumption of normality were transformed by several methods, and the transformations examined on normal probability plots. The transformation that yielded the most normal distribution was used in the analysis. Distance to water, trail or road, boulder, and the percent bare ground were transformed using the log transformation. Distance to shrub, and percents canopy, vegetative cover, rock, and litter were transformed with the square root transformation. The criterion for selection of variables in the DFA was maximization of Mahalonobis' distance between males and females, and only those variables significant at 0.05 (*F*-to-enter $\leq$ 0.05) were included. For this analysis, slope was converted into the following categories: 0-25, 26-50, 51-75, and $\geq$76%, numbered 1 through 4, respectively. The relatively small number of cases (7 males, 23 females) precluded splitting the data to derive the model with half and testing its classification success with the other half, as has been recommended (Morrison 1969, Williams 1983).

Aspect was converted into categories of 316-45, 46-135, 136-225, and 226-315 degrees. A chi-square goodness of fit test was used to test the hypothesis that the aspects of deer summer ranges were distributed randomly with respect to the 4 categories of compass direction. Small sample sizes precluded analysis by sex.

RESULTS

The summer ranges of 30 adult ($\geq$2 years old) deer (7 males, 23 females) fitted with radio-collars (Chapter 2) were described. Of these, all males and 16 females were captured on the winter range; 7 females were captured on the spring range. All males and 19 females summered on the west side of the Sierra Nevada; 4 females summered on the east side.

Univariate *F* tests on transformed variables indicated significant differences between male and female summer ranges in slope, elevation, distance to water, and percent litter ground cover (Table 4-1). The mean summer range elevation of males, 3169 m, was about 400 m higher than

Table 4-1. Descriptive statistics of summer habitat variables for male and female mule deer, and univariate F statistics of differences between the sexes, from the Sierra Nevada, California.

	Males (N = 7)		Females (N = 23)		Difference		
Variable	Mean	SE	Mean	SE		F	p
Elevation (m)	3168.86	160.82	2740.09	58.32	384.7	8.293	0.008
Distance to water (m)	46.14	34.13	212.96	39.21	-166.8	6.644	0.016
Slope category	3.57	0.50	2.26	0.22	1.5	6.428	0.017
Percent litter	21.14	7.91	41.13	3.63	-20.0	5.296	0.029
Percent canopy	13.14	5.00	31.17	4.31		3.666	0.066
Percent rock	30.71	6.44	18.48	2.62		3.594	0.068
DBH (cm)	17.84	2.65	28.37	2.58		3.541	0.070
Distance to trail (m)	1124.14	414.86	780.48	208.54		1.678	0.206
Percent vegetative cover	35.86	3.95	26.70	3.80		1.238	0.275
Percent bare ground	10.86	2.35	13.65	1.82		0.483	0.493
Distance to shrub (m)	5.06	1.40	4.31	0.75		0.475	0.496
Distance to boulder (m)	14.10	4.84	11.95	1.91		0.235	0.632
Aspect category	2.28	0.36	2.30	0.22		0.001	0.970

Table 4-2. Important variables distinguishing male and female mule deer summer habitats in the Sierra Nevada, California, 1984 and 1985, derived from linear discriminant anaysis. All variables are significant at the 0.05 level.

Variable	Standardized Canonical Coefficient	Interpretation
Elevation	0.624	Males summer at higher elevations
Distance to water	-0.605	Male summer ranges are nearer water
Slope category	0.575	Male summer ranges are steeper

that of females. [redacted] than females, [redacted] There was also a tendency (0.05 < $\underline{P}$ < 0.10) [redacted]

The linear discriminant model included 3 variables with Wilks' Lambda = 0.55 (R^2 = 0.45, $\underline{P}$ = 0.001) (Table 4-2). Group covariance matrices were equal (Box's $\underline{M}$ = 12.454, $\underline{P}$ = 0.13). With prior probabilities for males and females specified as equal to the proportion of each in the sample, i.e., males = 0.23 and females = 0.77, an overall classification success of 93.3% was achieved. Of the 7 males, 5 (71.4%) were correctly classified; all of the 23 females were correctly classified. Using prior probabilities approximating the sex ratio of adults in the population, i. e., males = 0.10 and females = 0.90, overall classification success was 90%. The classification success of males decreased to 4 of 7 (57.1%) and classification success of females remained 100%.

The standardized discriminant function coefficients indicated that [redacted] (Table 4-2). All of these coefficients were of comparable magnitude, indicating comparable importance of each variable to the discrimination, with elevation slightly more importo the discrimination, with elevation slightly more important than the others.

I could not reject the hypothesis that the summer ranges of radioed deer were distributed randomly with respect to category of compass direction (chi-square = 2.26, d.f. = 3, $\underline{P} > 0.25$).

The vegetative cover on the summer ranges was diverse. A total of 162 taxa were recorded on the 30 transects (Table 4-3; Appendix 1). Differences in plant species composition were evident between the eastern and western Sierra locations (e.g., in presence of moss), but in general, no clear patterns were apparent. The extreme diversity no doubt resulted from the large and diverse area covered by the transects. Of the 162 taxa identified, 129 (80%) were found on <4 transects (Appendix I).

DISCUSSION

In the linear discriminant analysis of male and female summer range characteristics, with the prior probabilities of group membership specified as approximately equal to the adult sex ratio in the population (10 males:90 females), 4 of the 7 males were classified correctly. From a strictly descriptive point of view (Williams 1983), this is an improvement over what one would get by chance alone, even given the upward bias inherent in the procedure (Morrison 1969). For this analysis, however, the ability to classify

Table 4-3. Plant species recorded on step-point transects of 100 points on summer ranges of 30 mule deer in the Sierra Nevada, California, 1984-85. Total hits recorded on each plant are presented by east side (n =4) and west side (n = 26) transects.

Plant Group/family	Species	Total hits		
		East	West	combined
MOSS:	Moss (unk.)	0	69	69
FERN:	*Cystopteris fragilis*	0	1	1
	Fern (unid.)	0	6	6
	Cryptogramma acrostichoides	0	3	3
	Onychium densum	0	1	1
	Pellaea Bridgesii	0	1	1
	Pteridium aquilinum	0	5	5
CONIFER:	*Abies concolor*	0	1	1
	A. magnifica	0	41	41
	Juniperus occidentalis	1	2	3
	Pinus monticola	0	3	3
	P. Murrayana	0	15	15
	P. albicaulis	2	11	13
	P. ponderosa	0	1	1
	Tsuga Mertensiana	0	26	2
Amaryllidaceae:				
	Allium obtusum	1	0	1
	A. validum	0	20	2
Cypraceae:				
	Cyperaceae (unk.)	0	1	1
	Carex sp.	3	43	46
	C. Rossii	5	0	5
Gramineae:				
	Grass (unid.)	92	764	856
	Oryzopsis hymenoides	3	0	3
	O. sp.	0	71	71
Juncaceae:				
	Juncus Nevadensis	0	10	10
Liliaceae:				
	Smilacina stellata	0	2	2
	Veratrum Californicum	0	8	8
Orchidaceae:				
	Habenaria dilata	0	2	2
	Dicot (unk)	3	0	3
Aceraceae:				
	Acer glabrum	0	1	1

Table 4-3. Continued.

Compositae:			
Composite (unk.)	0	4	4
Achillea lanulosa	0	9	9
Antennaria rosea	0	37	37
A. ummbrinella	0	6	6
Artemesia sp.	0	14	14
A. ludoviciana	0	95	95
A. tridentata	36	37	73
Aster alpigenus	0	8	8
Chrysopsis Breweri	0	2	29
Chrysothamnus sp.	3	0	3
C. nauseosus	2	0	2
Cirsium sp.	0	4	4
C. Andersonii	0	13	13
Erigeron sp.	0	22	22
E. Breweri	0	7	7
E. compositus	4	0	4
E. linearis	0	1	1
Eupatorium ocidentale	0	1	1
Haplopappus suffruticosus	0	2	2
Helenium Bigelovii	0	1	1
Hieracium gracile	0	8	8
H. horridium	27	1	28
Senecio sp.	0	13	13
S. aronicoides	0	9	9
S. Clarkianus	0	4	4
S. triangularis	0	5	5
Solodago Canadensis	0	4	4
Tetradymia sp.	0	6	6
T. canescens	1	0	1
Anaphalis margaritacea	0	4	4
Taraxacum officinale	0	6	6
Betulaceae:			
Alnus tenuifolia	0	34	34
Apocynaceae:			
Apocynum pumilum	0	1	1
Cruciferae:			
Arabis sp.	16	4	20
A. Lyallii	0	4	4
A. platysperma	0	13	13
Erysimum perenne	2	1	3
Streptanthus cordatus	0	1	1
S. tortuosus	6	1	7

Table 4-3. Continued.

Boraginaceae:			
Cryptantha sp.	1	0	1
Hackelia sp.	0	1	1
H. nervosa	0	7	7
Polygonaceae:			
Eriogonum sp.	4	28	32
E. incanum	4	2	6
E. microthecum	4	12	16
Oxyria digyna	0	4	4
Rumex paucifolia	0	4	4
Euphorbiaceae:			
Euphorbia sp.	0	1	1
Rubiaceae:			
Gallium aparine	0	4	4
Epilobium angustifolm	0	13	13
E. Oregonense	0	1	1
E. Pringleanum	0	2	2
Gayophytum sp.	1	0	1
Umbelliferae:			
Heradeum lanatum	0	2	2
Ligusticum Grayi	0	1	1
Osmorhiza occidentalis	0	14	14
Perideridia Bolanderi	0	8	8
Sphenosciadium capitellatum	0	1	1
Saxifragaceae:			
Heuchera rubesens	3	4	7
Ribes sp.	0	22	22
R. cereum	5	7	12
R. lasianthum	0	5	5
R. montigenum	0	49	49
R. Roezlii	0	3	3
R. velutinum	0	3	3
Leguminoseae:			
Lotus crassifolius	0	2	2
Lupinus sp.	0	9	9
L. Culbertsonii	0	12	12
L. latifolius	0	5	5
L. Lobbii	0	13	13
L. Lyallii	0	7	7
Vicia Californica	0	1	1
Primulaceae:			
Dodecatheon alpinum	0	4	4
D. Jeffreyi	0	1	1
D. redolens	0	2	2

Table 4-3. Continued.

Ericaceae:			
Arctostaphylos mariposa	0	48	48
A. patula	0	43	43
A. Nevadensis	0	41	41
Cassiope Mertensiana	0	1	1
Ledum glandulosum	0	14	14
Phyllodoce Breweri	0	156	156
Vaccinium nivictum	0	14	14
V. occidentale	0	24	24
V. parvifolium	0	6	6
Fagaceae:			
Castanopsis sempervirens	0	12	12
Quercus vaccinifolia	0	79	79
Q. dumosa	0	3	3
Scrophulariaceae:			
Castilleja sp.	0	6	6
C. Breweri	0	1	1
C. Applegatei	0	1	1
Mimulus sp.	0	5	5
M. nasutus	0	2	2
Pedicularis semibarbata	0	11	11
Penstemon sp.	1	19	20
P. Bridgesii	0	4	4
P. Davidsonii	13	0	13
P. heterodoxus	0	1	1
P. Newberryi	0	54	54
P. Rothrockii	0	7	7
Collinsia Torreyi	0	4	4
Rhamnaceae:			
Ceanothus cordulatus	0	6	6
C. velutinus	35	0	35
Rosaceae:			
Amelanchier pallida	0	2	2
Cercocarpus ledifolius	11	0	11
Fragaria platypetala	0	35	35
Holodiscus Boursieri	1	8	9
H. microphyllus	3	5	8
Petrophytum caespitosum	0	3	3
Potentilla sp.	0	1	1
P. Drummondii	0	1	1
Prunus sp.	0	4	4
P. emarginata	2	11	13
Purshia tridentata	12	0	12

Table 4-3. Continued.

Labiatae:				
	Monardella odoratissima	15	2	17
Hydrophyllaceae:				
	Phacelia hastata	3	0	3
	P. mutabilis	0	1	1
Polemoniaceae:				
	Phlox sp.	0	24	24
	P. diffusa	0	3	3
	P. Stansburyi	20	1	21
Salicaceae:				
	Populus tremuloides	12	3	15
	Salix sp.	0	52	52
	Salix orestra	0	3	3
Caprifoliaceae:				
	Sambucus caerulea	0	1	1
	Symphoricarpos sp.	0	2	2
	S. Parishii	0	17	17
	S. vaccinioides	26	26	52
	Lonicera conjugalis	0	4	4
Crassulaceae:				
	Sedum obtusatum	0	8	8
Ranunculaceae:				
	Thalictrum sp.	0	11	11
	T. Fendleri	0	15	15
	Aquilegia formosa	0	1	1
	Aconitum columbianum	0	5	5
Violaceae:				
	Viola purpurea	8	0	8
Unknown hits		13	122	134
Unknown species		5	13	18
Total	162	405	2703	3108

individuals is less important than establishing the fact that summer habitats of male and female mule deer do differ in the Sierra Nevada. Both univariate and multivariate analyses indicated significant differences between the sexes in habitat components. Elevation was the most important variable distinguishing the habitats, with distance to water and slope category of almost equal importance. This gives quantitative support to the reports by Russell (1932) and Dixon (1934) that larger, older bucks summer at higher elevations than do females. I also found that bucks were nearer to water, and on steeper slopes, than were does.

Even recognizing the exploratory rather than confirmatory nature of this study (Tukey 1980), these statistical results indicate the existence of a biological phenomenon that should be explored. Darwin (1873) discussed the differences in factors that contribute to reproductive success in males and females. These have been explored and greatly refined in more recent years. In mammals, the costs of reproduction to males are much less than the costs to females, and the two sexes have different "strategies" of maximizing reproductive success, i.e., the number of offspring an individual produces in its lifetime (Fisher 1958, Williams 1966, Trivers 1972, Wilson 1975). Male reproductive success is determined by the ability to gain access to and breed with females. Female reproductive success is determined by the number of offspring a female can bear and raise. These considerations have important consequences on body size, physiology and behavior (Glucksman 1974, Alexander et al. 1979, Clutton-Brock et al. 1982). In ungulates, the different strategies of each sex for maximizing individual reproductive success could be reflected in habitat differences.

In the Sierra Nevada, summer is the period of the most abundant nutritional resources. During summer, male and female deer have different constraints and responsibilities regarding reproduction. Females are bearing and rearing young, tasks of great nutritional demands (Pond 1977, Robbins 1983). Males, in contrast, need to grow in body and antler size to compete for estrus females during rut (Kucera 1978, Clutton-Brock et al., 1979). Both sexes must avoid predators, and females also must avoid losing offspring to predators. That females on average are at lower elevations and on gentler slopes than are males, and are possibly in vegetatively more dense habitats (Table 4-1), could result from their high summer nutritional requirements, a need for more concealment cover from predators, or both. The pattern of female mule deer selecting lower areas of more dense cover relative to areas occupied by males was also described by King and Smith (1980) in a mountainous area of Utah. That it is not elevation or relative position <u>per se</u> that is important in separating males and females is apparent from the work by Scarbrough (1985) and Ordway and Krausman (1986) in desert mountain ranges in Arizona. There, males usually were below females, and often in flat areas away from the mountainous areas preferred by females. This suggests that concealment may be the important factor for females.

Several authors have described habitats used by male ungulates as being of lower quality than those of females (Charles et al. 1977, Geist and Petocz 1977, Watson and Staines 1978, McCullough 1979, King and Smith 1980, Staines et al. 1982, Bowyer 1984). Quality in this context usually meant forage quality, and it has seemed paradoxical that males would abandon areas of good forage for inferior ones. McCullough (1979) suggested that the relationship between animal density and resources in the more marginal areas may resolve this paradox. Following this reasoning, Bowyer (1984) noted to the lower animal density in the habitats of male deer in southern California, and argued that forage per individual deer did not differ in the habitats used by males and females. No studies have yet satisfactorily addressed the hypothesis that male deer consume a diet of lower quality than females, although red deer stags did have lower rumen nitrogen levels in the winter than did hinds (Clutton-Brock et al. 1982). Beier (1987) reported that female white-tailed deer had higher fecal nitrogen than than did males, but the interpretation of fecal nitrogen remains problematic (Chapter 5).

Many of these studies have looked at habitat or dietary differences between the sexes during the winter, or during the period of seasonally least abundant resources. Regarding summer deer habitat in the Sierra Nevada, anecdotal observations support the contention that the higher elevation areas occupied by males are not necessarily inferior to those of the lower elevation areas of females in providing nutritional resources. For example, in late August and September 1984, near the end of the growing season and during the period of lowest moisture availability, fecal pellets collected from male deer at 3170 m were moist and soft, resembling those found in the spring when diets were composed of succulent new growth. These deer had found an area with a series of terraces with little springs and moist soil that provided succulent herbaceous vegetation into the fall.

At least in years of good snowfall, such moist areas may be common at higher elevations. Wehausen (1980) discussed the influence of snowpack on the length of the growing season in the Sierra Nevada. He reported that the timing of the yellowing of high elevation meadows in the fall in the Sierra Nevada varied with snowpack the previous winter, and suggested that a large snowpack extends the growing season for plants that are dependent on snowmelt both by providing water and by differential timing of melting of snow over various patches of vegetation. Although these comments concerned habitats used by mountain sheep (Ovis canadensis), they are relevant to summer areas used by mule deer at higher elevations. Male deer, unencumbered by fawns, may be able to take advantage of long-lasting, high quality forage in open, dispersed, high elevation areas.

Predation is another factor implicated in habitat differences between the sexes in ungulates (McCullough 1979, King and Smith 1980). The reasoning is that female deer and their young are much more vulnerable to predation than are the larger males, and thus females are restricted to habitats which facilitate the avoidance of predators. This hiding strategy (Lent 1974), however, may involve a tradeoff with other resources, particularly forage. Edwards (1983) documented the impacts on the diets of female moose caused by their need to move in the spring to avoid areas areas with wolves (Canis lupus). Cow moose on Isle Royale moved to small islands offshore, where wolves did not go, prior to parturition. At that time, the vegetation on these islands was phenologically behind that on the main island due to local climatic factors. Male moose remained on the the main island and occupied areas with higher quality forage. Thus, due to a need to avoid wolves, females occupied areas of lower forage quality than did males in the summer.

I suggest that predator avoidance may be a more important factor in habitat differences between summering male and female mule deer in the Sierra Nevada than are nutritional considerations. It may be that females are trading off some nutritional rewards for the additional protection from predators offered by lower elevation habitats with denser vegetation. This hypothesis could be tested by a study comparing male and female diets through the summer; however, any such work would need to control for possible effects of animal density.

CHAPTER V. DIETS AND NUTRITION

Body size and morphology greatly influence the types of vegetation in the herbivore diet (Janis 1976, Parra 1978, Hanley 1982, Demment and Van Soest 1985). In his classification of cervids by morphophysiological feeding type, Hofmann (1985) placed deer of the genus Odocoileus among the concentrate feeders. These animals, typically of relatively small size, are adapted to a diet that selects for highly digestible plant parts, i.e., those with a high cell contents/cell wall ratio. Hobbs et al. (1983) found that mule deer (O. h. hemionus) fit Hoffman's category of concentrate selectors, if added to them was the characteristic of rapid passage time of ingesta.

High quality forage contains the greatest soluble carbohydrates and protein, the least lignin, and is the type most rare in the environment (Demment and Van Soest 1985). Although energy requirements of mammals are scaled approximately to the 0.75 power of body weight (Kleiber 1975), the relatively large body size of Odocoileus (relative to, for example, Capreolus) requires larger absolute amounts of energy and nutrients. This, combined with highly seasonal environments in many parts of their range, in which high quality forage is seasonally scarce, results in periods of nutritional stress, during which energy is derived from stored fat and a maintenance diet. During winter, the adequacy of the diet and the amount of stored fat relative to energy demands, which are largely determined by length and severity of the winter, determine the survival of individuals and influence reproduction.

Diets of deer of the genus *Odocoileus* in North America have been studied extensively (see reviews in Klein 1970, Wallmo 1981*a*, and Halls 1984). These deer are able to exist on a wide variety of forage species. Kufeld et al. (1973) listed more than 700 plants reported in the diets of Rocky Mountain mule deer (*O. h. hemionus*) throughout their range. Diets vary regionally, locally, and seasonally, but some overall patterns are evident. In the Great Basin region, big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*) have long been recognized as major components of deer diets (Cliff 1939, Smith 1950, Hoskins and Dalke 1955, Richens 1967). Wallmo and Regelin (1981) reported that in the review by Kufeld et al. (1973), the second and fifth most frequently cited components of deer diets were big sagebrush and antelope bitterbrush; both species were common in the present study area (Chapter 2). Leach (1956) demonstrated the importance of both *Artemisia* and *Purshia* in diets of deer throughout the Great Basin area of California. Dasmann and Blaisdell (1954) related fawn production and survival to intensity of browsing on *Purshia* in northeastern California and northwestern Nevada, and suggested that *Purshia* can serve as an indicator species in deer management programs. Burrell (1982) reported that bitterbrush was highly preferred by mule deer in eastern Washington. However, its decline in the diet, both across sites as bitterbrush density declined and within sites as winter progressed, did not affect herd survival because of the presence of alternative food, primarily buckwheat (*Eriogonum* spp.).

In addition to knowing species composition of herbivore diets, investigators have wanted to know the quality of the diet. Diet quality has proved to be an elusive concept, involving nutrient concentration and accessability, and presence of compounds such as attractants and toxins (Crawley 1983). Given the complexities of the issue, perhaps the lack of a widely recognized measure is not surprising. The ultimate measure of food quality is herbivore fitness (Crawley 1983). A diet that produces a large, positive value of *r*, or rate of population growth, is of high quality. One that produces a small or slightly negative *r* is of low quality, and one that produces a large, negative *r* is toxic (Crawley 1983).

The difficulty of measuring *r* in wild vertebrate populations has lead to attempts to develop other ways of measuring diet quality. One approach has involved attempting to identify a chemical constituent of feces that is correlated with diet quality. However, the search for a fecal indicator of dietary quality that is both reliable and practical for field use has not yet produced consensus. Fecal nitrogen (FN) has been proposed as an appropriate index of diet quality because it has been shown to be positively correlated with such measures as forage intake, dietary protein and digestibility, and weight changes (reviewed in Leslie and Starkey 1985 and Beier 1987). Objections to FN have been based on the fact that secondary plant metabolites such as tannins can bind with dietary protein, and thus produce elevated FN in diets that otherwise would be considered of low quality (Mould and Robbins 1981, Holechek et al. 1982, Robbins et al. 1987, Hobbs 1987, but see Leslie and Starkey 1987).

Another chemical that has been proposed as an indicator of dietary quality is diaminopimelic acid (DAPA) (Nelson et al. 1982). This is an amino acid residue of rumen bacterial fermentation that is not absorbed by the ruminant, and passes out in the feces. Because it is correlated with diet digestible energy, it may be an appropriate indicator of the adequacy of an herbivore's diet.

The objectives of the present study were (1) to examine winter diets of Rocky Mountain mule deer from the eastern Sierra Nevada, California, during several years in which climate and plant growth varied, (2) to present information on spring and summer range diets, and (3) to evaluate suggested indicators of dietary quality in light of differences in plant species composition of the diet and measures of animal condition and reproduction.

METHODS

Fecal pellets were collected from seasonal ranges of mule deer wintering on the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, California, and summering throughout some 1200 sq. km of higher elevations in the Sierra Nevada (Chapters 3 and 4). On the winter range, fresh fecal pellets were collected monthly from January (BM) or February (SG) to April 1984 and November through April in 1985 through 1987 (SG) or 1988 (BM). Collections were made in the middle of each month, usually within a period of 1 or a few days. Additional collections were made in early April and early May 1985 and 1987, and in mid-May 1985. Each composited collection consisted of 5 pellets from at least 40 different defecations from 4 or 5 areas on each winter range.

Each composited fecal collection was mixed, stored in an individual paper bag, and air-dried. From each composite sample, 50 pellets were removed at random and sent to the Composition Analysis Laboratory, Colorado State University, for determination of plant composition by microhistological identification of plant fragments (Sparks and Malachek 1968). Plant fragments were identified to genus, and composition was expressed as percent relative density (Sparks and Malachek 1968). Fifty pellets/composite sample also were sent to the Wildlife Habitat Laboratory, Washington State University, for determination of fecal crude protein by the Kjeldahl method (Assoc. Off. Anal. Chem. 1980) and fecal DAPA (Czerkawski 1974).

Additional pellet collections were made less systematically during April and May 1984-87 on a spring holding area near the town of Mammoth Lakes, about 50 km northwest of the winter range at about 2400 m elevation (Chapter 3). Fresh pellets also were collected opportunistically during June-September 1984-85 on deer summer ranges, and in October 1984-86, during fall migration on migration routes over the Sierra crest (Chapter 3). These collections consisted of 4 or 5 pellets from each of 10 to 40 individual defecations; from 20 to 50 pellets were taken from each composited collection for species composition and chemical analyses.

Precipitation data were supplied by the National Weather Service station at the Bishop airport, some 24 km east of the winter range.

As an index of forage growth, annual bitterbrush leader growth was measured by personnel from the U. S.

Bureau of Land Management and the California Department of Fish and Game in October or November, near or after the cessation of plant growth but before the arrival of deer onto the winter range. During 1983-87 on the BM range, the lengths of 30 new terminal twigs were measured to the nearest 1.27 cm (0.5 inch) on 5 plants on each of 6 randomly located transects. I used the average from each plant in the analysis of the data.

In discussing diet composition by forage class, I included sedges (Carex) and rushes (Juncus) in the graminoids, and trees (Abies, Juniperus, Pinus, Quercus, and Salix) in the shrubs. Unless stated otherwise, these were all minor components of the diet. Because the data on species composition were derived from single samples composited from many individual defecations at each collection period, no variances could be calculated. This prohibited statistical tests of differences in relative proportions of species in the samples over time or between herds.

To evaluate the relationship between FN and DAPA and dietary quality, I regressed fresh-kill weights, eviscerated carcass weights, log kidney-fat indices (LNKFI), fetal hindfoot lengths, and weights of adult does or their fetuses collected during March of 1984 through 1988 on the BM range (dependent variable; Chapter 6) on monthly FN or DAPA from the winter preceeding the collections (independent variable). I also used multiple regression with a stepwise inclusion of variables (November through March FN or DAPA). To decrease problems asssociated with multicollinearity, tolerance was set at 0.01 (Norusius 1986). The rationale for the regression analyses was that if FN and DAPA are useful indicators of dietary quality, they should be associated with body size, condition, reproduction, or some combination of these. In other words, by knowing FN or DAPA, one should be able to make predictions about animal condition or reproduction. I also examined the correlations between FN and DAPA and the percent composition of the major species in the winter diet.

RESULTS

Diet Composition

<u>Winter</u>.--Diets of deer from both herds were >93% shrubs during all months they were on the winter range, except for the BM March 1988 diet, which had about 86% shrubs (Tables 5-1 and 5-2). Grasses (<u>Bromus</u> and <u>Poa</u>), sedges (<u>Carex</u>), and a few forbs, notably <u>Eriogonum</u>, completed the winter diet as minor components, and were most freqent in late winter and spring. Small amounts (<2%) of material from trees occurred in some of the samples from the Sherwin Grade deer, with the exception of February 1985, when <u>Juniperus</u> was 3.25% of the Sherwin Grade diet. The other tree genera identified were <u>Pinus</u> and <u>Quercus</u>,

Table 5-1. Percent composition of winter diets of Rocky Mountain mule deer on the Buttermilk winter range, Inyo County, California, by 3 forage classes, 1984-88, as determined by microhistological analysis of fecal pellets. A dash indicates that no sample was taken that period.

Year	Collection period								
Forage class	Nov	Dec	Jan	Feb	Mar	1 Apr	15 Apr	1 May	15 May
1984									
Grass	-	-	0.48	1.51	1.82	-	0.73	-	-
Forb	-	-	0.79	0.00	2.06	-	5.46	-	-
Shrub	-	-	98.73	98.49	96.12	-	93.81	-	-
1985									
Grass	0.00	0.45	0.00	0.56	1.22	3.93	4.27	0.35	0.00
Forb	0.00	0.00	0.29	0.00	1.70	0.29	0.00	1.21	0.00
Shrub	100.00	99.55	99.71	99.44	97.08	95.78	95.73	98.44	100.00
1986									
Grass	0.00	0.94	0.34	0.76	2.17	0.64	1.63	-	-
Forb	0.00	0.00	0.00	0.34	1.89	1.73	4.37	-	-
Shrub	100.00	99.06	99.66	98.90	95.94	97.63	94.00	-	-
1987									
Grass	0.68	0.00	2.92	0.00	0.41	1.33	2.55	0.37	-
Forb	0.00	1.28	0.00	0.43	0.00	0.00	0.28	0.00	-
Shrub	99.32	98.72	97.08	99.57	99.59	98.67	97.17	99.63	-
1988									
Grass	0.03	2.25	0.82	0.68	4.27	-	1.16	-	-
Forb	0.32	1.24	0.49	5.52	9.28	-	3.15	-	-
Shrub	99.38	96.51	98.2	93.8	86.45	-	95.69	-	-

Table 5-2. Percent composition of winter diets of Rocky Mountain mule deer on the Sherwin Grade winter range, Inyo and Mono Counties, California, by 3 forage classes, 1984-87, as determined by microhistological analysis of fecal pellets. A dash indicates that no samples were taken that period.

Year Forage class	Collection period Nov	 Dec	 Jan	 Feb	 Mar	 1 Apr	 15 Apr
1984							
Grass	-	-	-	0.86	0.92	-	3.85
Forb	-	-	-	1.47	0.88	-	0.37
Shrub	-	-	-	97.67	98.20	-	95.78
1985							
Grass	0.00	0.27	0.74	0.40	1.87	0.62	2.88
Forb	0.00	0.00	0.00	0.32	0.29	2.49	4.73
Shrub	100.00	99.73	99.26	99.28	97.84	96.89	92.39
1986							
Grass	0.00	0.00	0.77	0.00	0.97	-	3.02
Forb	0.00	5.66	0.00	0.00	0.00	-	0.00
Shrub	100.00	94.34	99.23	100.00	99.03	-	96.98
1987							
Grass	0.00	0.00	0.34	0.00	0.40	0.29	0.36
Forb	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Shrub	100.00	100.00	99.66	100.00	99.60	99.71	99.64

The other tree genera identified were *Pinus* and *Quercus*, the latter probably from nearby residential plantings.

Four shrubs comprised most of the winter diet: big sagebrush, antelope bitterbrush, blackbrush (*Coleogyne ramosissima*), and Gregg's ceanothus (*Ceanothus Greggii*). Trace amounts of *Ephedra nevadensis* and *Rosa* sp. were present in some samples. The relative amounts of each shrub changed within and between years on the winter range (Figures 5-1 and 5-2). Purshia was most frequent in the diets of both herds during their first few months on the winter range, and again in April. Artemisia was most common in mid-winter. *Ceanothus* and *Coleogyne* showed much lower and more variable levels in the diet, although *Coleogyne* typically was most common in mid-winter. An exception to this was March and April of 1988, when *Coleogyne* was 49% and 38% of the BM diet, respectively (Figure 5-1).

There was a strong negative relationship between the amounts of *Purshia* and *Artemisia* in the diet (Figure 5-3). The correlation between these plants in BM diets was less than in the SG diets mainly because of 2 extreme points, March and April 1988. Excluding those yielded $\underline{r}^2 = 0.89$; excluding 1987-88 entirely yielded $\underline{r}^2 = 0.91$. This generally close, negative relationship between *Artemisia* and *Purshia* in the diets reflected a shift in the relative proportions of each in the diet over the course of the

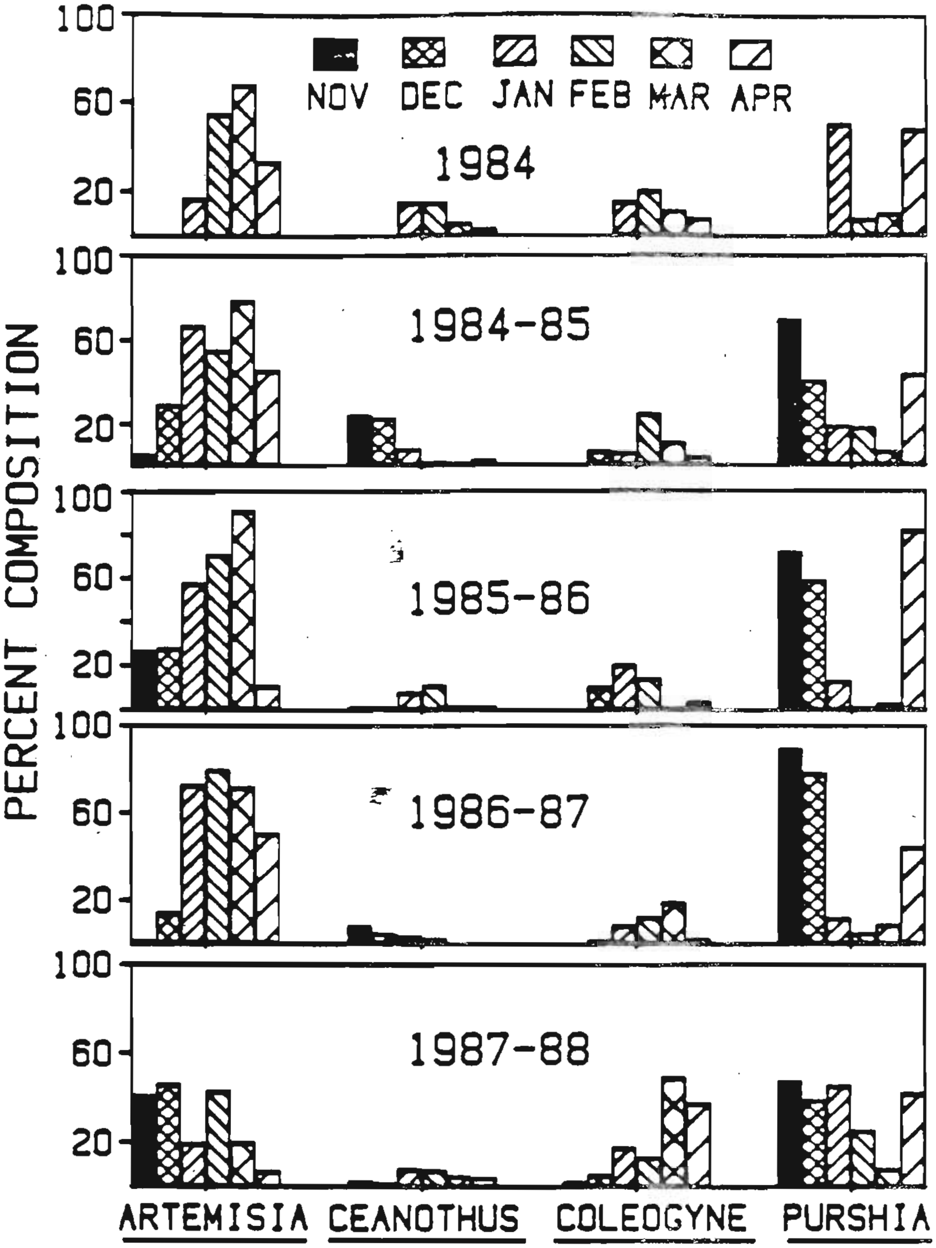

Figure 5-1. Percent composition of 4 shrubs in the winter diet of mule deer on the Buttermilk winter range, Inyo County, Calif., 1984 through 1988.

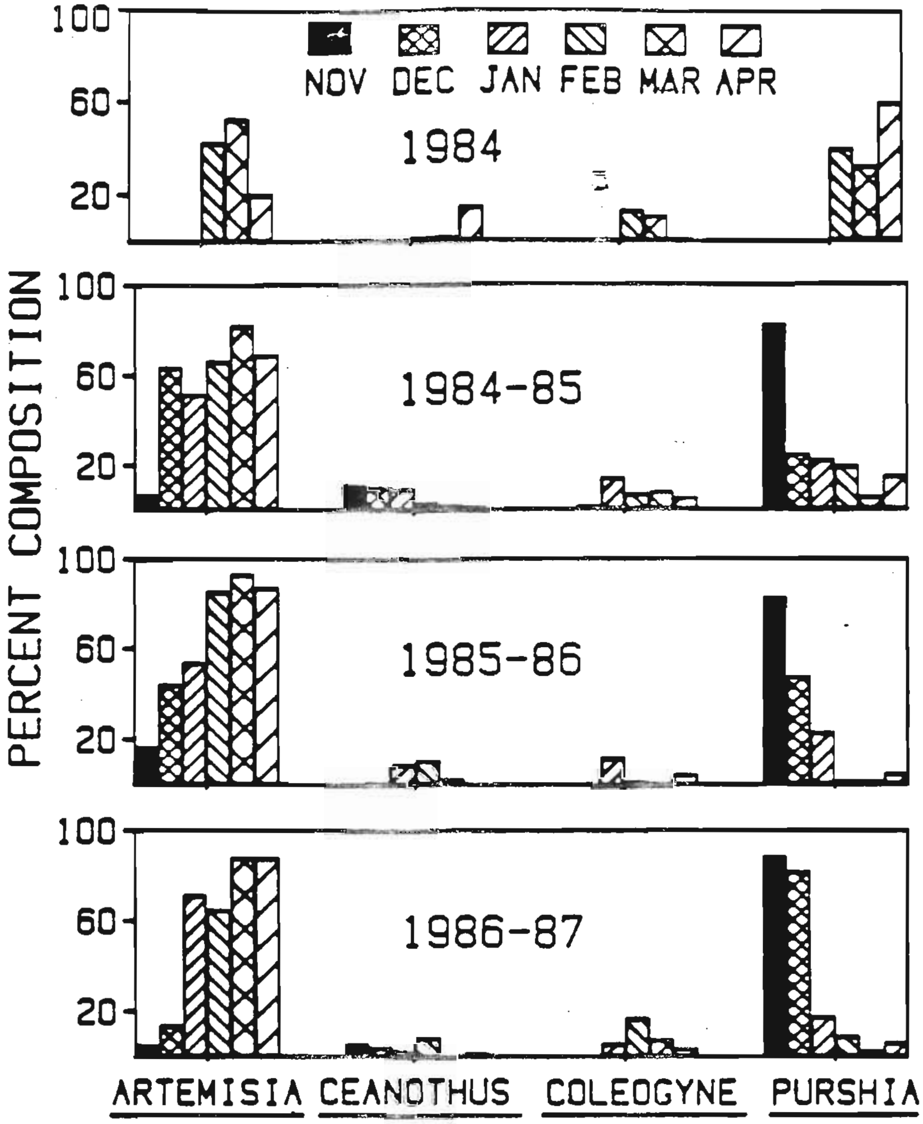

Figure 5-2. Percent composition of 4 shrubs in the winter diets of mule deer on the Sherwin Grade winter range, Inyo and Mono Counties, Calif., 1984 through 1987.

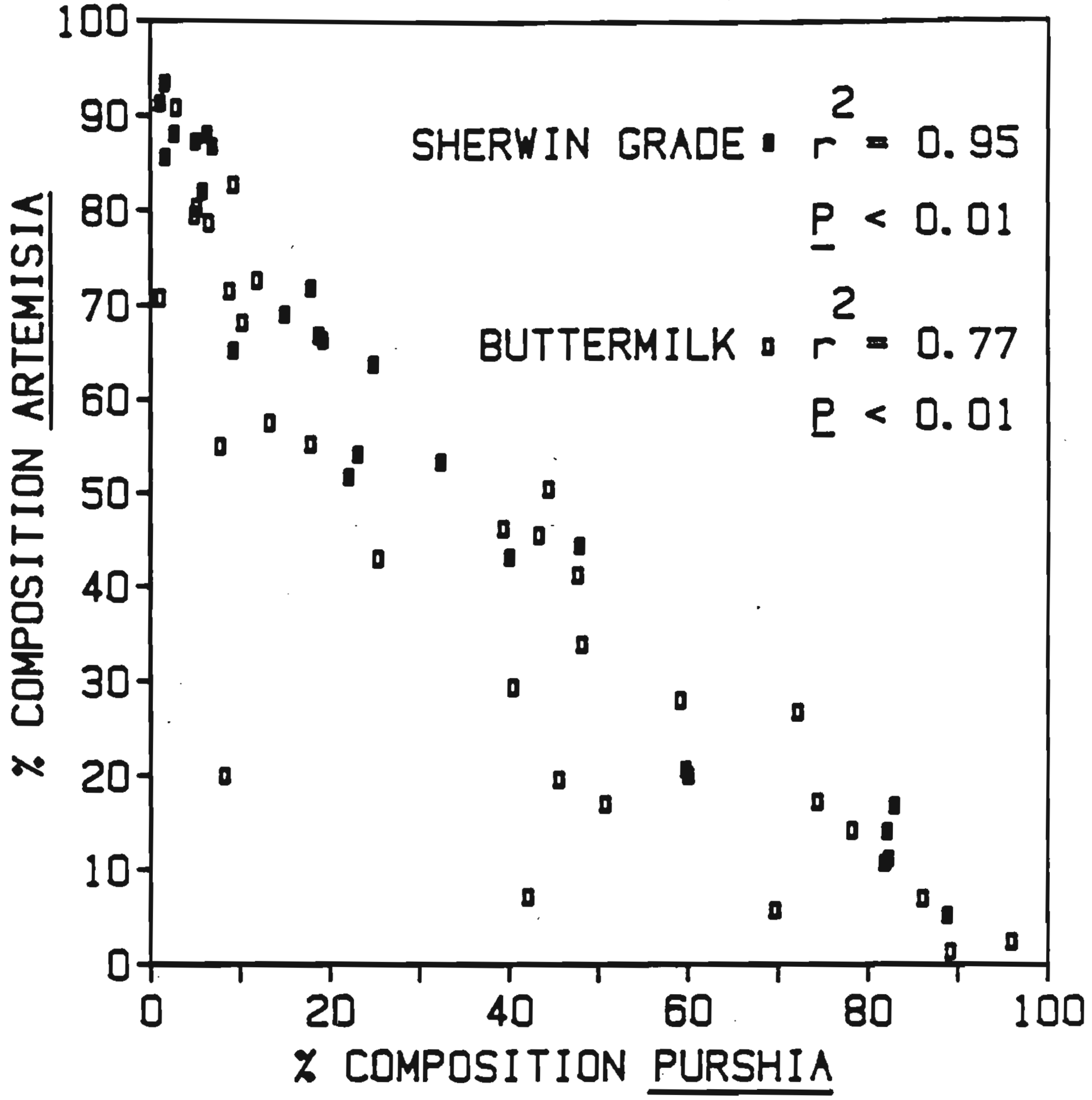

Figure 5-3. Percent composition *Artemisia* plotted against percent compositon *Purshia* in winter diets of mule deer on the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono Counties, Calif., 1984 through 1988.

winters. The temporal pattern of the shift of the winter diets from *Purshia* to *Artemisia* and back becomes apparent when the percent composition of each is plotted monthly for the years of study (Figures 5-4 and 5-5). In all years, November diets were largely *Purshia*; as winter progressed, it was replaced by *Artemisia*. The intensity of browsing on *Purshia* was reflected in the columnar and umbrella-shaped growth forms of plants common on both ranges, and by frequent observations of deer on their hind legs reaching for *Purshia* leaves.

Differences within and between years in the timing and extent of this dietary shift are apparent from the plot of the ratio of the percent *Purshia* to the percent *Artemisia* in the diet by collection period for the years 1984 through 1988 on the BM range (Figure 5-6). This *Purshia*/*Artemisia* ratio exhibits a generally U-shaped pattern throughout the winter, with *Purshia* more common in early winter and spring, *Artemisia* predominant in mid- and late winter, and *Purshia* again most frequent in the spring. Differences among years, however, are apparent. Most noticeably, the diet of the deer on the BM range in November of 1987 had nearly as much *Artemisia* as *Purshia*; the February and March diets had less *Artemisia* than in previous years and much more *Coleogyne* (Figure 5-1). This is likely related to the very poor growth of *Purshia* the previous year (Figure 5-7).

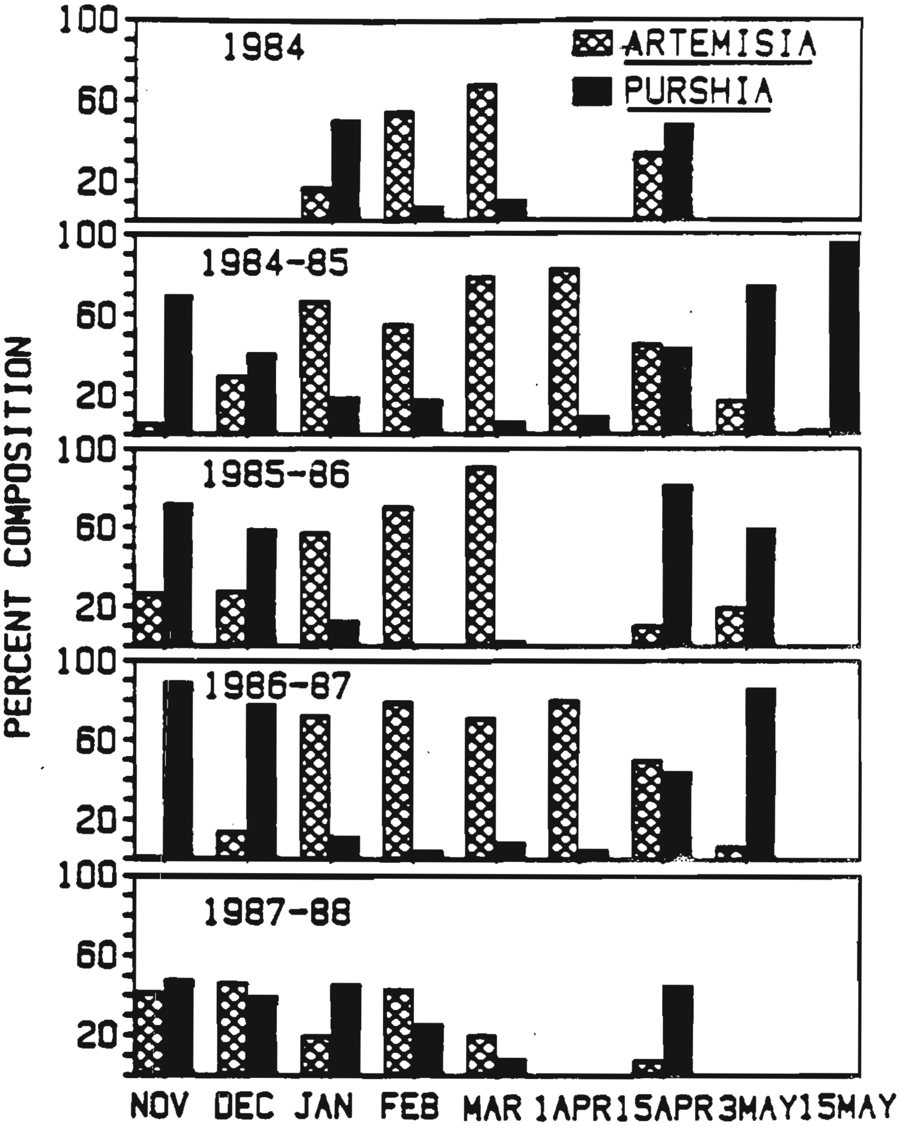

Figure 5-4. Percent composition of _Artemisia_ and _Purshia_ in winter diets of mule deer on the Buttermilk winter range, Inyo County, Calif., 1984 through 1988.

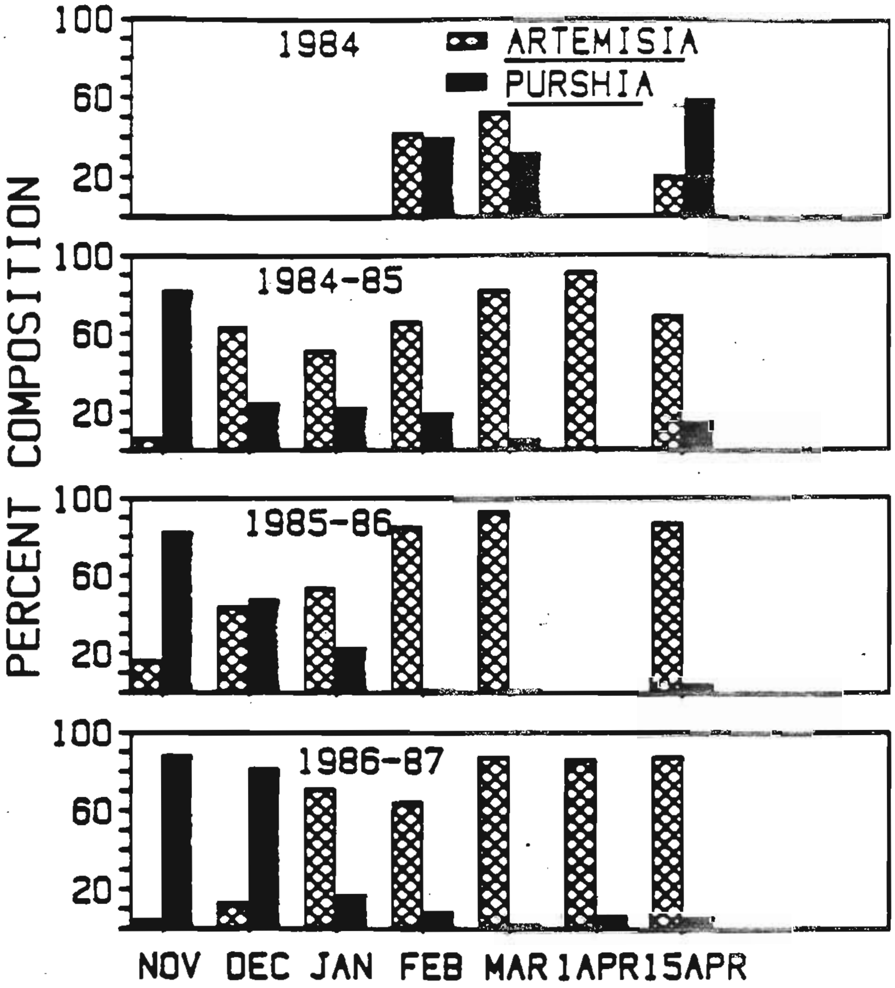

Figure 5-5. Percent composition of <u>Artemisia</u> and <u>Purshia</u> in winter diets of mule deer on the Sherwin Grade winter range, Inyo and Mono Counties, Calif., 1984 through 1987.

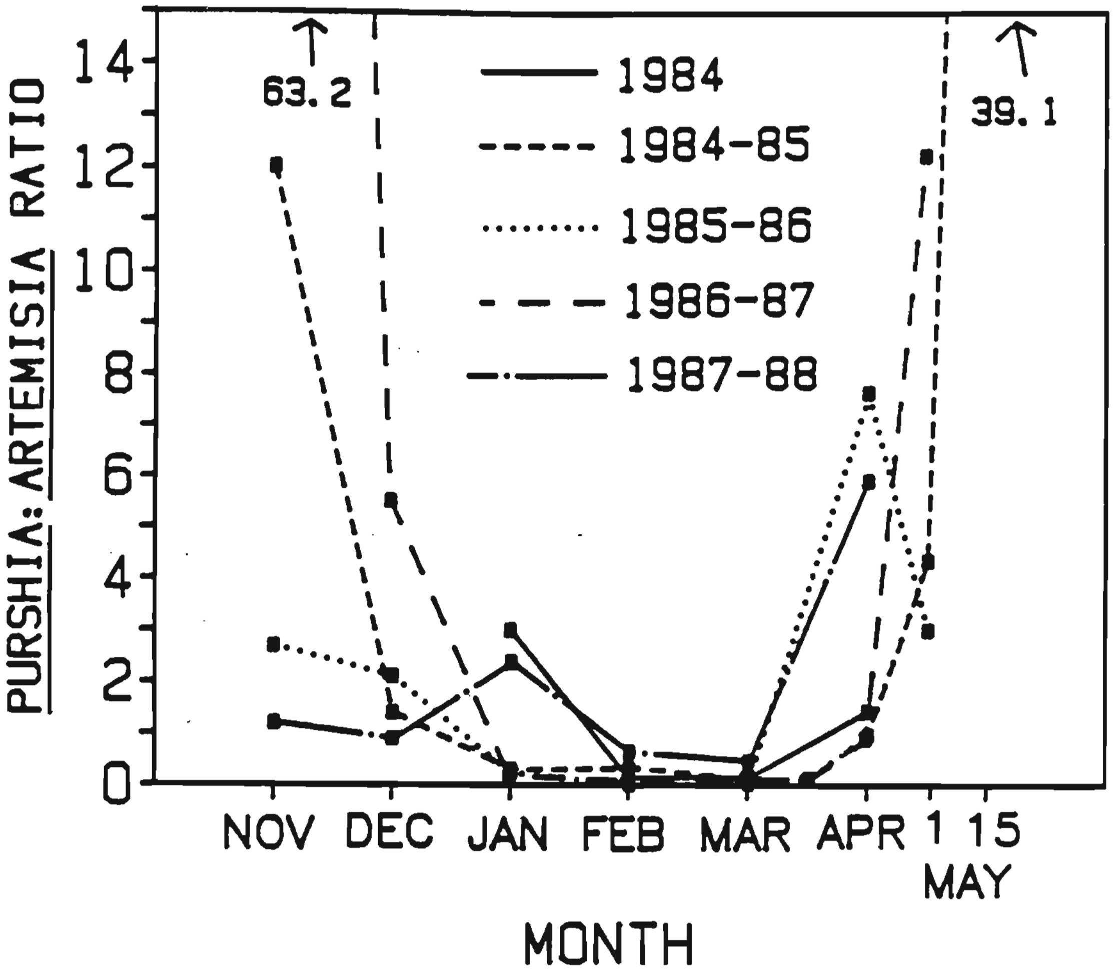

Figure 5-6. The ratio of the percent composition _Purshia_ to the percent composition _Artemisia_ in the winter diets of mule deer on the Buttermilk winter range, Inyo County, Calif., 1984 through 1988.

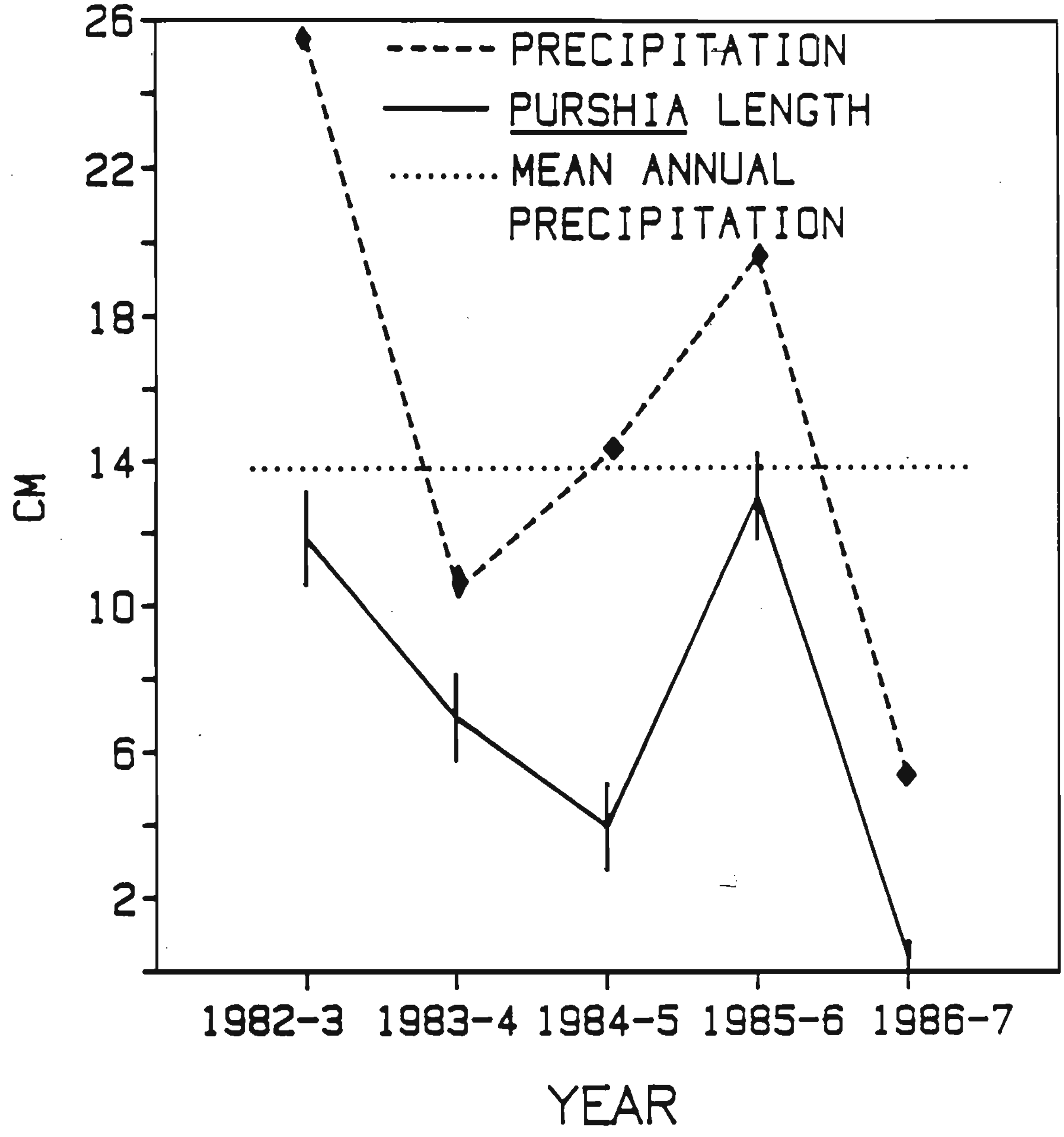

Figure 5-7. Annual precipitation, July through June 1982 to 1987, measured at the Bishop Airport, and annual growth of *Purshia* terminal twigs (mean ± 95% CI) on the Buttermilk winter range each corresponding year, and mean annual precipitation 1951 through 1987, Inyo County, Calif.

There was a highly significant relationship between annual (July-June) precipitation and *Purshia* growth measured the following October ($R^2 = 0.51$, $P < 0.001$). There was also a positive correlation between growth of *Purshia* and the *Purshia*/*Artemisia* ratio in November for the years 1984 through 1987 ($r_s = 1$, $P = 0.05$). Thus, the extremely low production of *Purshia* in 1987, due to low rainfall during 1986-87, meant that little *Purshia* was available for deer when they arrived on the winter range in October and November of 1987. By February 1988, the deer were feeding heavily on *Coleogyne*, considered a very poor forage (Provenza et al. 1983).

There was a rapid switch of diet back to *Purshia* in early April evident among the BM deer, coincident wih the beginning of spring growth (Figure 5-4). That this was an abrupt switch was evident in 1985 and 1987, when pellets were collected bimonthly during late winter. In a 2-week period from early to mid-April in both those years, percent composition of *Purshia* in the diet increased from <10% to >40%. In all years on the Buttermilk range, *Purshia* was >40% of the diet by mid-April. This was not the case among the SG animals; only in 1984 did April diets of SG deer contain >15% *Purshia*.

Spring.--On the spring range, shrubs again were the most important components of the diet (Table 5-3). *Pur-*

Table 5-3. Percent composition of taxa comprising more than 1% of the diet of Rocky Mountain mule deer on a spring holding area near Mammoth Lakes, Mono County, California, 1985-87, as determined by microhistological analysis of fecal pellets.

	Year and date of sample							
	1985			1986			1987	
Taxon	13 Apr	3 May	15 May	17 Apr	2 May	15 May	28 Apr	22 May
Grass/sedge:								
Carex	1.27	2.26	0.00	0.00	0.35	5.82	0.00	0.00
Juncus	0.00	0.00	0.00	0.00	0.00	2.22	0.00	0.00
Poa	0.42	0.00	0.00	1.59	0.51	0.00	0.00	0.00
Total grass	2.08	2.69	0.59	1.95	0.86	8.43	0.00	0.00
Forbs:								
Cirsium	0.00	3.59	0.00	0.00	0.00	0.00	0.00	0.00
Total forb	1.21	4.05	0.58	0.34	0.00	0.66	0.00	0.00
Shrubs:								
Artemesia	20.48	23.04	15.26	38.80	28.74	27.27	19.12	2.91
Ceanothus	33.53	60.08	20.21	22.67	5.76	43.28	0.00	8.63
Purshia	42.29	10.14	61.61	36.24	63.67	19.97	80.11	88.46
Total shrub	96.71	93.26	97.08	97.71	98.52	90.52	100.00	100.00

shia, Artemisia, and Ceanothus velutinus comprised >90% of the diet in all samples; each varied in relative proportion, but in no discernable pattern. Grasses and forbs were minor components in all spring samples.

Summer.--Shrubs appeared less frequently in summer diets, but were still common, comprising between 44% and 95% of the diet (Table 5-4). More grasses and forbs were in the summer samples, and relative frequencies of various taxa varied widely, probably reflecting both local and seasonal effects. Carex and Poa were among the most common graminoids in any sample, and Lupinus was the most common forb. Among the shrubs, Ceanothus was common; although species were not identified microhistologically, this was probably a mixture of C. cordulatus and C. velutinus, both of which are common in the summer range areas of the Sierra Nevada. Salix was the other shrub present in large amounts. Artemisia and Purshia were present in small amounts, reflecting the low availability of these plants on most summer ranges.

Fall.--Pellet collections during or immediately after fall migration showed variable frequencies of several taxa, although shrubs were again the most important forage class (Table 5-5). Artemisia, Ceanothus, Purshia, and Salix were most prevalent, but no pattern was evident from the samples.

Table 5-4. Percent composition of taxa comprising more than 1% of the diet of Rocky Mountain mule deer on summer ranges in the central Sierra Nevada, California, 1985-86, as determined by microhistological analysis of fecal pellets.

	Year and month of sample						
	1984				1985		
Taxon	Jun	Jul	Aug	Sep	Jun	Jul	Aug
Grass/sedge							
Agropyron	0.55	0.00	0.00	0.00	0.39	1.04	3.47
Bromus	0.00	0.49	1.83	2.01	0.00	0.00	4.89
Carex	5.83	2.78	2.38	5.12	1.78	3.28	24.13
Eleocharis	6.62	0.00	0.00	0.00	0.00	0.00	1.18
Oryzopsis	0.55	0.00	0.00	0.00	0.00	0.00	1.11
Poa	0.00	0.56	0.00	0.00	1.88	0.57	11.29
Stipa	2.58	0.00	0.00	0.00	0.00	0.00	0.00
Total grass	16.13	3.83	4.21	7.61	4.05	4.89	46.60
Forb							
Astragalus	0.55	0.00	0.00	0.00	0.00	1.10	0.00
Composite	0.62	1.48	0.00	0.00	0.00	0.00	1.10
Epilobium	0.00	1.05	0.00	0.00	0.00	0.00	0.00
Eriogonum	2.88	0.00	0.00	0.00	0.00	0.00	0.00
Fern	0.00	0.00	0.00	0.00	0.00	0.00	4.49
Lupinus	0.00	0.53	6.15	28.99	0.00	0.00	1.69
Phlox	0.00	0.00	0.00	0.00	0.68	1.67	2.71
Total forb	5.54	3.06	6.62	28.99	0.68	2.77	9.99
Shrub							
Abies	0.00	0.00	0.00	0.00	0.00	1.04	0.52
Artemesia	3.51	0.56	3.08	1.09	1.07	0.00	1.11
Ceanothus	65.06	7.29	60.62	40.12	3.37	8.20	1.10
Purshia	8.57	1.97	5.66	7.00	7.80	1.07	0.00
Pinus	0.00	6.09	1.83	6.20	0.58	0.00	0.00
Quercus	0.00	0.00	0.00	0.00	0.45	2.24	0.59
Rosa	0.00	0.00	0.00	0.00	0.00	6.22	5.01
Salix	0.00	76.64	17.40	5.78	82.00	70.32	35.61
Total shrub	77.14	93.11	88.59	60.19	95.27	89.09	43.94

Table 5-5. Percent composition of taxa comprising more than 1% of the diet of Rocky Mountain mule deer during fall migration, Mono County, California, 1984-86, as determined by microhistological analysis of fecal pellets.

	Year and month of sample			
	1984	1985		1986
Taxon	Oct	Sep	Oct	Oct
Grass/sedge				
Agropyron	0.52	0.64	1.14	0.00
Bromus	4.64	0.00	0.00	0.00
Carex	0.00	38.33	3.98	1.08
Oryzopsis	0.00	1.15	1.91	0.00
Poa	0.00	1.77	2.92	4.95
Total grass	5.16	41.89	9.95	6.59
Forb				
Lupinus	4.38	0.00	7.97	4.45
Medicago	2.00	0.00	0.00	0.00
Oenothus	0.00	2.97	0.00	0.00
Phlox	0.00	0.00	1.93	0.00
Total forb	7.29	3.59	10.45	4.45
Shrub				
Artemesia	15.62	10.43	51.62	5.14
Ceanothus	49.73	1.65	2.33	15.57
Coleogyne	1.58	1.25	0.00	0.00
Pinus	1.58	3.64	8.58	0.51
Populus	0.00	1.15	2.94	0.00
Purshia	13.92	7.65	6.79	67.74
Quercus	5.12	0.00	0.00	0.00
Salix	0.00	28.11	4.25	0.00
Symphoricarpos	0.00	0.00	3.08	0.00
Total shrub	87.55	54.52	79.59	88.96

Fecal Nitrogen

FN showed distinct seasonal patterns over the years of study. With the exception of the winter of 1987-88, the monthly fecal nitrogen levels were similar for both the BM and SG deer, and showed similar changes over the winter (Figures 5-8 and 5-9). On the BM range in November 1984 through 1986, FN was between 1.8% and 1.9%. It subsequently decreased through January or February to about 1.5%. In March FN typically began to rise, and in April and May FN was 2.5-3.5%. In the winter of 1987-88 on the BM range, however, November FN was 1.3%, and then decreased to 0.91% in December, the lowest ever measured. FN remained below that observed in previous years into the spring of 1988.

On the spring range near Mammoth Lakes during April and May, FN rose from about 2.2% to >3% (Figure 5-10). These spring values, however, were consistently lower than FN from pellet samples collected within a few days from animals still on the winter range (Table 5-6). For example, at the beginning of May on the BM range in 1985, 1986, and 1987, FN was 3.53%, 2.86%, and 2.43%, respectively; the corresponding values from the spring range were 2.30%, 2.26%, and 2.29%. Thus, the transition from winter range to spring range was accompanied by a decrease in FN.

On the summer range, FN was highest during June, with values of about 3.5% in both 1984 and 1985 (Figure 5-10).

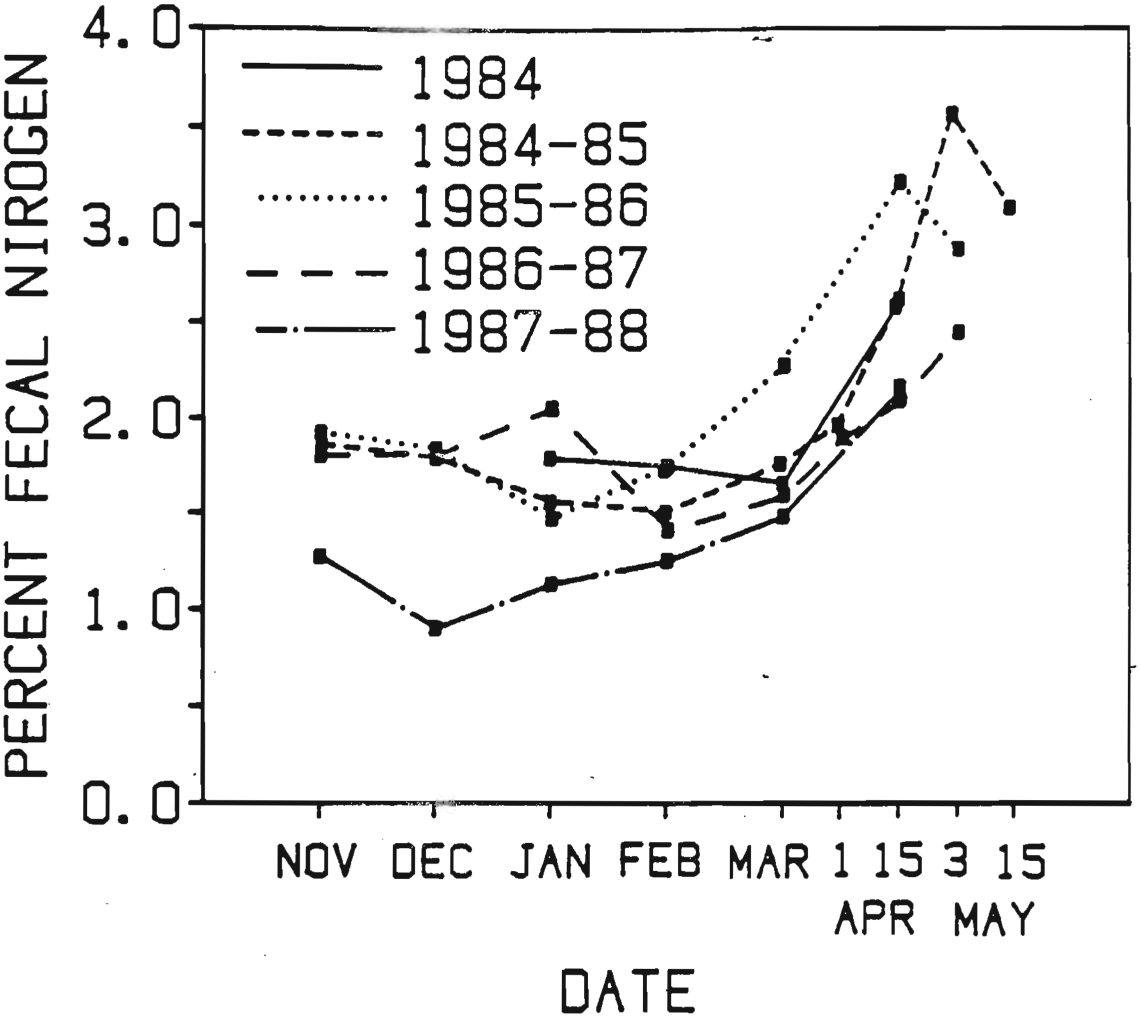

Figure 5-8. Nitrogen (%) in composited mule deer fecal samples from the Buttermilk winter range, Inyo County, Calif., 1984 through 1988.

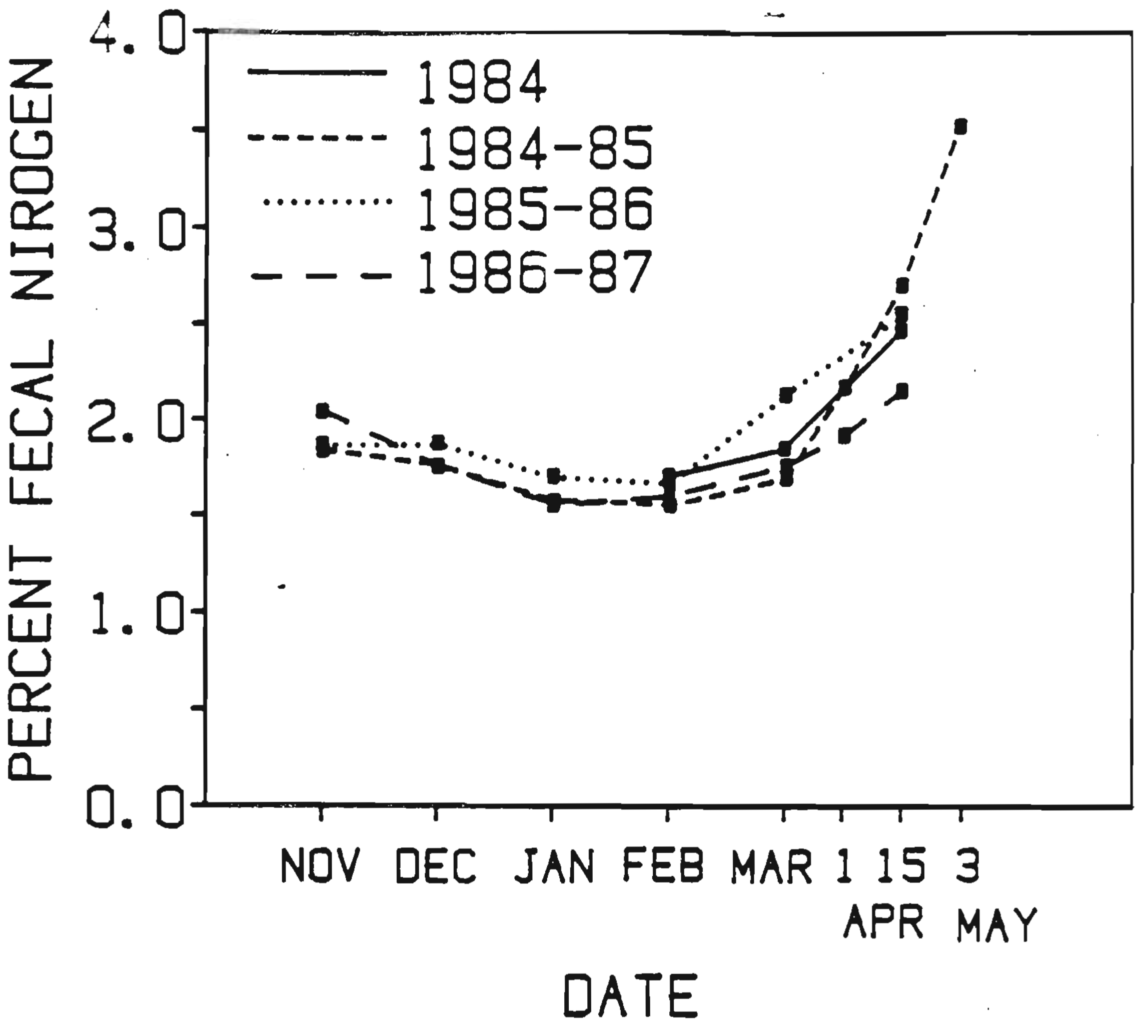

Figure 5-9. Nitrogen (%) in composited mule deer fecal samples from the Sherwin Grade winter range, Inyo and Mono Counties, Calif., 1984 through 1987.

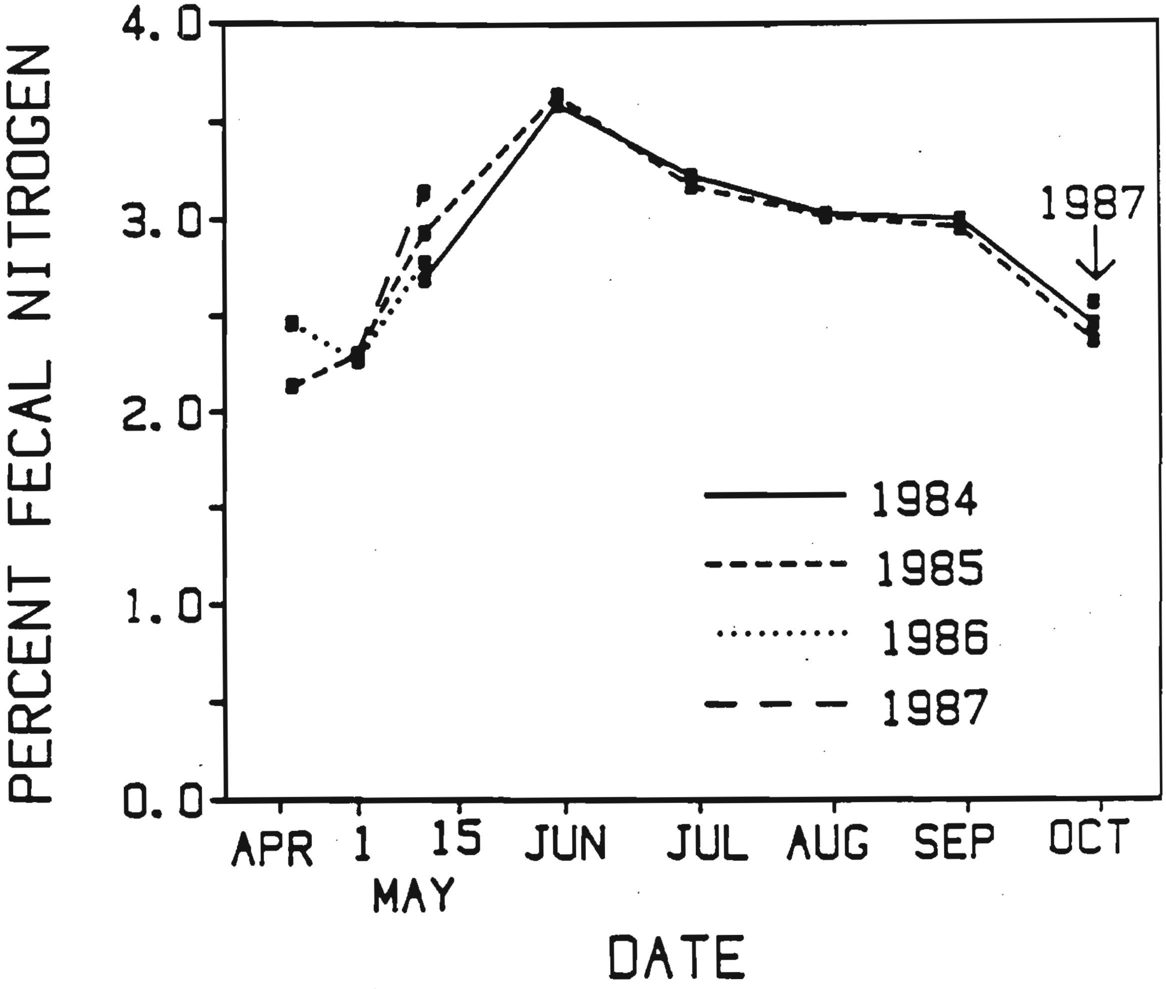

Figure 5-10. Nitrogen (%) in composited mule deer fecal samples from a spring range near Mammoth Lakes (April and May), summer range areas in the central Sierra Nevada (June through September), and during fall migration (October) near Mammoth Lakes, Calif., 1984 through 1987.

Table 5-6. Percent fecal nitrogen (FN) and concentration of fecal diaminopimelic acid (DAPA, mg/g) in composited samples of fecal pellets collected contemporaneously on the Buttermilk winter range (BM) and a spring holding area, Inyo and Mono Counties, California, during spring 1985 through 1987.

		FN		DAPA	
Year	Date	BM	Spring	BM	Spring
1985	15 Apr	2.54	2.14	0.495	0.624
	3 May	3.53	2.30	0.921	0.537
	15 May	3.05	2.93	0.937	0.883
1986	15 Apr	3.21	2.46	0.866	1.005
	1 May	2.86	2.26	1.131	0.906
1987	1 May	2.43	2.29	0.500	0.500

FN subsequently decreased through September, with very similar values observed during both years. During migration in October of 1984 through 1986, FN also was notably consistent, varying between 2.36% and 2.55%.

Fecal DAPA

The seasonal patterns of fecal DAPA were similar to those of FN, but somewhat more variable (Figures 5-11, 5-12). In November, DAPA ranged from 0.415 to 0.600 mg/g. DAPA profiles differed between winters, with some years, e. g., 1984-85 and 1986-87, showing decreases through the winter and the other years remaining approximately constant. In contrast to FN, DAPA in the winter of 1987-88 was not lower than in other years. DAPA increased in the spring in all years.

The relationship between DAPA from contemporaneous collections on the winter and spring ranges was not consistent (Table 5-6). In mid-April of 1985 and 1986, DAPA from collections from the BM winter range was lower than that from the spring range. In early May of 1985 through 1987, DAPA on the winter range was greater than or equal to that on the spring range.

DAPA showed a gradual decrease through the summer and fall, although again differences between years were apparent (Figure 5-13).

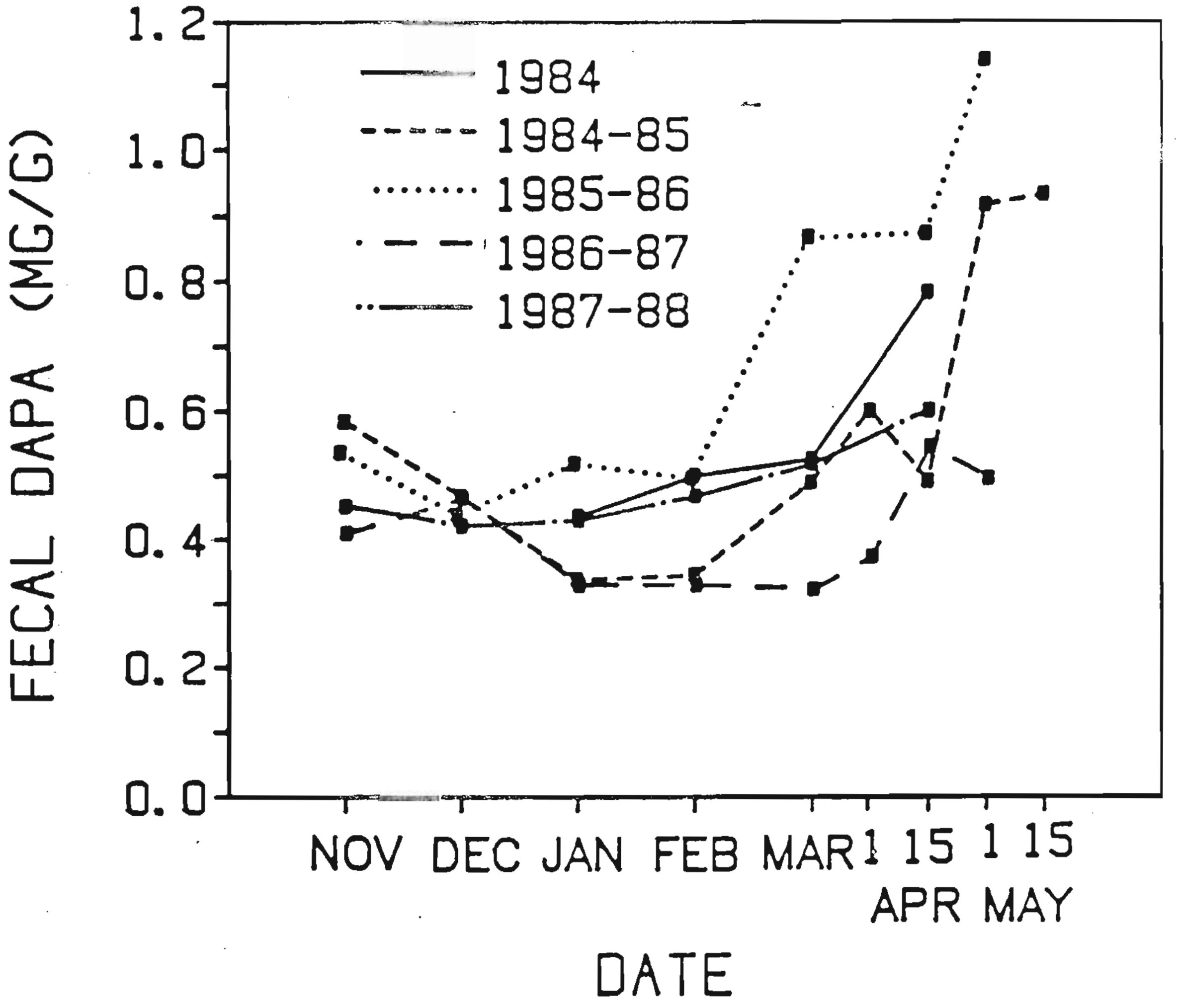

Figure 5-11. Diaminopimelic acid (DAPA; mg/g) in composited mule deer fecal samples from the Buttermilk winter range, Inyo County, Calif., 1984 through 1988.

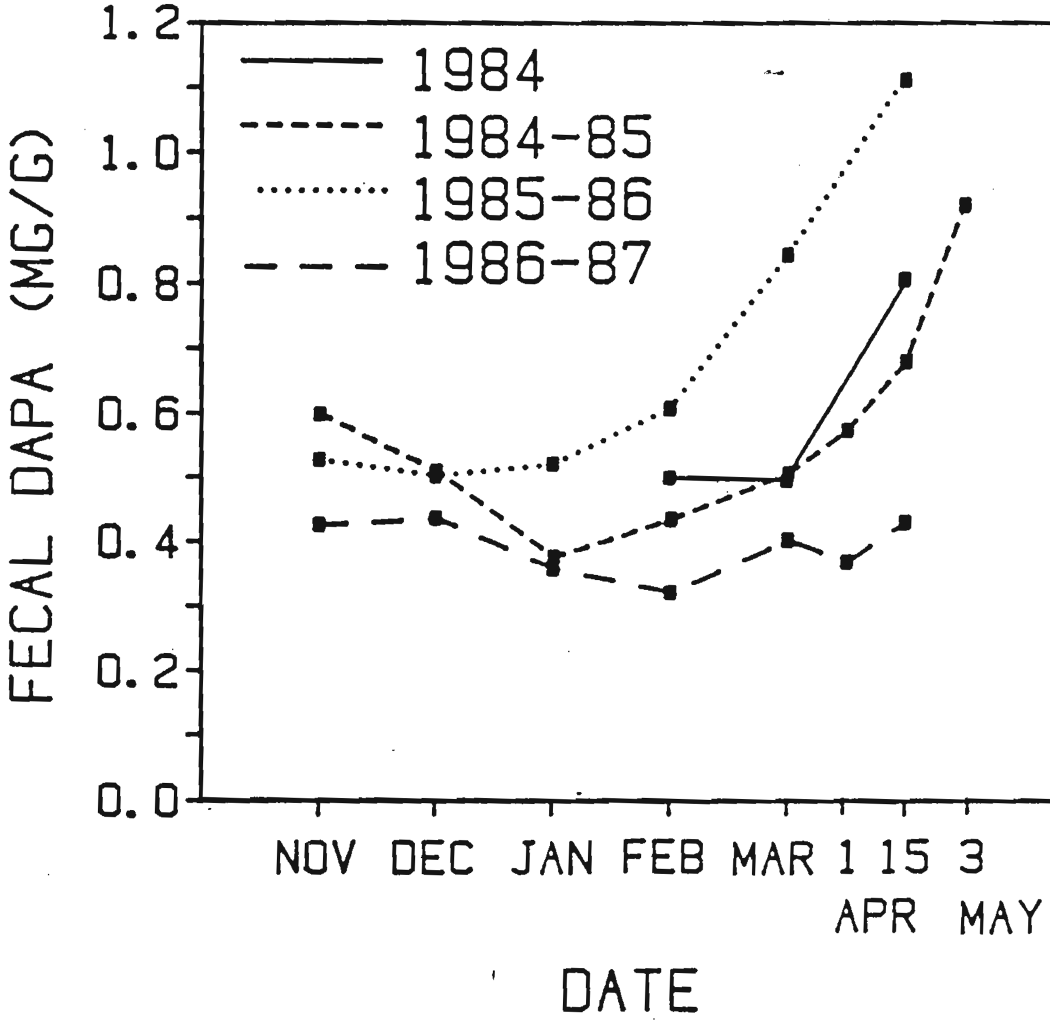

Figure 5-12. Diaminopimelic acid (DAPA; mg/g) in composited mule deer fecal samples from the Sherwin Grade winter range, Inyo County, Calif., 1984 through 1987.

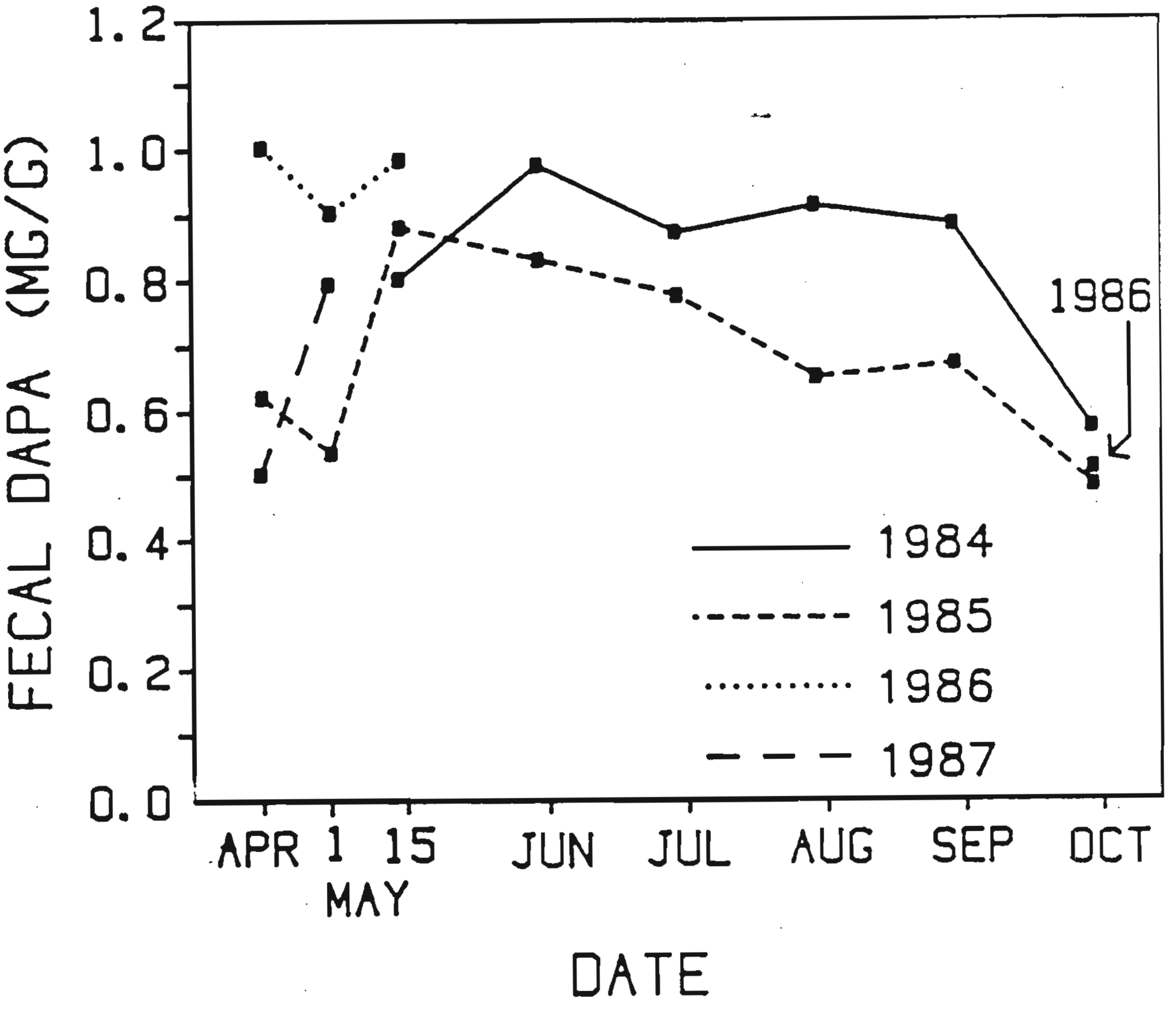

Figure 5-13. Diaminopimelic acid (DAPA; mg/g) in composited mule deer fecal samples from a spring range near Mammoth Lakes (April and May), summer range areas in the central Sierra Nevada (June through September), and during fall migration (October) near Mammoth Lakes, California, 1984 through 1987.

FN and DAPA as Indicators of Dietary Quality

FN and DAPA concentrations in pellet samples were correlated ($r = 0.79$, $P < 0.001$). Simple linear regressions of the measures of condition and reproduction on monthly FN and DAPA values revealed no clear relationships (Tables 5-7, 5-8). Although several of the slopes were different from zero, in few of those cases was the amount of explained variance (R^2) sufficient to be of biological significance. In no case did FN or DAPA explain more than 9% of the variance in body weights or >21% of the variance in KFI. March FN and March DAPA showed the closest relationship to any measure, and that was with fetal hindfoot length. However, the association was negative; higher FN and DAPA were associated with smaller fetuses.

Multiple regressions using monthly FN and DAPA to predict condition or reproduction revealed multicollinearity among the predictor variables, indicated informally by the simple correlation coefficients (Table 5-9). However, multicollinearity has little effect on inferences about the predictive value of the regression equation (Neter et al. 1985). Using monthly FN in multiple regressions to predict condition (body weight or KFI) produced no improvement in R^2 over simple linear regression (Table 5-10). A regression equation including March and January FN, however, did account for nearly half the vari-

Table 5-7. Simple linear regressions of several measures of body condition and reproduction (Y) on monthly fecal nitrogen (FN) (X) from mule deer fecal pellets on the Buttermilk winter range, Inyo County, Calif. Measures of condition and reproduction were from adult does collected in March of 1984 through 1988. FN was from monthly (January through March 1984, November through March 1984 through 1988) composited fecal samples prior to the March collections during each respective year. Only slopes (b) significantly ($P < 0.10$) different from zero are shown.

Y	X	R^2	b	$P(b = 0)$	n
Fresh-kill weight	Nov			0.37	66
	Dec			0.45	66
	Jan			0.34	83
	Feb			0.34	83
	Mar			0.17	83
Eviscerated weight	Nov	0.056	-7.19	0.054	67
	Dec	0.056	-4.66	0.054	67
	Jan			0.94	84
	Feb			0.57	84
	Mar			0.27	84
LNKFI	Nov	0.121	1.21	0.002	67
	Dec	0.166	0.88	0.001	67
	Jan	0.203	1.27	<0.001	74
	Feb	0.047	1.18	0.035	74
	Mar			0.82	74
Fetal hindfoot	Nov	0.067	-15.16	0.046	60
	Dec			0.18	60
	Jan	0.059	10.68	0.048	67
	Feb	0.253	-38.97	<0.001	67
	Mar	0.344	-32.25	<0.001	67
Fetal weight	Nov	0.048	-68.52	0.091	60
	Dec			0.29	60
	Jan	0.068	61.43	0.032	67
	Feb	0.200	-193.90	<0.001	67
	Mar	0.270	-152.08	<0.001	67

Table 5-8. Simple linear regressions of several measures of body condition and reproduction (*Y*) on monthly diaminopimelic acid (DAPA) (*X*) from mule deer on the Buttermilk winter range, Inyo County, Calif. Measures of condition and reproduction were from adult does collected in March of 1984 through 1988. DAPA was from monthly (January through March 1984, November through March 1984 through 1988) composited fecal samples prior to the March collections during each respective year. Only slopes (*b*) significantly ($P < 0.10$) different from zero are shown.

Y	*X*	R^2	*b*	P(*b* = 0)	*n*
Fresh-kill weight	Nov			0.260	66
	Dec			0.795	66
	Jan			0.805	83
	Feb			0.149	83
	Mar			0.391	83
Eviacerated weight	Nov	0.071	-30.5	0.029	67
	Dec	0.053	-88.2	0.033	67
	Jan			0.107	84
	Feb	0.084	-31.3	0.007	84
	Mar			0.970	84
LNKFI	Nov			0.779	67
	Dec	0.199	17.0	<0.001	67
	Jan	0.041	-2.9	0.046	74
	Feb	0.045	-2.7	0.069	74
	Mar	0.025	-36.2	0.090	74
Fetal hindfoot	Nov	0.210	-102.9	<0.001	60
	Dec	0.047	-6.9	0.097	60
	Jan	0.245	-109.1	<0.001	67
	Feb	0.137	-76.7	0.002	67
	Mar	0.392	-52.5	<0.001	67
Fetal weight	Nov	0.245	-585.8	<0.001	60
	Dec			0.140	60
	Jan	0.199	-523.7	<0.001	67
	Feb	0.126	-390.6	0.003	67
	Mar	0.334	-258.0	<0.001	67

Table 5-9. Correlation matrix of variables used in multiple regression of measures of condition and reproduction on diaminopimelic acid (DAPA) and fecal nitrogen (FN) from mule deer fecal pellets collected monthly on the Buttermilk winter range, Inyo County, California. Measures of condition and reproduction were from adult does collected in March of 1985 through 1988. FN was from monthly (November through March) composited fecal samples prior to the March collections during each respective year. Variables are: LVWT, fresh-kill weight; EVWT eviscerated carcass weight; LNKFI, log KFI; FTHF, fetal hindfoot length; FTWT, fetal weight.

FN OR	MONTH OF PELLET COLLECTION									
DAPA	NOV	DEC	JAN	FEB	MAR	LVWT	EVWT	LNKFI	FTHF	FTWT
DAPA										
NOV	1	0.132	0.198	0.103	0.522	-0.140	-0.281	0.038	-0.449	-0.482
DEC		1	-0.814	-0.947	-0.581	-0.033	-0.271	0.468	0.240	0.215
JAN			1	0.952	0.928	-0.043	0.149	-0.319	-0.531	-0.472
FEB				1	0.812	-0.013	0.202	-0.417	-0.421	-0.383
MAR					1	-0.094	0.012	-0.209	-0.651	-0.602
LVWT						1	0.660	-0.054	0.139	0.219
EVWT							1	0.106	0.137	0.222
LNKFI								1	0.213	0.959
FTHF									1	0.180
FTWT										1
FN										
NOV	1	0.989	0.625	0.820	0.680	-0.108	-0.241	0.370	-0.252	-0.212
DEC		1	0.728	0.734	0.574	-0.095	-0.240	0.410	-0.166	-0.129
JAN			1	0.146	-0.044	0.009	-0.107	0.444	0.264	0.294
FEB				1	0.977	-0.122	-0.135	0.119	-0.548	-0.486
MAR					1	-0.116	-0.084	0.016	-0.613	-0.548
LVWT						1	0.660	-0.054	0.139	0.219
EVWT							1	0.106	0.137	0.222
LNKFI								1	0.213	0.959
FTHF										0.180
FTWT										1

Table 5-10. Multiple regressions of several measures of body condition and reproduction ($\underline{Y}_i$) on fecal nitrogen (FN) ($\underline{X}_i$) from mule deer fecal pellets on the Buttermilk winter range, Inyo County, California. Measures of condition and reproduction were from adult does collected in March of 1985 through 1988. FN was from monthly (November through March) composited fecal samples prior to the March collections during each respective year. Only slopes ($\underline{b}_i$) significantly ($\underline{P}$ < 0.05) different from zero are shown.

$\underline{Y}_i$	$\underline{X}_i$	Multiple $\underline{R}^2$	$\underline{b}_i$	$\underline{P}(\underline{b}_i = 0)$	$\underline{n}$
Fresh-kill weight	N.S.				
Eviscerated weight	N.S.				
LNKFI	Jan	0.18	1.1	<0.001	65
Fetal hindfoot	Mar		-32.7	<0.001	58
	Jan	0.45	11.5	<0.001	
Fetal weight	Mar		-155.4	<0.001	58
	Jan	0.36	68.2	<0.001	

ance in fetal hindfoot length. Using monthly DAPA, 42% of the variance in hindfoot length was explained by a regression that included only March (Table 5-11). This was only a slight increase over the 39% explained by the simple linear regression using March DAPA to predict fetal hindfoot length (Table 5-8). Statistically significant relationships between monthly FN and DAPA and several of the other measures also existed. However, the lower coefficients of determination of these relationships render their utility as indicators of diet quality questionable.

One might also expect a correlation between major species in the diet and nutritional indicators. In the 34 composited fecal samples from the BM range between 1984 and 1988, there was a positive correlation between the percent *Purshia* in the diet and both FN (*r* = 0.51, *P* = 0.002) and DAPA (*r* = 0.41, *P* = 0.02). There was a negative correlation between the percent *Artemisia* in the diet and both FN (*r* = -0.35, *P* = .04), and DAPA (*r* = -0.33, *P* = .059). Thus, the associations between the chemical indicators of diet quality and diet composition, although not especially close, were in the direction predicted from knowledge of feeding preferences.

On a more gross scale, the winters of 1985-86 and 1987-88 were the worst for these deer. Measures of condition and reproduction, as well as population size, dropped

Table 5-11. Multiple regressions of several measures of body condition and reproduction ($\underline{Y}_i$) on diaminopimelic acid (DAPA) ($\underline{X}_i$) from mule deer fecal pellets on the Buttermilk winter range, Inyo County, California. Measures of condition and reproduction were from adult does collected in March of 1985 through 1988. DAPA was from monthly (November through March) composited fecal samples prior to the March collections during each respective year. Only slopes ($\underline{b}_i$) significantly ($\underline{P}$ < 0.05) different from zero are shown.

$\underline{Y}_i$	$\underline{X}_i$	Multiple $\underline{R}^2$	$\underline{b}_i$	$\underline{P}(\underline{b}_i = 0)$	$\underline{n}$
Fresh-kill weight	N.S.				65
Eviscerated weight	Nov Dec	0.11	-29.1 -81.2	0.022 0.010	66
LNKFI	Dec	0.21	17.4	<0.001	66
Fetal hindfoot	Mar	0.42	-52.5	<0.001	59
Fetal weight	Mar	0.36	-259.6	<0.001	59

(Chapter 6). This is the kind of situation that should be reflected by an index of nutritional well-being. FN did reflect the poor condition of the deer in the winter of 1987-88, but not in 1985-86 (Figure 5-8). DAPA in 1985-86 was as high or higher than in any other year, and in 1987-88 it was intermediate (Figure 5-11). Thus, there was no consistent relationship between these chemicals and other indicators of herd status.

DISCUSSION

The accuracy of the microhistological technique for determining herbivore diets has been questioned (Gill et al. 1983). The criticism most relevant to the present descriptions of winter diets involves error resulting from a large proportion of shrub stems relative to leaves in the diet. Stem material has a lower ratio of identifiable to unidentifiable fragments, and thus would be underrepresented in fecal analysis, which necessarily quantifies only what is identifiable (Holochek 1982). Although this is doubtless a valid criticism in some circumstances, it is less relevant here. Whether the measured differences in relative proportions of various components of the winter diets were produced by real changes in species, from *Purshia* to *Artemisia* and back, or by changes in plant parts consumed, from leaves to stems, is less important than the fact that such changes occurred at all. Whether the animals were eating mainly Purshia stems in mid-winter, which were not identified microscopically, or mainly Artemisia, an evergreen plant with parts of constant identifiability, it means that a diet shift occurred. This shift was from the leaves of a favored, highly nutritious plant species to either a less nutritious part of the same species, or to a different species.

Further, it is most likely that the measured diet shift was in fact produced by a shift between forage species. Such has been reported from other areas using different techniques to determine diet. Leach (1956) examined stomach samples from deer from several areas in eastern California and found that bitterbrush was common only in the early winter and spring, and sagebrush was most heavily used in the winter. In Montana, Wilkins (1957) examined rumen contents and observed deer feeding, and reported a similar pattern of decreasing use of bitterbrush and increasing use of sagebrush over the winter. He related this to the heavy use of bitterbrush in the fall; when it became less available, animals used sagebrush. Tueller (1979) reported a similar pattern in Nevada evident from rumen samples. In Colorado, using a bite-count technique with tame deer, Carpenter et al. (1979) found heavier use of Artemisia as winter progressed. Thus, I do not think the diet switches measured with the fecal method reported here are simply artifacts of the technique, but rather reflect real changes in the diet, which reflect changes in availability of Purshia.

Other sources of error in the fecal technique, e.g., those associated with large forb components in the diet (Gill et al. 1983), are less important in the present case, because of the low availability of forbs during winter in this area. Fecal samples from spring and summer may have underestimated forbs.

Large within- and between-year differences in species composition in the diet were seen, particularly involving Purshia and Artemisia. Although no statistical tests of these differences could be performed, Anthony and Smith (1974) reported that pellet collections from 15 deer were sufficient to describe seasonal diets of deer in Arizona. The present data are based on at least 40 pellet groups per composited sample, and thus likely reflect real changes is species composition in the diet.

Bissell et al. (1955) suggested that sagebrush may have a deleterious effect on ruminant digestion through the effect of oils on rumen microbes; this phenomenon was subsequently confirmed by Nagy et al. (1964). Bissell et al. (1955) and Carpenter et al. (1979) related heavy (ca. 30%) use of sagebrush to weight loss in deer, and Longhurst et al. (1968) and Wallmo and Gill (1971, in Carpenter et al. 1979) related heavy use of sagebrush to heavy mortality in populations of wild deer. This deleterious effect exists despite the otherwise favorable nutrient content of sagebrush (Short et al. 1966). Reliance on sagebrush by deer in the present study was associated with poor body condition, poor reproduction, and a declining deer population (Chapter 6). In the winter of 1987-88, following the year with the lowest precipitation and least *Purshia* growth, *Coleogyne* constituted 49% and 38% of the March and April diets, respectively (Figure 5-1). This emphasizes the extreme nutritional stress of that year. *Coleogyne* is regarded as a poor forage due to its low protein, high fiber, and spinescent growth form (Provenza et al. 1983); in the present situation, it represents a starvation diet.

FN and DAPA showed consistent seasonal changes throughout the years. From a mid-winter low, they rose through the spring to maxima in May or June, and then declined through the summer and fall to low winter values. Kie and Burton (1984) found similar patterns of FN and DAPA in 2 herds of migratory black-tailed deer (*O. h. columbianus*). They reported similar summer maximum FN values of 3.0-3.5%. However, the lowest FN they reported for winter (2.1%) was above the typical values of 1.6-2.0% measured in the present study, and much higher than the minimum of 0.9% recorded here. Elliott (1982) also reported seasonal fluctuations of FN in Columbian black-tailed deer (O. h. columbianus) in coastal California, but FN (% protein divided by 6.25) was much higher than in the present study, varying between 2.90% in August and 5.65% in March. The timing of this fluctuation also reflected the local conditions of summer drought and winter plant growth.

The DAPA values reported by Kie and Burton (1984) were consistently higher than those in this study. For example, they reported typical December through April DAPA concentrations of about 0.7 mg/g; I found winter DAPA to be between 0.42 and 0.52 mg/g. Goldsmith (1988) reported seasonal variations in FN and DAPA from several pronghorn (Antilocapra americana) populations. Summer maximum FN for pronghorn ranged from 2.42 to 2.69%, somewhat lower than for the deer in the present study, and winter minima were 1.32 to 1.45%, also slightly lower. DAPA from pronghorn ranged from 0.58 to 0.82 mg/g in summer and 0.30 to 0.40 in winter, comparable to the present observations.

Kie and Burton (1984) related FN to animal condition in a general way, stating that 1 herd with lower FN in November and December was in somewhat poorer condition than the other. DAPA values showed no differences. Poor nutrition was not thought to be a factor in the pronghorn populations examined by Goldsmith (1988). I found that the lowest FN, in 1987-88, occurred in the winter following the year with the lowest precipitation and forage growth (Figures 5-7 and 5-8), and during which the deer had the lowest KFI (Chapter 6). However, in the winter 1985-86, also following a dry year and during which the deer were in very poor condition, FN was not obviously different from the other years of better precipitation and condition.

I found no close univariate relationships between the fecal chemicals and any measure of animal condition or fetal size (Tables 5-7 and 5-8). The strongest associations were between both FN and DAPA in March and fetal hindfoot length. These relationships were negative, the opposite of what would be predicted if higher fecal concentrations of these chemicals indicate a higher quality diet. One would predict that animals on a good diet, being better nourished, would have larger offspring, either from earlier onset of estrus in well-nourished does, more rapid fetal growth, or both (Verme 1963, Mansell 1974, Burrell 1982).

Multiple regression including both March and January FN revealed a somewhat stronger relationship between FN and fetal size, with these 2 variables accounting for nearly half the variation in fetal hindfoot length (Table 10). Multiple regression analysis revealed a somewhat less strong relationship between March fecal DAPA and fetal hindfoot (Table 5-11). Using several months of dietary information is reasonable biologically, because fat reserves late in winter are certainly a function of the conditions the animals experienced in the preceeding months. Regression coefficients in a multiple regression depend upon variables not in the equation, as well as those present. Thus, a straightforward interpretation of the regression coefficients, particularly in the presence of multicollinearity among the independent variables, is impossible. Some of the more obvious independent variables not in the equation that may have had an influence on the dependent variables in this case include winter weather, summer and migratory range conditions, deer population size and resulting intraspecific competition, and perhaps cumulative effects of previous years.

It is evident that FN and DAPA do have some relationship to diet. The correlations between FN and DAPA and the percents of *Purshia* and *Artemisia* in the diets, albeit not particularly high, were in the expected direction to indicate diet quality, i.e., positive for *Purshia* and negative for *Artemisia*. During the winter of 1987-88, in which the deer were under the greatest nutritional stress, FN levels were the lowest observed. The seasonal patterns evident in FN and DAPA concentrations also indicated a relationship between these chemicals and diets. Lowest in winter, increasing in spring to their highest levels in early summer, and then gradually decreasing through the fall, FN and DAPA concentrations mirrored patterns of plant growth and thus dietary quality. In addition, this seasonal pattern also argues against FN being merely a reflection of the concentrations phenolic compounds in the diet. If this were the case, FN should be lower in the spring and summer, and higher in winter. That the present winter FN and DAPA values were lower than those reported by Kie and Burton (1984) also is consistent with what is known about about population trend. The data reported here were from a population in steep decline (Chapter 6). Kie and Burton (1984) do not report trend for the populations they studied, but it is likely that it was stable or slowly declining (Kie et al. 1982).

However, the absence of close relationships of FN and DAPA to direct measures of animal condition and reproduction, and the weak associations among FN and DAPA and diet components, suggest that they will not serve as quick and easy indicators of nutritional well-being. Although there obviously is some relationship between these chemicals, plant growth, and diet, the ability of a deer manager to make evaluations of herd status simply from knowledge of FN and DAPA remains unlikely.

There are several approaches that might be helpful to elucidate further the relationships among FN and DAPA and animal diets, condition, and reproductive output. Because the present data were from a population in serious decline, observed FN and DAPA relationships may reflect only this. Knowing what happens with FN and DAPA when the population increases would provide comparative data to those from the decline, and could put the present data into perspective. Continued study of the present population during its current crash through eventual recovery, then, is recommended. Presumably, population growth will occur following a period of wet years.

Calculation of variance in FN and DAPA among individuals or sampling periods was not possible in the present study due to the composite nature of the pellet samples. This in turn was due to the study design, attempting to assess a composite index of diet quality, as well as to economic and logistic constraints. Although analyzing individual defecations would rapidly inflate the costs, this should be done to enable a determination of variation across individuals, and across time.

Variance in condition and reproduction indicated that all deer were not equal, and that individual differences did exist. Knowing variations in fecal chemistry from a sample of known, presumably captive deer on different quality diets could provide another means of understanding these relationships.

CHAPTER VI. PRODUCTIVITY AND POPULATION DYNAMICS

Macnab (1983, 1985) recommended that issues in wildlife management be resolved by experimentation to test hypotheses. One of the issues they discussed was that of 2 alternative models of the dynamics of populations of large herbivores, named the Harvestable Surplus Model and the ICC Harvest Model. The former holds that harvesting does not reduce a population from its maximum sustainable level or K carrying capacity (KCC; McCullough 1979); rather, harvesting simply substitutes for natural mortality. In contrast, the ICC ("I" carrying capacity) Harvest Model predicts that harvest will reduce population size below KCC and increase yield due to greater per capita resources in the remaining population. The essential point is that reducing density increases productivity.

These ideas, founded on the work of Pearl (1924) and going back at least to Malthus, stem from the observation that populations produce new members in a geometric progression. Concepts arising from this have been presented with varying degrees of formality in the wildlife management field for decades. Chapman (1928) developed the concept of "biotic potential" acting against "environmental resistance" to determine population size. Leopold (1933) discussed the "harvestable surplus" produced by wildlife populations. Scott (1954) discussed the sigmoid or logistic curve as a model for the growth of animal populations, and emphasized that the abscissa on such a curve can properly be relative animal density as well as time. His observation that "...there seems to be an unfortunate and growing lag between the significant advances in knowledge of population phenomena, and their practical application in the field of game management" (Scott 1954:482) has been verified repeatedly in the subsequent decades. Gross (1969) discussed the relationship between maximum harvest and maximum population size, based on a logistic or density-dependent pattern of growth. Caughley (1976, 1977) developed the topic in a largely theoretical way, and McCullough (1979) did the same empirically. Yet among contemporary wildlife managers, the notion of carrying capacity and its related concepts such as yield and harvestable surplus remain "slippery shibboleths" (Macnab 1985).

Ignoring immigration and emigration, the size of a population at any time is a function of natality and mortality. If density dependent forces operate to regulate population size, natality and mortality rates must change with population size. Thus, proximal mechanisms regulating population size can involve reproductive output, e. g., pregnancy and fetal rates, and fetal sizes. The ultimate cause, however, is density in relation to resources.

Changes in reproductive output with changes in animal density or resources have often been reported. Cheatum and Severinghaus (1950:184) observed that "alteration of deer densities in relation to available forage appears to find expression in altered rates of deer reproduction" in white-tailed deer (*O. virginianus*). Leopold et al. (1951:120) asked "...how does hunting or removal of part of the animals induce higher production of fawns in the surviving breeding herd?", and stressed density in relation to resources ("carrying capacity") in their response. This was echoed by Longhurst et al. (1952). Robinette et al. (1955) reported higher fertility among mule deer does from areas of better summer range. Julander et al. (1961) reported that mule deer from poor habitats had lower ovulation rates and body weights than deer from areas of better summer range. Teer et al. (1965) found an inverse relationship between density of white-tailed deer and reproductive performance. Gross (1969) discussed data from several studies indicating a negative relationship between reproductive output and density in deer and elk (*Cervus elaphus*). Verme (1969) confirmed the relationship between nutrition and reproduction in captive white-tailed deer.

All of these studies of wild populations were observational in nature; none included any experimental manipulation to test hypotheses. In contrast, McCullough (1979) manipulated the density of a wild population of white-tailed deer in a 464-ha reserve to test density effects on population parameters. His conclusion (McCullough 1979:190), that "...reproductive effort in the George Reserve deer herd is a function of available resources as expressed through the physiological condition of the females", mirrored those of the previously cited workers.

This part of the present study was an attempt to extend the experimental approach of McCullough (1979) to a large, wild population of migratory mule deer. The objective was to test the effects of a reduction in animal density on reproductive output. The experimental density manipulation was achieved through a public antlerless hunt on one segment of the population. The prediction was that in the years following the antlerless hunt, measures of reproduction and condition would be greater in the hunted segment than in the unhunted control. Additional related objectives were to measure precipitation, growth of favored forage, and diets in both herds, and to relate these to the demographic response of the animals.

METHODS

Study Area

The population of study was composed of the Buttermilk (BM) and Sherwin Grade (SG) deer herds, which winter on adjacent ranges at the base of the estern escarpment of the

Sierra Nevada approximately 20 km west of Bishop, California (Chapter 2).

Antlerless Hunt

Between 20 December 1984 and 13 January 1985, an antlerless hunt was held on the Sherwin Grade range during 3 4-day hunt periods. Two hundred permits were issued to public hunters. All deer reported killed in the hunt were examined, and data on age, condition and reproduction were taken. The BM deer were left as an unhunted control. The SG herd was chosen because it was smaller than the BM herd, thus the removal of a fixed number of animals would more likely have a noticeable effect on per capita resources of the herd. During this study, both herds were hunted under bucks-only regulations as usual during October.

Collections

To assess reproduction and condition, deer from both BM and SG winter ranges were shot by personnel of the California Department of Fish and Game (CDFG) during 14-20 March 1984, 12-20 March 1985, 11-13 March 1986, 23-30 March 1987, and 21-22 March 1988. Some deer also were taken on 24-25 April 1984 on the BM range. Number of adults taken in any year/herd sample ranged from 9-20. To promote unbiased sampling, the collecting teams were instructed to take the first killing shot at identifiable adult females, disregarding apparent condition, age, presence of fawns, etc. This, combined with the large amount of movement and mixing of the animals caused by the activities of the collecting teams, gave confidence to the randomness of the collected samples. Taking of female yearlings when possible also was instructed.

All deer were brought to a field processing station, measured, and weighed with a spring scale to the nearest pound. Reproductive tracts (uterus with any fetuses and ovaries) and right kidneys were removed, labelled, placed in individual plastic bags, and refrigerated; those not examined within a few days were stored at -17 deg C. Mandibles were removed for age estimation by tooth wear and replacement (Larson and Taber 1980); some also were aged by molar (Ransom 1966) and incisor (Low and Cowan 1963) cementum analysis.

In the laboratory, ovaries were sectioned by hand and examined macroscopically for the presence of corpora lutea (Cheatum 1949, Kirkpatrick 1980). Fetuses were counted, sexed, and weighed to the nearest 0.1 g; left fetal hindfoot was measured after Cheatum and Morton (1946) and Chattin (1948). For the analyses of fetal size, I used only those fetuses from does killed in March; in the cases of litter sizes of 2, I used measurements only from the larger fetus. In the analyses of pregnancy rates, I used animals from March and, in 1984, April. For analyses of condition, I used the fresh-kill and eviscerated carcass weights and kidney fat index (KFI; Riney 1955) only from those adults taken in March.

Population Size

The CDFG made total counts of both herds from a Bell Jet Ranger helicopter on 27 January 1985, 8 January 1986, 6 January 1987, and 11 January 1988. All flights were made shortly after snowfall to enhance visibility of the animals from the air and to enable the outer limits of the deer range to be established by the absence of deer tracks. In addition to the pilot, there were 2 observers and 1 data recorder. The ranges were flown in succession, at speeds of about 30-60 km/hr, and an attempt was made to count every individual. As indicated by radio-telemetry, all deer had reached their respective winter ranges by the time the censuses were conducted (Chapter 3). Rates of population growth, *r*, were calculated as the slope of the regression of the natural log of population size on time in years (Caughley 1977).

Precipitation and Vegetation

CDFG and BLM personnel measured new twig growth of antelope bitterbrush (*Purshia tridentata*) in October or November, near or after the cessation of plant growth but before the arrival of deer onto the winter range. During 1983-87 on the BM range, the lengths of 30 new terminal twigs were measured to the nearest 1.27 cm (0.5 inch) on 5 plants on each of 6 randomly located transects. During 1983-5 and in 1987 on the SG range, the lengths of 15 new twigs on 5 plants on each of 5 randomly located transects were similarly measured; no data were taken in 1986 on the SG range. I used the average from each plant in the analysis of BM data, and the average from each transect in the analysis of SG data.

The National Weather Service supplied precipitation data from the weather station at the Bishop airport, some 24 km east of and 300 m lower than the winter ranges. I assume that these data are strongly correlated with, although likely somewhat lower than, rainfall on the winter ranges. I present precipitation by "rain year", 1 July through 30 June of the following calendar year.

RESULTS

Condition

There were no significant differences in ages of adult deer in the collections as estimated by tooth wear and replacement, either by year ($\underline{F}$ = 1.811; 4, 14 df; $\underline{P}$ = 0.130) or herd ($\underline{F}$ = 0.125; 1, 145 df; $\underline{P}$ = 0.724), nor was there a significant herd by year interaction ($\underline{F}$ = 0.052; 4, 145 df; $\underline{P}$ = 0.995). Although fresh-killed carcass weights of adult does were not significantly different between herds ($\underline{F}$ = 1.994; 1, 150 df; $\underline{P}$ = 0.160), the differences among years were significant ($F = 4.695$; 4, 151 df; $P = 0.001$), as was the herd by year interaction ($F = 2.724$; 4, 151 df; $P = 0.032$) (Figure 6-1). To remove the effects pregnancy may have had on body weights, I compared eviscerated carcass weights of all does (Figure 6-2). Again, differences among years were significant ($F = 7.745$; 4, 151 df; $P < 0.001$), but differences between herds were not ($F = 0.529$; 1, 151 df; $P = 0.468$), nor was the year by herd interaction ($F = 1.527$; 4, 151 df; $P = 0.197$).

KFI showed large differences over years (Figure 6-3). Variances of KFI were heterogeneous over years (Bartlett-Box $F = 24.644$, $P < 0.001$; Norusius 1986). The distributions of KFI, especially in 1984, were positively skewed; most deer had relatively low KFI's, and a few had high KFI's. Log-transformation of KFI yielded homogeneous variances (Bartlett-Box $F = 1.460$, $P = 0.212$;), and the log-transformed KFI (LNKFI) was used in the subsequent analyses. Two-way analysis of variance indicated that LNKFI differed over years ($F = 14.509$; 4, 139 df; $P < 0.001$) and between herds ($F = 4.240$; 1, 139 df; $P = 0.041$), with no significant herd by year interaction ($F = 0.319$; 4, 139 df; $P = 0.865$).

Reproduction

All adult SG females were pregnant in all years with the exception of 1988, when 18 of 19 were pregnant (Figure

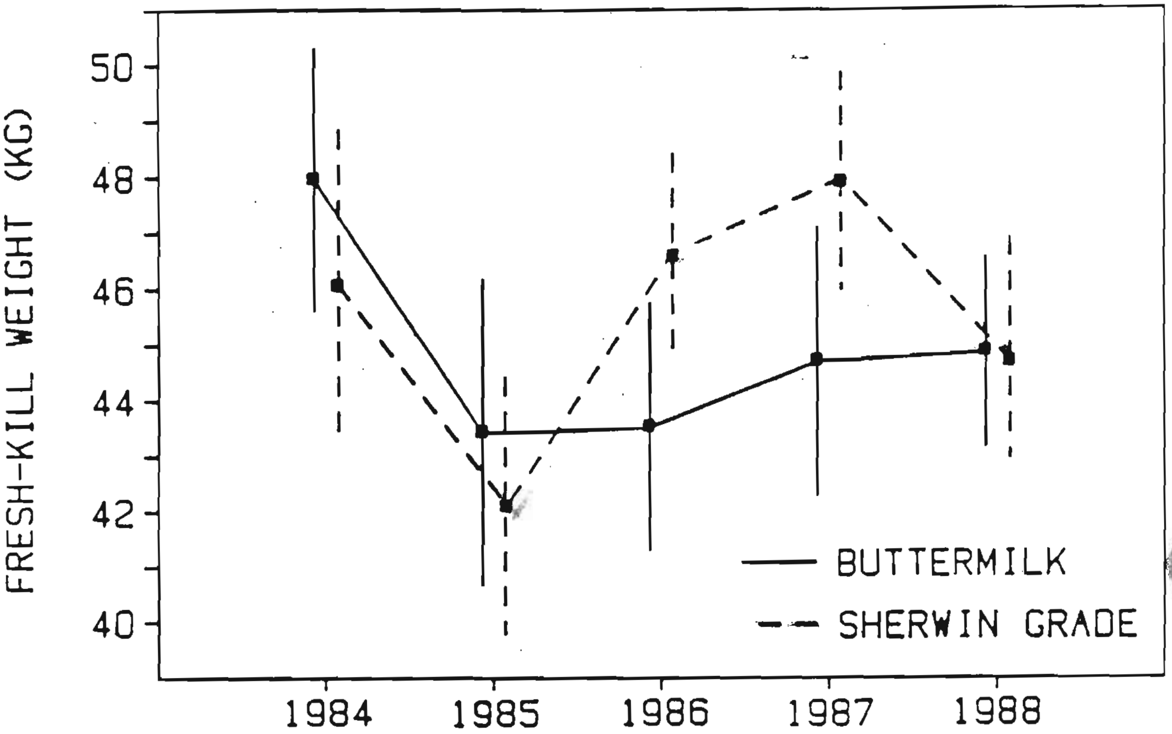

Figure 6-1. Fresh-kill weight (mean ± 95% CI) of adult female mule deer from the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, Calif., March 1984 through 1988. Sample sizes are shown near means.

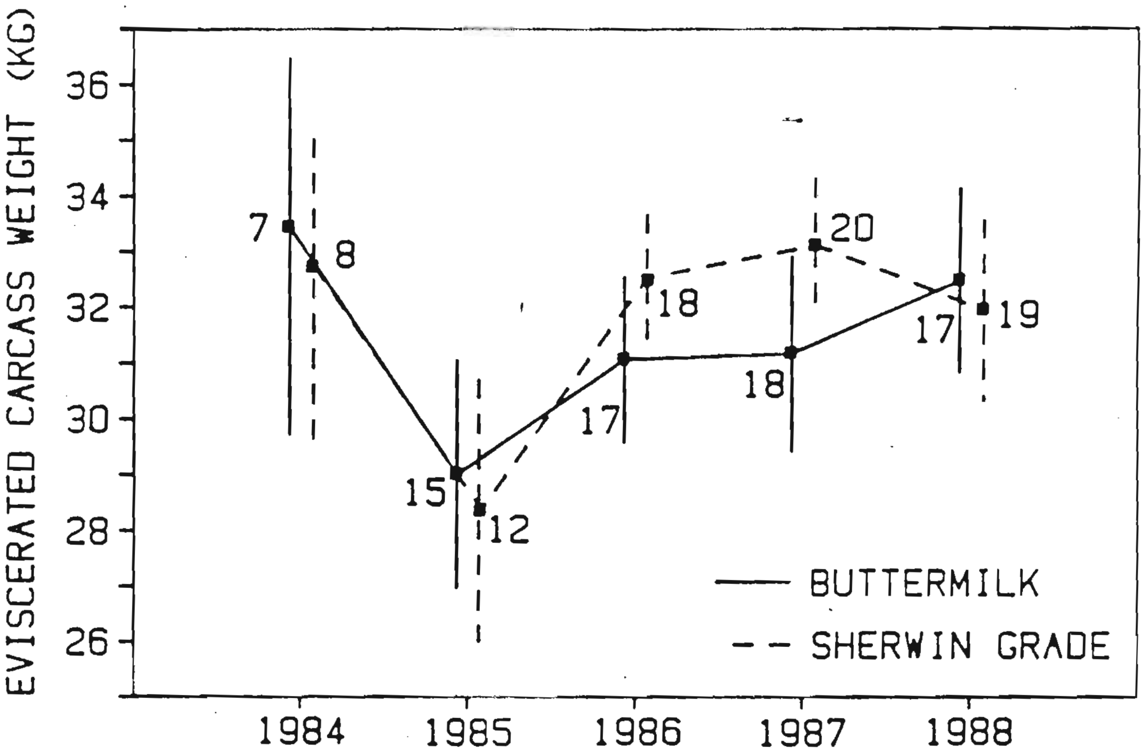

Figure 6-2. Eviscerated carcass weights (mean + 95% CI) of adult female mule deer from the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, Calif., March 1984 through 1988. Sample sizes are shown near means.

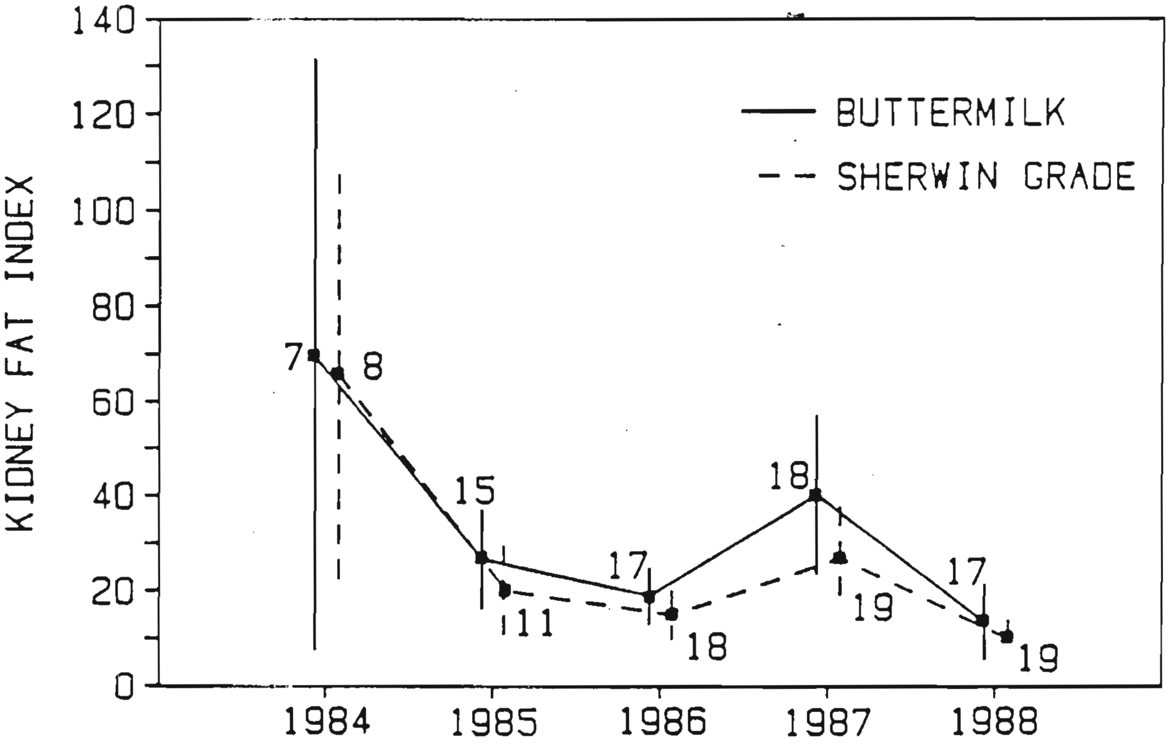

Figure 6-3. Kidney fat indexes (mean + 95% CI) from adult female mule deer from the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, Calif., March 1984 through 1988. Sample sizes shown near means.

6-4). Among BM adults, the pregnancy rate dropped from 100% in 1984 to 71% in 1986, then increased to 100% in 1988. The proportions of BM and SG does pregnant in 1986, 12 of 17 and 18 of 18, respectively, were significantly different ($\underline{P} < 0.01$, Rohlf and Sokal 1981, Table 23). Both yearling females in the 1984 BM sample, and 1 of 3 in the 1988 BM sample, were pregnant, all with singlets. In 1986 and 1987, none of the 3 and 2 BM yearlings, respectively, was pregnant, nor was any of the 3, 2, or 1 SG yearlings pregnant 1985, 1986, and 1988. No yearling was present in any other sample collection.

Mean fetal rate among adult BM does declined from an average of 1.88 fetuses/doe in 1984 to 1.06 in 1986, increased to 1.42 in 1987, then decreased to 1.29 in 1988 (Figure 6-5). Variances over years in BM fetal rates were not homogeneous (Bartlett-Box $\underline{F} = 3.321$, $\underline{P} = 0.010$); furthermore, counts of fetuses probably were not normally distributed at the sample sizes used. I therefore tested differences over years with the Kruskal-Wallis test (Sokal and Rohlf 1981), which indicated statistically significant differences over years in the BM deer ($\underline{H} = 12.14$, 4 df, $\underline{P} = 0.016$), but not among SG deer ($\underline{H} = 6.09$, 4 df, $\underline{P} = 0.19$). The fetal rates among BM deer in 1984 and 1986 were different (Mann-Whitney $\underline{U} = 226$, $\underline{P} = 0.005$).

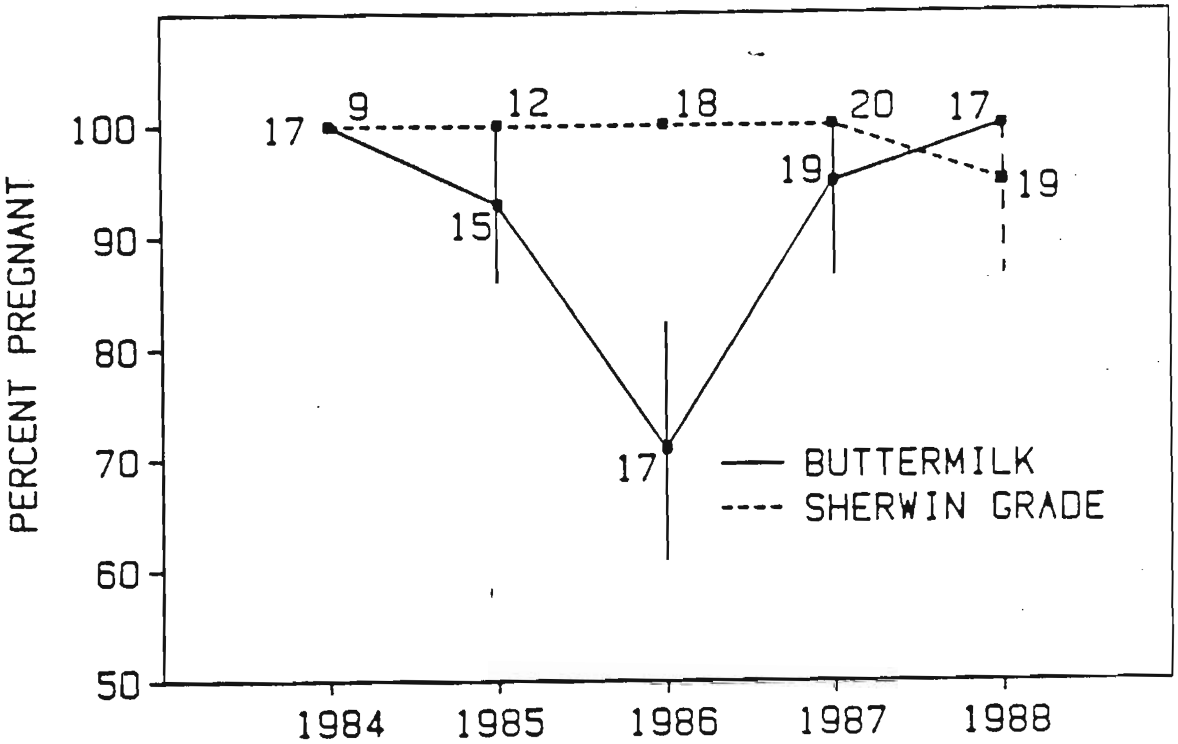

Figure 6-4. Pregnancy rates (mean ± SE) of adult female mule deer from the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, Calif., March 1984 through 1988. Sample sizes shown near means.

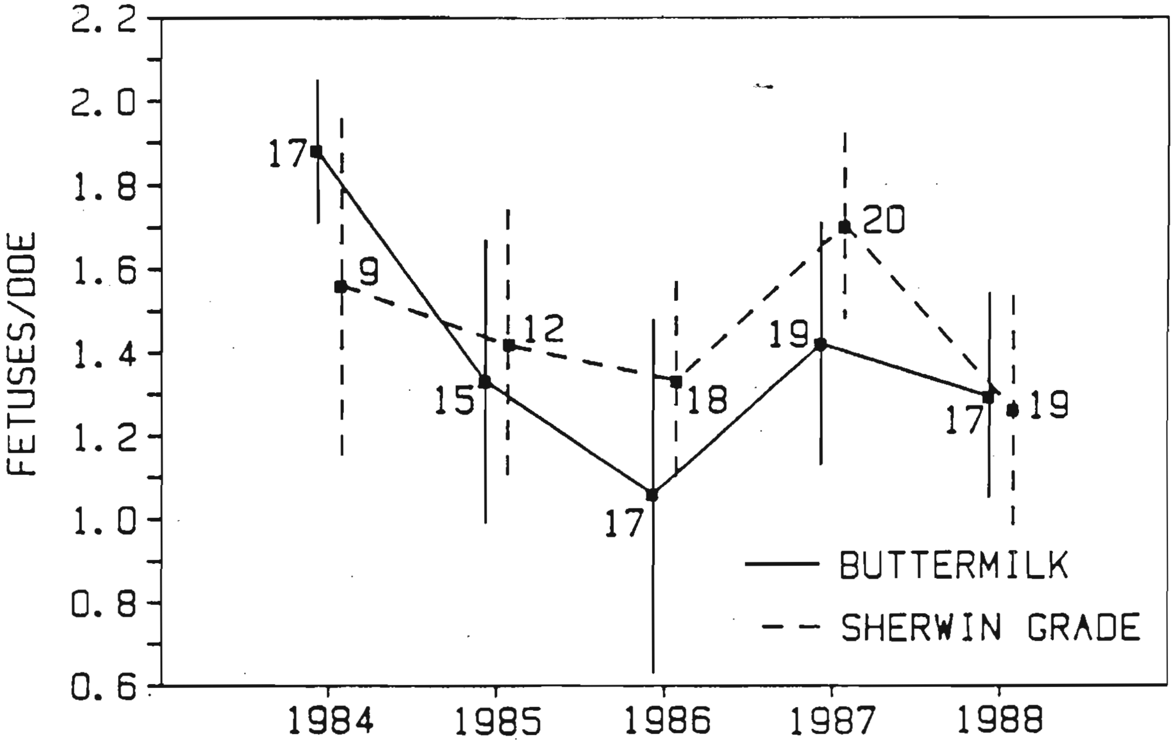

Figure 6-5. Fetal rates (mean ± 95% CI) of adult mule deer from the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, Calif. Sample sizes shown near means.

Excluding does that did not breed, litter sizes of pregnant does varied over years in the BM deer (Kruskal-Wallis $\underline{H} = 9.56$, 4 df, $\underline{P} = 0.049$) but not in the SG deer ($\underline{H} = 5.42$, 4 df, $\underline{P} = 0.247$) (Figure 6-6). Thus, does varied their reproductive output in 2 ways: by breeding or not, and by varying litter size.

Two-way analysis of variance indicated that fetal hindfoot length varied significantly over years ($\underline{F} = 12.788$; 4, 133 df; $\underline{P} < 0.001$) and between herds ($\underline{F} = 5.516$; 1, 133 df; $\underline{P} = 0.020$) (Figure 6-7). There also was a significant herd by year interaction ($\underline{F} = 2.746$; 4, 132 df; $\underline{P} = 0.031$).

Census

Total numbers counted in the BM and SG herds dropped about 50% and 60%, respectively, between 1985 and 1988 (Figure 6-8). Buttermilk deer declined from 3657 in 1985 to 1879 in 1988, with the decline evident in the last two years. Sherwin Grade totals decreased from 2321 to 931, with declines in all years. This represents a mean observed $\underline{r}$ of -0.23 on the BM range and -0.30 on the SG range during January 1984 to January 1988.

Precipitation and Vegetation

Two-way analysis of variance indicated no difference between twig growth of bitterbrush on BM and SG ranges in 1983-85 and 1987 ($\underline{F} = 0.01$; 1, 125 df; $\underline{P} = 0.95$). In

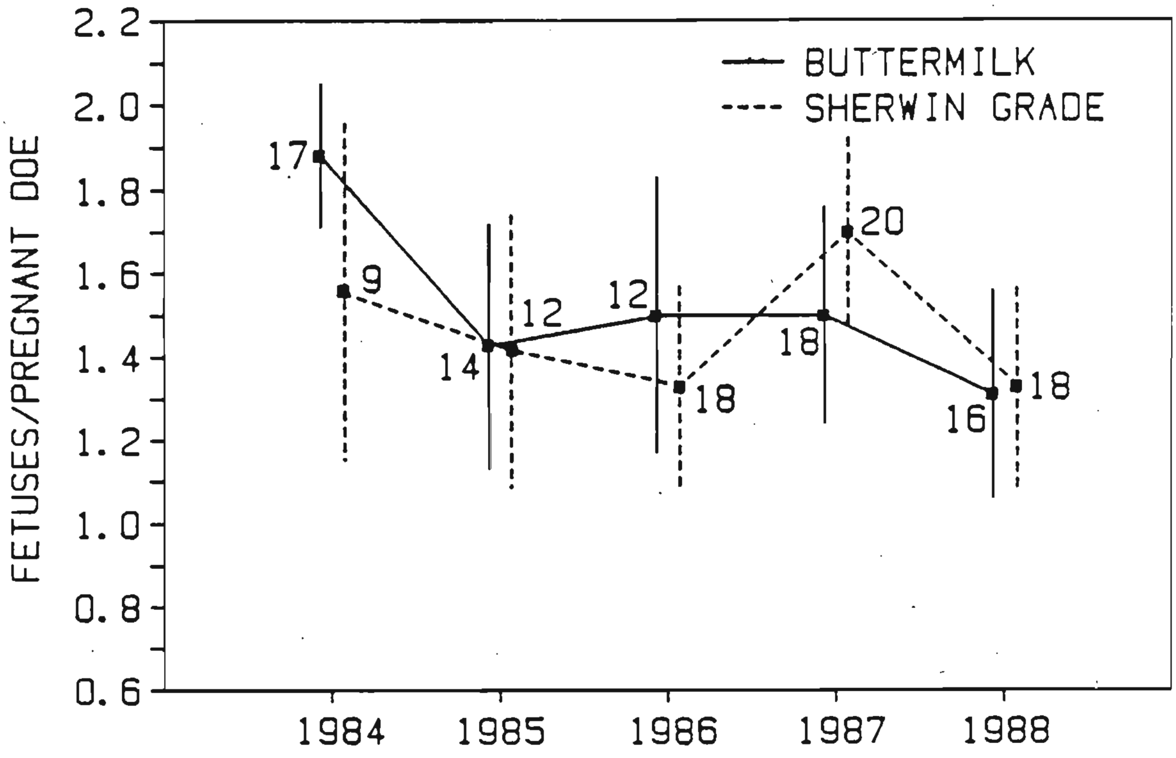

Figure 6-6. Fetal rates (mean + 95% CI) of pregnant adult mule deer from the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, Calif. Sample sizes shown near means.

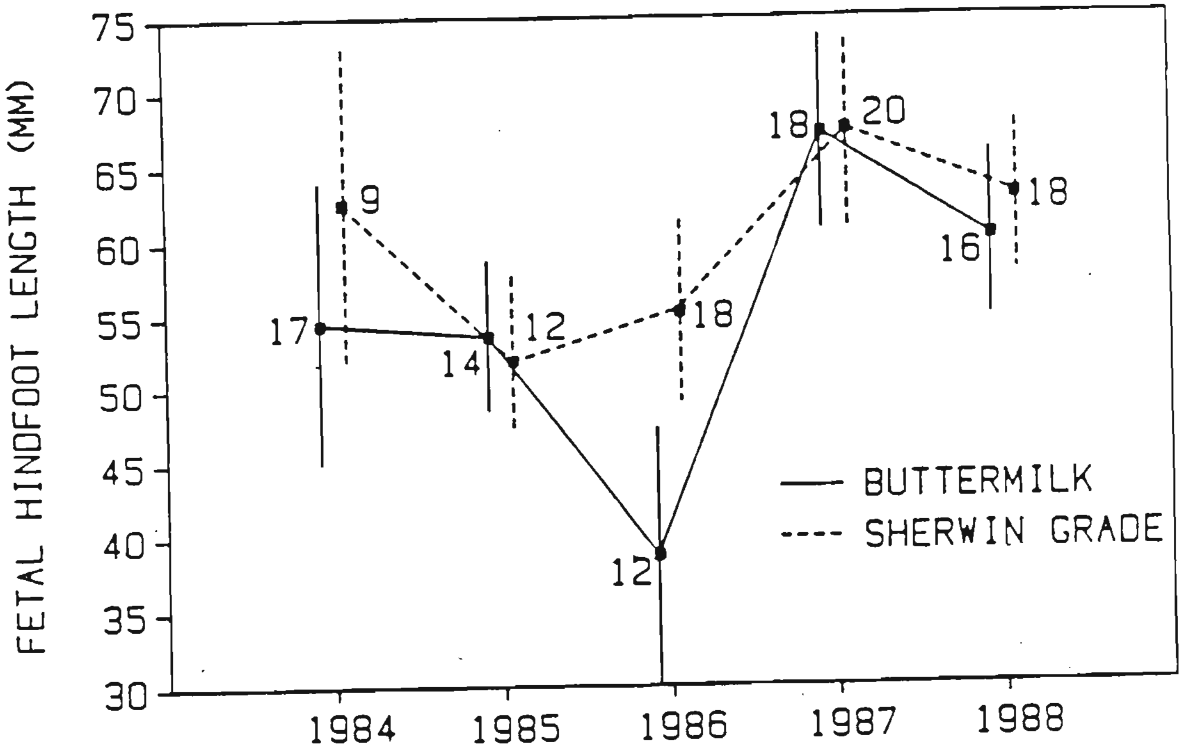

Figure 6-7. Hindfoot lengths (mean ± 95% CI) of fetuses carried by adult mule deer collected on the Buttermilk (BM) and Sherwin Grade (SG) winter ranges, Inyo and Mono Counties, Calif., in March of 1984 through 1988. Sample sizes shown near means.

From Kucera (1989)

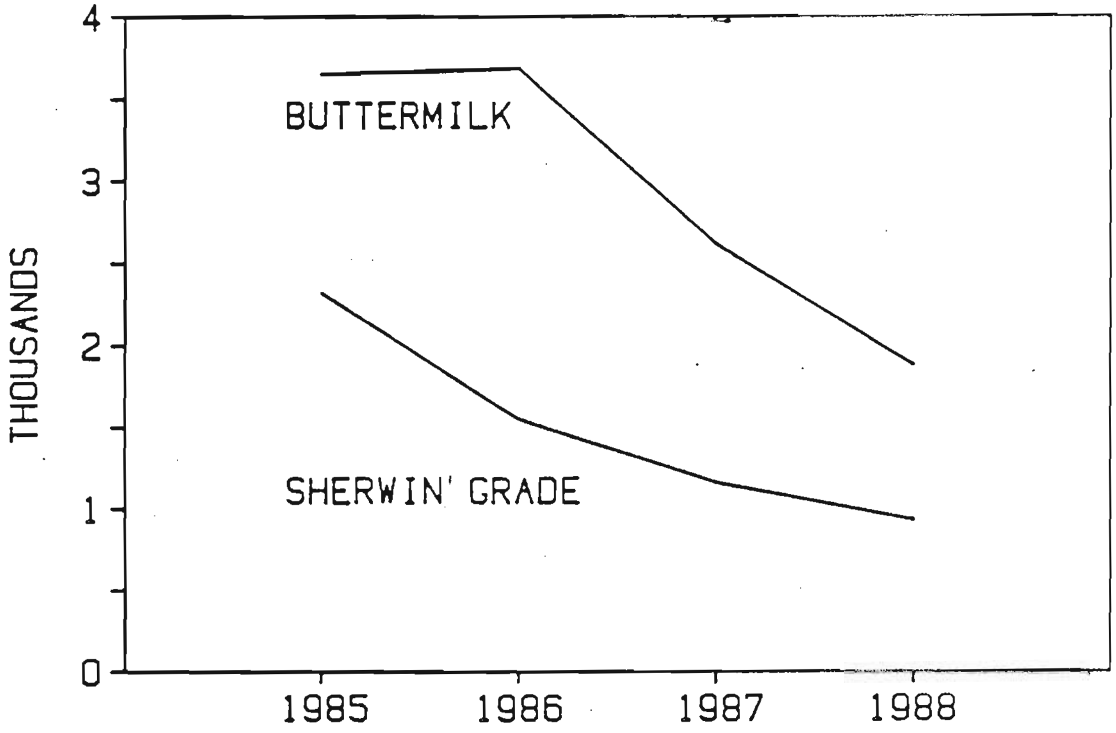

Figure 6-8. Numbers of mule deer counted on the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono Counties, Calif., in January 1985 through 1988.

subsequent analyses I used only the more complete data from the BM range. Differences in bitterbrush growth over years were highly significant ($\underline{F}$ = 75.01; df = 4, 140; $\underline{P} < 0.001$) (Figure 5-7).

Mean annual precipitation at the Bishop airport during the years 1982 through 1987 was 16.9 cm (range 5.3-25.4 cm, standard error 3.0; Figure 5-7), very close to the mean (14.5 cm), range (3.8-45.8), and standard error (3.0 cm) measured in 1951 through 1987 (Chapter 2). Annual precipitation for the years 1951 through 1987 was not autocorrelated (Durban-Watson $\underline{D}$ = 2.41, $\underline{n}$ = 37, $\underline{P} < 0.01$).

Annual bitterbrush growth largely mirrored the precipitation total in the year preceeding plant growth (Figure 5-7). Heavy precipitation in 1982-3 was followed by a large growth of forage in 1983, available to deer in the winter of 1983-4. The same occurred in 1985-86. Between these years was a period of declining forage production. The drought year of 1986-87 resulted in almost no new twig growth of Purshia. The only measurable, i.e., >1 cm, twig growth in the fall of 1987 was on 3 plants that occurred near perennial springs.

Relationships between Precipitation and Purshia Growth, and Deer Reproduction and Condition

Simple linear regression indicated that more than half of the variation in annual growth of bitterbrush in the years 1983 to 1987 was explained by the previous year's precipitation ($\underline{R}^2 = 0.52$, $\underline{P} < 0.001$). The direct relationships among either of these variables and measures of condition and reproduction, however, were much weaker. Simple linear regressions of fresh-kill weights, eviscerated carcass weights, fetal hindfoot lengths and litter sizes on mean annual Purshia growth and total annual precipitation the previous year were either non-significant or resulted in $\underline{R}^2 < 0.09$. LNKFI was related to both Purshia growth and precipitation ($\underline{R}^2 = 0.26$ and 0.25, and $\underline{P} < 0.001$ and $\underline{P} = 0.006$, respectively).

DISCUSSION

Both deer herds declined during the time of this study, with numbers in January 1988 being about half of what they were in January 1985. This was presaged by the decrease in KFI's between March of 1984 and 1985 (Figure 6-3). Due to the connective tissue around the kidney, a KFI below about 15% indicates essentially no kidney fat, and is approximately the level at which deer begin to deplete femur marrow fat for energy (Harris 1945, Riney 1955, Hanks 1981, Kie et al. 1984). In March of 1985, 1986, and 1988 both BM and SG deer had mean KFI's of between 10% and 27%, which indicated the extremely poor condition of both herds. Further, these samples were necessarily biased toward those deer expected to be in better condition, i.e., those that survived the winter. The deer in worst condition no doubt were already dead when the collections were made in March. Asynchronicity in nutritional status has been observed in deer during starvation experiments and has been suspected in wild populations (deCalesta et al. 1977). Such asynchronicity may be inferred from a large variance in KFI, such as seen in 1984. In subequent years, both means and variances were low, indicating that most deer were near the edge of starvation.

The trend in KFI was also seen in pregnancy rates, fetal rates, and fetal sizes, especially among BM deer (Figures 6-4, 6-5, 6-6, 6-7). The importance of maternal nutrition to reproduction has been demonstrated repeatedly (Verme 1965, 1977; Julander et al. 1961; Robinette et al. 1973; Ozaga and Verme 1982). The high values of the measures of reproduction in March of 1984 followed a wet year with high forage production in 1982-83, which itself was preceeded by several years of average or above average precipitation (Chapter 1). Specifically regarding fetal sizes, maternal nutrition can influence the onset of estrus, thus affecting age and size of fetuses measured at a given time (Verme 1965, Mansell 1974). Maternal nutrition can also affect the rate of fetal growth. Although Verme (1963) found effects of maternal condition on the size of fetuses of penned white-tailed deer (_O. virgin-_

ianus) only in the last third of gestation, Bartmann (1986) found that fetal growth rates of wild mule deer differed according to winter severity. Thus, the differences in sizes of fetuses measured in March of the years of this study were related to maternal condition through timing of breeding, differential fetal growth, or both.

Another possible explanation of the yearly differences in fetal size, especially in the BM 1986 sample, is that low buck ratios caused delayed breeding. CDFG herd composition counts indicated 7 bucks:100 does on the BM winter range in the fall of 1985. One hypothesized cause of small fetal size in 1986 was that so few males in the population might be unable to impregnate the females within a short period of time. This would result in smaller, i.e., younger, fetuses in March, and fewer pregnancies. Presence of males also may induce early estrus in deer (Verme et al. 1987). However, the same buck ratio occurred the subsequent year, when pregnancy rates, fetal rates, and fetal sizes all increased. This makes it unlikely that too few bucks in the population caused the poor reproduction observed in the BM 1986 sample.

My original hypothesis was that the deer populations were at ecological carrying capacity, and that a density reduction in one would lead to an increase in reproductive output and condition relative to the other. An underlying assumption of this hypothesis was the presence of a relatively stable environment. Within this environment, the deer population was assumed to interact with relatively stable food resources to determine deer numbers and reproductive output around some kind of density-dependent equilibrium. In other words, the assumption was of fixed resources determining a fixed carrying capacity.

This assumption was false. Precipitation in the study area was extremely variable, and the growth of a major forage species of deer was correlated with precipitation. KFI was the only measure of reproduction or condition that was related to precipitation or forage growth, and even these relationships were weak. However, the absence of close relationships between precipitation or vegetation and condition and reproduction could have been because the population was declining so rapidly. A reversal of population trend may be necessary to derive predictions of population performance from knowledge of precipitation or plant growth.

Regarding the differences between the BM and SG herds in 1984 to 1986, particularly in pregnancy rates (Figure 6-4), fetal rates (Figure 6-5), and fetal size (Figure 6-8), it is likely that the drought-caused reproductive crash seen in the BM deer was avoided by the SG deer because of the density reduction of the latter in 1985. This is consistent with the population decrease from 1985 to 1986 in the SG herd, in contrast to the stable BM population size during the same period (Figure 6-8). Subsequently, numbers of both herds decreased through 1988, when both were similar in reproduction and condition. Although assigning causality is weakened by the absence of replicates of the "treatments", i.e., density reduced and not reduced, the differences seen in the BM and SG herds in the year following the antlerless hunt were consistent with predictions. Following several years of decreasing precipitation and forage, the BM deer showed decreases in body weight, pregnancy rate, fetal rate, and fetal size in 1986. The SG deer, under the same environmental conditions, but having been reduced in number the previous year, showed lesser or no such changes. In subsequent years, both herds were identical. Thus, the effects of the drought, evident in the BM animals, were ameliorated in the SG herd.

The confidence with which one can be sure that a modest reduction in numbers resulted in no change in reproductive output in the presence of declining nutritional resources, however, seems less important to understanding the workings of this this system than the fact that there was such a dramatic decline in deer numbers over the course of this study. The concept of density dependence, within which the hypothesis was framed, may be insufficient for a complete understanding of the dynamics of extremely variable systems. In such situations, an equilibrium may never be achieved and KCC may be more a statistical abstraction than a reality. Wehausen et al. (1987) demonstrated the contribution of several factors, including precipitation and disease as well as animal density, to variation in lamb recruitment in a mountain sheep (*Ovis Canadensis*) population in the California desert. In Australia, Caughley et al. (1987) studied rainfall, plant, kangaroo (*Macropus rufus* and *M. fuliginosus*), and domestic sheep dynamics in arid rangelands. Caughley (1987) argued that when the coefficient of variation (standard deviation divided by the mean; CV) of annual precipitation exceeds 30%, the concept of ecological carrying capacity, against which changes in herbivore density are evaluated to examine density dependence, loses its usefulness and inhibits understanding of the dynamics of the system.

There are many ecological differences between the precipitation-vegetation-herbivore systems of Australia and the eastern Sierra Nevada of California. Rainfall in Australia was unpredictable by month and year; in the present study area, annual total precipitation was unpredictable, but highly seasonal, with most occurring in winter (Chapter 1). The vegetation in Australia was composed mainly of ephemerals, annuals, and short-lived perennials. In the eastern Sierra Nevada, the major winter forage species were long-lived perennials. Kangaroos were sedentary, and aseasonal or mildly seasonal breeders. Deer in the Sierra are emphatically migratory (Chapter 3), and strongly seasonal breeders.

In both areas, however, the important common factor was low and variable precipitation and its effect on plant growth. In Australia, average annual precipitation was 236 mm, with a CV of 45%. Bishop, California, averaged 145 mm annual precipitation, with a CV of 61%. In neither area was the amount of precipitation correlated with that of previous years. The CV of plant biomass in Australia was 100%; the CV of annual mean *Purshia* twig growth on the BM range between 1983 and 1987 was 75%. Further, some aspects of the Great Basin Desert Shrub-migratory mule deer system in the eastern Sierra may enhance its variability. Precipitation, although seasonal, was lower and more variable than that in Australia. Mule deer, because of their seasonal breeding, cannot respond as rapidly to favorable conditions as kangaroos, with their aseasonal or less seasonal breeding, post-partum estrus, shorter estrous cycles, and delayed implantation (Shepherd 1987). This variable precipitation, and the probable lag in reproductive response to favorable conditions, may serve to increase the variability of the system and make the concept of ecological carrying capacity even less meaningful in the eastern Sierra Nevada than in arid Australia. However, there are management strategies appropriate to such a variable system, and which may dampen the characteristically large fluctuations in herbivore numbers (Chapter 8).

Caughley (1987) referred to the "centripetality" of the Australian system, to avoid confusion arising from the term "stability". In a centripetal system, "...the forces causing temporal variation may be so powerful, continual and multidirectional that the ´equilibrium´ is seldom or never occupied...a centripetal system is one that would come to equilibrium if it were not buffeted continually" (Caughley 1987:161).

Centripetality in Australia was maintained by 2 negative feedback loops, without which the system would break down. One involved plant biomass and plant growth: above a certain biomass, plant growth slows, then stops, The other feedback loop involved kangaroo biomass and plant biomass: as kangaroo numbers increased, they ate more, plant biomass decreased, and kangaroo numbers decreased. A third potential feedback loop, between kangaroos and natural predators, was eliminated by European settlers.

Centripetality in the present population of deer is yet to be established. There are no direct measurements of feedback between plant biomass and plant growth, nor between animal density and plant growth. The presence of a third feedback loop, between deer and predators, especially mountain lions (*Felis concolor*) and possibly coyotes (*Canis latrans*), and its effect on centripetality, are also unknown, but potentially important (Chapter 8). The present study covered only a period of negative growth, so there is no way to determine if this system is centripetal, chaotic, or moving toward the loss of its largest herbivore. One would predict that following several wet years, the population will increase, tracking forage supplies, until the next drought reduces the population again. Given the variability in precipitation, another drought seems a certainty, and any management policies need to recognize this. Tracking the population during a recovery may allow evaluation of the system's centripetality, allow understanding of its dynamics during a period of growth, and guide management policies and actions.

CHAPTER VII. FETAL SEX RATIOS

Trivers and Willard (1973) predicted that females could adjust offspring sex ratios to maximize their own genetic representation in future generations. Specifically, they suggested that in polygynous mammals in which male reproductive success varies more than that of females, in which parental investment can influence condition of young, and in which such early condition advantage confers later breeding success, females in good condition should have more males. This follows because in such polygynous species, males of larger body or weapon size or greater strength will be more successful in reproduction than smaller competitors. Thus, a female with the ability, i.e., one with sufficient resources or "condition", to make a larger investment in offspring relative to other females in the population should tend to produce males. Because most females breed, maternal investment in female offspring has relatively less influence on female offspring reproductive success.

Trivers and Willard (1973) used caribou (*Rangifer tarandus*) in the formulation of their model, and cervids seem particularly appropriate animals in which to look for adaptive sex ratio variation. Their polygynous breeding systems, their dependence on vegetation which may vary widely in quantity and quality, and the wealth of information about them make cervids likely candidates to display such a phenomenon. This model of adaptive variation of offspring sex ratio has been challenged, refined and modified since its proposal. Verme (1965, 1969, 1985) examined reproductive data from penned white-tailed deer (*Odocoileus virginianus*) and found a relationship opposite to that predicted by Trivers and Willard: malnourished females produced an excess of males, and those in better condition produced an even sex ratio or an excess of females. Verme (1983) examined results from the literature on the genus *Odocoileus* and found a negative correlation between fecundity rate (fawns/adult doe), as an indicator of maternal condition, and proportion of male fawns. He also found that among breeding fawns, and in litters of 1, males were more frequent, which he interpreted as being counter to the Trivers and Willard hypothesis.

McCullough (1979) found that sex ratio varied with population density, and presumably maternal condition, in a wild population of white-tailed deer, but also in a direction opposite from that predicted by the Trivers and Willard model. At low densities, these deer produced more females; at high densities, more males. McCullough (1979) posited a model to explain this based upon the differential timing of offspring production during the lives of males and females. Because females begin reproducing at a younger age than do males, a female that produced a female at a low population density, at the beginning of a period of population growth, would already have many descendents by the time a son born at the same time would achieve dominance status and begin to reproduce.

DeGayner and Jordan (1987) examined fetal sex ratios in well-nourished white-tailed deer and reported a negative relationship between proportion of male fetuses and age of mother. They negated nutritional causes, and invoked a social explanation. Assuming that (1) age is related to dominance, (2) dominant females control favorable patches of fawning habitat and can influence a daughter's acquisition of such, and (3) males disperse from natal areas, older females can increase their fitness by producing more females, which will inherit their own favorable habitat. Young females have no such control over habitat inheritance, and thus should favor male offspring. These authors found no relationship between maternal age and proportion of males in single litters.

In wild reindeer (R. t. tarandus), Skogland (1986) found that smaller mothers from poor range produced more males and larger mothers from good range produced more females, again counter to Trivers and Willard's (1973) model.

Clutton-Brock et al. (1986) investigated offspring sex ratio relationships in red deer (Cervus elaphus), and found that this species does conform to the predictions of Trivers and Willard (1973). High-ranking mothers were more likely to produce males. The males born to dominant females were more reproductively successful than females, and females of subordinate mothers were more successful than males. High maternal rank was also associated with larger body size, and larger body size was associated with larger offspring weight. Additional support for the Trivers and Willard (1973) predictions comes from studies on bison (Bison bison; Rutberg 1986), wood rats (Neotoma floridana; McClure 1981), and coypus (Myocaster coypus; Gosling 1986a).

Williams (1979) proposed a model for the optimization of offspring sex ratio for a species in which litter size is usually 2, but which can vary from 1 to 3, and in which males are slightly more expensive to produce. According to this model, as the ability to provide maternal investment increases, the sex ratio and litter size should go from 1 female to 1 male to twin females to mixed sex twins to male twins. McGinley (1984) and Gosling (1986b) discussed this "fractional offspring hypothesis", and Gosling (1986b:895) stressed the need for precise information about parental investment ability to avoid a "Panglossian interpretation investment ability to avoid a "Panglossian interpretation of every offspring sex-ratio result".

Myers (1978) reviewed the data cited by Trivers and Willard (1973) in support of their hypothesis and found them wanting. For example, the difference in sex ratios of deer produced after mild and harsh winters (Robinette et al. 1957) discussed by Trivers and Willard was not statistically significant. Myers (1978) proposed an alternative hypothesis based upon differential mortality of the sexes, and predicted that animals in poor condition will produce more of the cheaper sex, in order to maximize number of offspring.

Caley and Nudds (1987) hypothesized that local resource competition better explains the male bias of sex ratios produced by nutritionally stressed Odocoileus mothers. According to this reasoning, the overall costs of producing females, which remain on the maternal range for several years, are greater than the costs of producing males, which disperse as yearlings. These authors also speculated that the Odocoileus and Rangifer sex ratio data do not fit the Trivers and Willard model because of the lower variance in reproductive success between the sexes in these species relative to Cervus and Bison (Lott 1981, Rutberg 1986).

The objective of the present paper is to examine fetal sex ratios in a large, wild population of mule deer (*O. hemionus*) and test the predictions of Trivers and Willard with respect to the influence of maternal condition on sex ratio of offspring.

METHODS

Deer from the Buttermilk and Sherwin Grade deer herds, Inyo and Mono Counties, California (see Chapter 2), were collected by personnel of the California Department of Fish and Game each year during March, 1984 through 1988, and April, 1984. The primary purpose of the collections was to assess condition and reproduction in these animals. To minimize bias in the sampling, shooters were instructed to take females without regard to apparent condition, presence of fawns, etc. Only litters from adult females, i.e., ≥2 yrs old, were used in the present analysis. Fetuses were approximately 2-3 months old, and were readily sexed by external genitalia. The total sample included 163 litters and 233 fetuses. Number of litters varied between years from 26 to 36. Eight females were not pregnant. Fresh-kill weight was determined in the field, and right kidnys removed to determine kidney fat index (KFI; Riney 1955). Mandibles were removed, and age was estimated by tooth wear and replacement (Larson and Taber 1980).

In analyses involving fetal sizes, only March collections ($N = 151$) were used. I used analysis of variance to examine differences in fresh-kill weight, eviscerated carcass weight, KFI, and age among groups defined by litter size and sex ratio. I examined group variances for homogeneity, and used log transformations on any data where the assumption of homogeneity of variances was not met with untransformed data. I used the Newman-Keuls test in multiple comparisons of group means.

RESULTS

There were 117 males and 116 females among the 233 fetuses sampled. Among the 78 litters of 2 (47.9%), the frequencies of sex ratio categories differed from binomial expectation ($G = 8.304$, 2 df, $P < 0.025$; Figure 7-1). Among litters of 2, twin females occurred more often than would be expected by chance, and twin males and mixed sex litters ocurred less often. Among the 77 single litters (47.2%), males were significantly more frequent than females ($G = 5.80$, 1 df, $P < 0.025$).

Average annual fetal sex ratio was uncorrelated with average annual fetal rate over the 5 years of study ($P = 0.80$). There was no relationship between fetal sex ratio and maternal age, considering all litters together, or with twin and single litters considered separately (Figure 7-2).

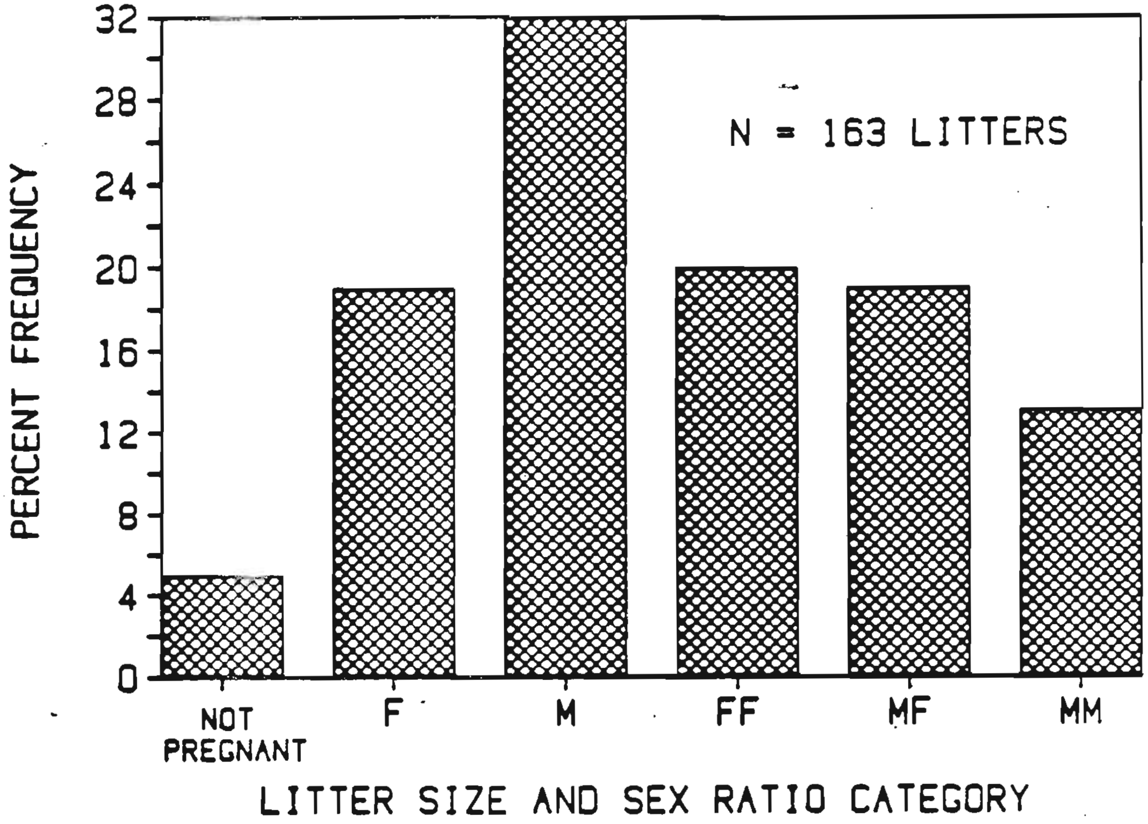

Figure 7-1. Frequency distribution of litter size and sex ratio categories from adult female mule deer collected on the Buttermilk and Sherwin Grade ranges, Inyo and Mono Counties, Calif., 1984 through 1988. Categories are as follows: F, single female; M, single male; FF, twin females; MF, mixed twins; MM, twin males.

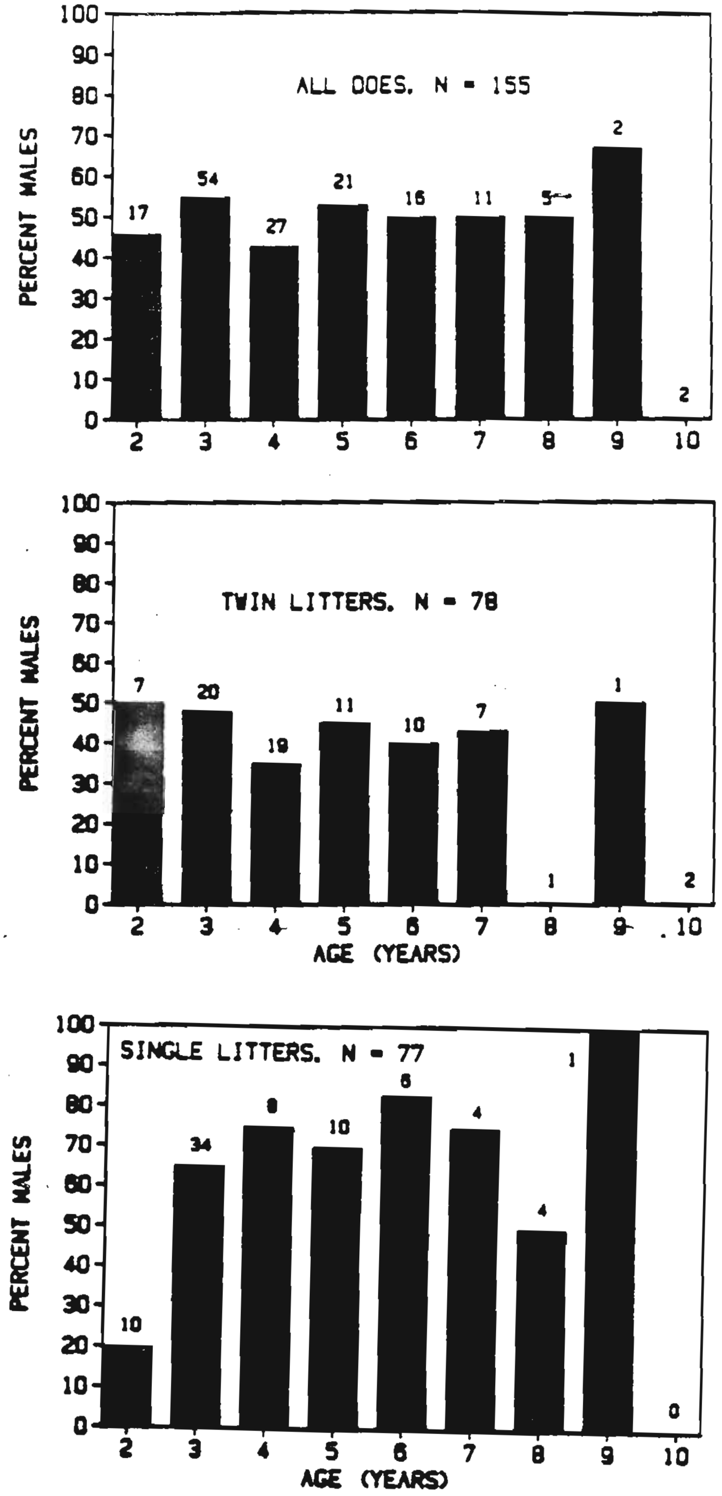

Figure 7-2. Sex ratios of mule deer fetuses by age of mother and litter size, from deer collected on the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono Counties, Calif., 1984 through 1988.

Fresh-kill weights of does differed among litter size and sex ratio categories (*F* = 6.90; 5, 153 df; *P* < 0.0001). Females with twin litters were heavier (*P* < 0.05) than females with single litters or non-breeding females. Among females with twin litters, there were no significant differences among the various sex-ratio categories. There were no significant differences among fresh-kill weights of females with single males, single females, or those not breeding.

Arranging litter categories according to the scheme of Williams (1979) revealed that the relationship between maternal weight and offspring number and sex ratio was what would be predicted (Figure 7-3). The heaviest mothers tended to produce male-biased litters.

KFI also was asociated with litter category (*F* = 4.48; 5, 152 df; *P* = 0.0008). Females with twin males had significantly higher log KFI's than any other category except non-breeding females, and this was likely a result of sample size (Figure 7-4). Females with the greatest KFI's tended to have litters of 2 males; females with mixed litters, or those with 2 females, had lower and approximately equal KFI's. Females with single litters and those not pregnant had the lowest KFI's.

Twin male litters were heavier than litters of twin females (*t*= 2.16, *P* =0.036, 2-tailed), with mixed litters

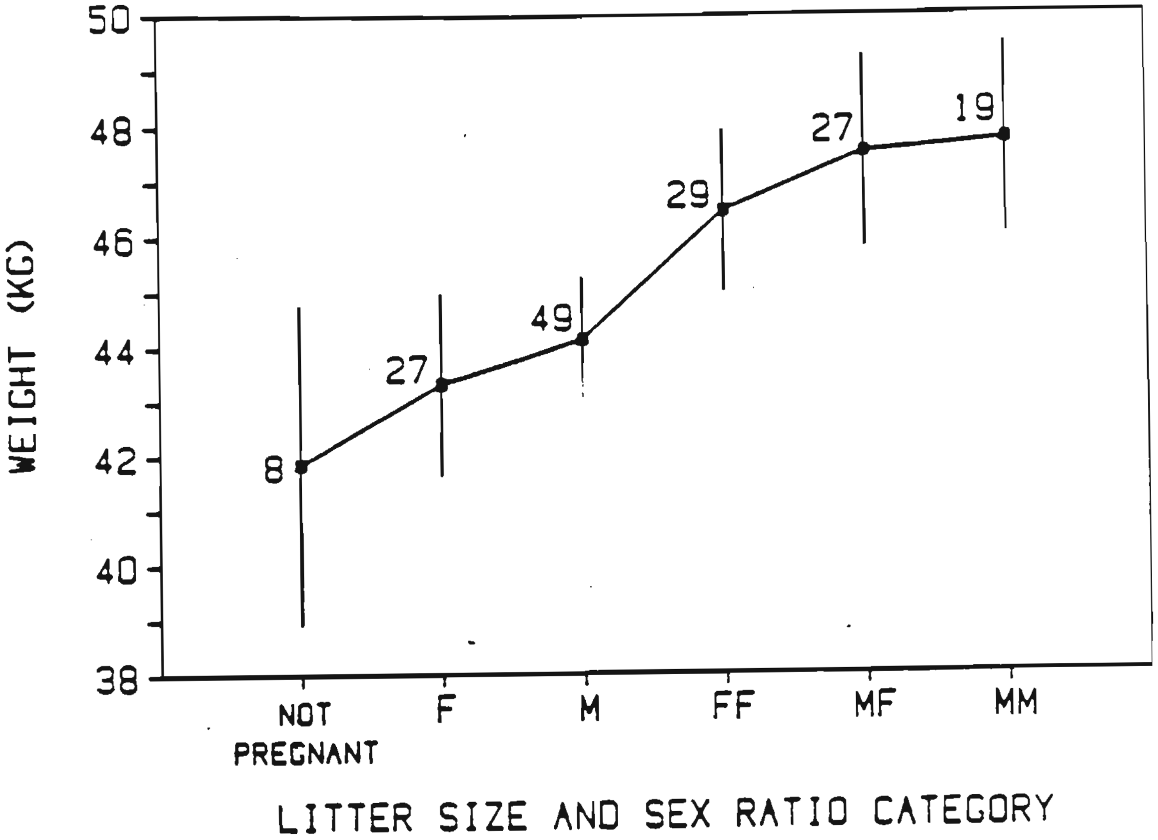

Figure 7-3. Weights (mean ± 95% CI) and sample sizes of adult female mule deer collected on the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono Counties, Calif., 1984 through 1988, arranged by litter size and sex ratio category as follows: F, single female; M, single male; FF, twin females; MF, mixed twins; MM, twin males.

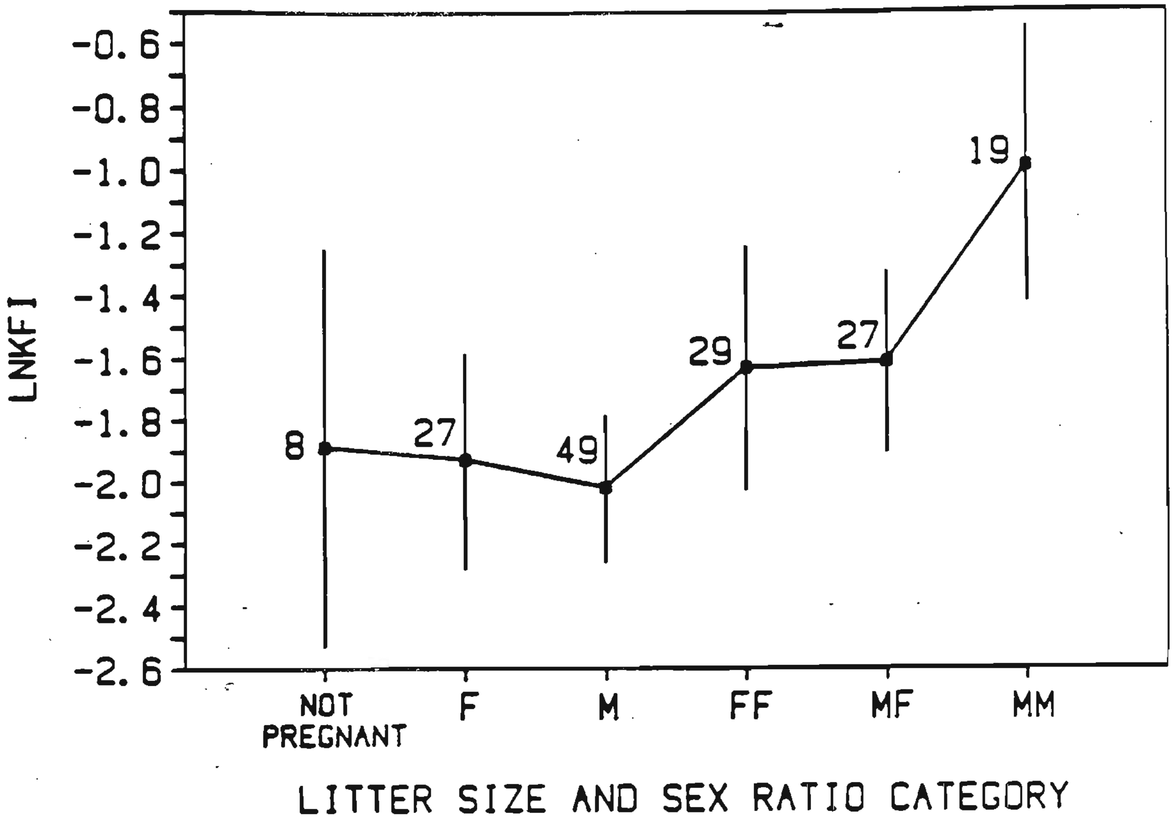

Figure 7-4. Logged kidney fat indexes (LNKFI; mean ± 95% CI) and sample sizes of adult female mule deer collected on the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono counties, Calif., 1984 through 1988, arranged by litter size and sex ratio category as follows: F, single female; M, single male; FF, twin females; MF, mixed twins; MM, twin males.

being intermediate (Figure 7-5). Within mixed litters, males and females did not differ in weight (_t_ = 1.10, _P_ = 0.28, 2-tailed). Single male litters were not significantly heavier than single female litters (_t_ = 0.81, _P_ = 0.423, 2-tailed).

DISCUSSION

Berman (1988) suggested that a population under nutritional stress may be necessary to exhibit condition-related sex-ratio variation. The present data were from a population in rapid decline (Chapter 6), in which most of the deer were in very poor condition when collected for study, and thus would be appropriate to examine for adaptive variation in offspring sex ratio.

Although the sex ratio of all fetuses in the present study was unity (117 males:116 females), patterns were evident when sex ratios of fetuses were plotted against measures of maternal condition. These measures may be closely related to maternal investment ability (MI), although it must be remembered that fetal sex is determined at the time of conception. It is then that any influence of maternal condition on offspring sex ratio is exerted. In the present case, conception was several winter months before sexes were identified, which is sufficient time for changes in weight and fat deposits to occur. However, weight and fat in December or January and in March likely

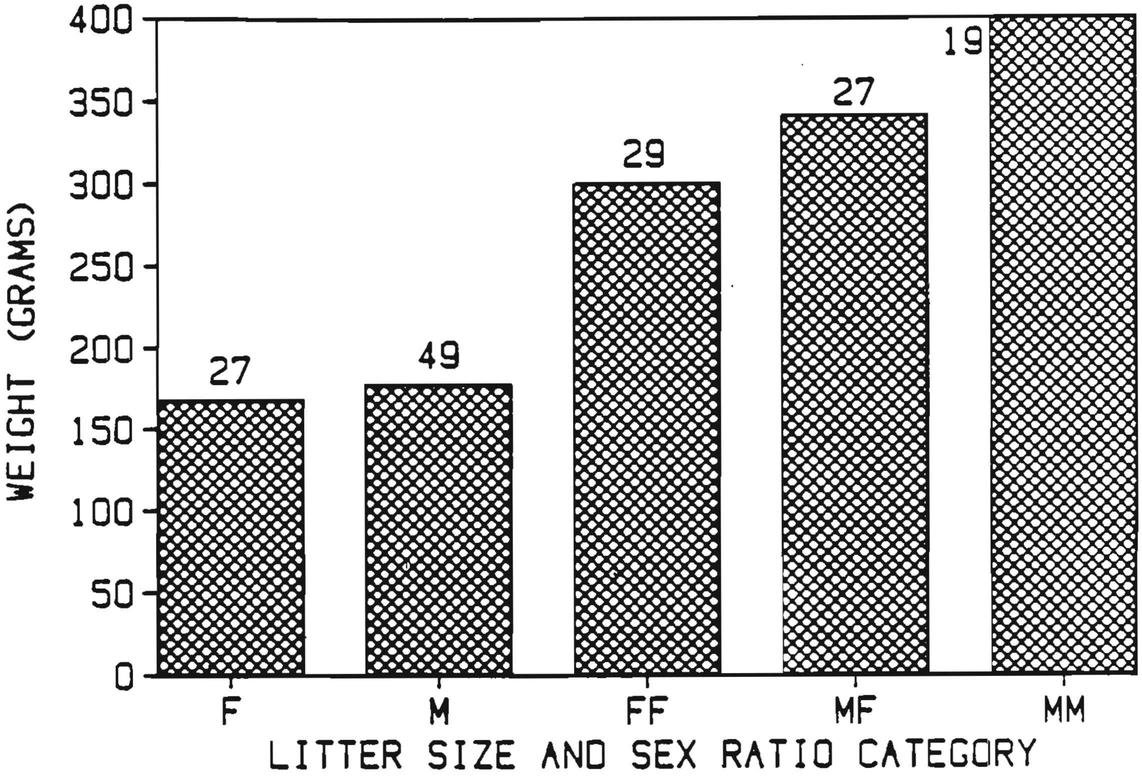

Figure 7-5. Mean weights of litters from adult mule deer collected on the Buttermilk and Sherwin Grade winter ranges, Inyo and Mono Counties, Calif., in March of 1984 through 1988, arranged by litter size and sex ratio category as follows: F, single female; M, single male; FF, twin females; MF, mixed twins; MM, twin males.

are correlated, and thus weight and fat measured in March should reflect conditions earlier.

Across all individuals, the heaviest and fattest mothers tended to have litters of 2 (Figures 7-3 and 7-4). Within this litter size category, fetal sex ratios were female-biased (Figure 7-1). Lighter and thinner mothers tended to have litters of 1, and these were biased toward males. The lightest does did not breed.

According to the Williams (1979) model, which assumes a higher cost of male offspring, male singlets should be more frequent than female singlets in a species with a usual litter size of 2. Among litters of 2, twin females should be most common, followed by mixed litters and twin males. This follows the distribution of (MI), with a mode at the level of MI that can produce twin females. This pattern is exactly what I observed, in a species that conforms to the requirement of the Williams model (Figure 7-1). That single males were the most common litter category overall easily accords with the fractional offspring hypothesis. The necessary assumption is that the mode of the distribution of MI was shifted to a lower level in this nutritionally stressed population, corresponding to that level sufficient to produce male singlets, but insufficient to produce twin females (Figure 7-6).

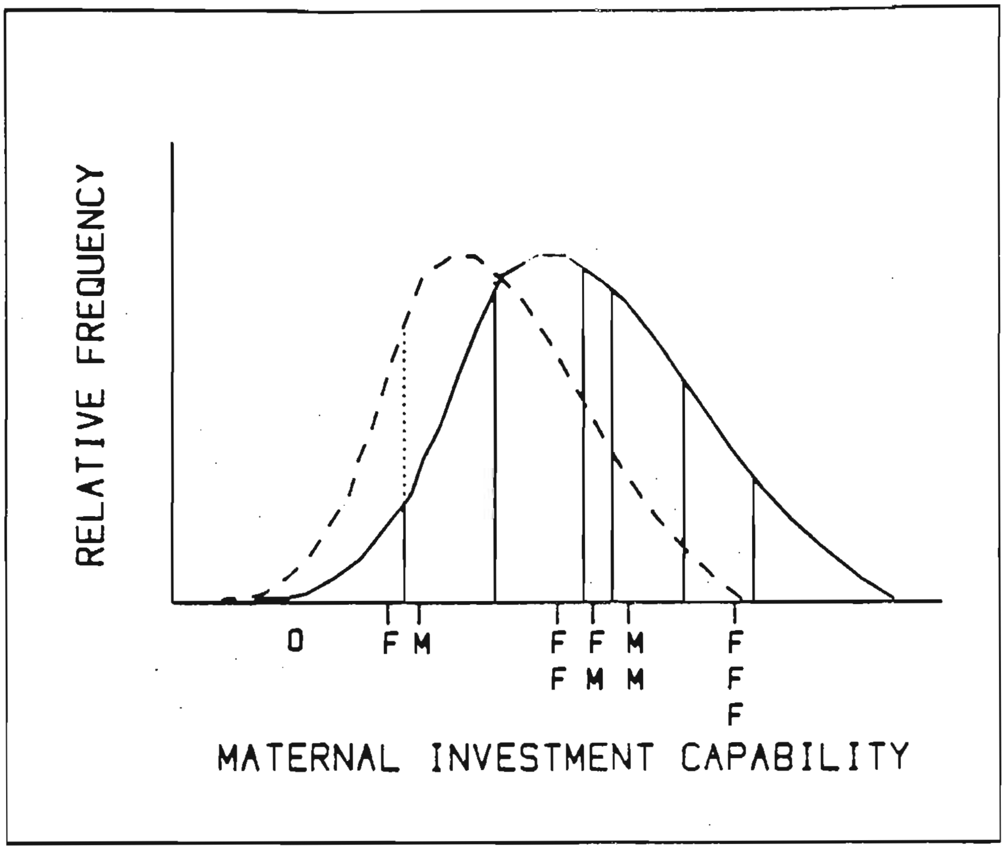

Figure 7-6. Conceptual model of the distribution of maternal investment capability in a species with a usual litter size of 2 (solid line) and in the present, nutritionally stressed population (broken line), after Williams (1979). Vertical lines separate categories of maternal investment sufficient to produce litters of the following categories: 0, not pregnant; F, single female; M, single male; FF, twin females; MF, mixed twins; MM, twin males; FFF, female triplets. A female offspring is assumed to cost 1.0, and a male 1.1, units.

The assumption of the Williams (1979) model that males are more expensive than females to produce seems reasonable, at least through birth. That males were more expensive was apparent in this study from the weights of litters of twin females and twin males, although sex differences in single litters were not statistically significant (Figure 7-3). On average, in March, or after approximately 2-3 months of gestation, litters of twin males weighed about 100 g, or 33%, more than litters of twin females. Single male fetuses weighed approximately 14.1g, or about 8%, more than females. At birth, mule deer male fawns were reported to be significantly heavier than females (Robinette et al. 1973). Differences in post-natal and post-weaning costs between sexes of offspring in mule deer are unknown, but involve considerations of sex differences in nursing frequencies and duration, metabolism, growth rates, dispersal patterns, and mortality.

McCullough's (1979) explanation of observed patterns of sex ratio variation in white-tailed deer involved the timing and pattern of reproduction in males and females. According to this "differential timing of reproduction" hypothesis, at low population density, i. e., under relatively good nutritional conditions, offspring sex ratios should favor females. Under such good conditions, female offspring would be more reproductively successful because they would begin breeding immediately; males are excluded socially from breeding until they attain sufficient dominance. At high density, under poor nutritional conditions, males should be favored. They would be more reproductively successful than females if a natural disturbance (e. g., fire or storms), retarded succession and improved habitat for this subclimax species by the time a male achieved sufficient size and status to begin breeding.

The nutritional conditions during this study can only be described as bad, yet the overall fetal sex ratio was unity. However, among litters of 2, associated with heavier and fatter mothers, the sex ratio was biased toward females (Figure 7-1). Among single litters, produced by the lightest and thinnest mothers, males predominated. Thus, while the population-wide fetal sex ratio was even, female offspring predominated among the most fecund deer. Within this category of twin litters, there was a non-significant tendency for males to be produced by heavier and fatter mothers. Thus, the present results conform both to the fractional offspring and to the differential timing of reproduction hypotheses. These need not be mutually exclusive. The former may involve how reproductive effort is allocated among litter size and sex ratio category; the latter involves an ecological context within which selective forces operate.

Caley and Nudds (1987) proposed the local resource competition hypothesis to explain the lack of conformity of data from white-tailed deer to the predictions of Trivers and Willard (1973). They speculated that males are ultimately the cheaper sex to produce, because they disperse as yearlings, and thus total maternal investment in them is less, even if pre-weaning investment is greater. This assumes that the animals in question are year-round residents of matrilinearly inherited home ranges. Within these home ranges, the potential for competition during periods of resource scarcity would be reduced for a female that had produced males, which disperse, relative to a female with female offspring residing near her. This situation does not exist with migratory mule deer in the mountainous west. For these animals, the time of resource scarcity occurs during periods when animals are concentrated on winter ranges. Any possibility of differential competition arising from the existence of male vs. female offspring would be overwhelmed due to the number of unrelated animals sharing the range. On summer (natal) ranges, from which male offspring would disperse and on which females presumably remain, the potential for competition would seem to be much less, because of greatly lower animal density and greater vegetative resources. Thus, local resource competition is unlikely to play an important role in the adaptive variation of offspring sex ratios, at least in migratory mule deer.

I found no relationship between maternal age and fetal sex ratio. Thus, the present data are in accord with the condition-based model of Williams (1979), and conform to the differential timing of reproduction model of McCullough (1979). They also support, if non-significantly, the prediction of Trivers and Willard (1973): within this nutritionally stressed population of mule deer, offspring of lighter females tended to be female, and offspring of heavier females tended to be male, both in single and twin litters.

CHAPTER VIII. MANAGMENT CONSIDERATIONS

Deer in the eastern Sierra Nevada exist in an unpredictably variable environment, particularly on the winter range. Wet years with copious forage growth are interspersed with drought, in no obvious pattern. Little is known about the variation in quality of summer habitats. Because these occur in higher and wetter areas where animals are much less concentrated, however, fluctuations in summer range quality are probably of less importance to the dynamics of deer populations than those on the winter range. The results of the density reduction on the Sherwin Grade (SG) herd supported the contention that, within this variable environment, density can influence reproduction and condition. The impacts of the drought were less severe on the SG than the Buttermilk (BM) deer. Thus, there are opportunities for management to lessen the great fluctuations in population size and decrease the chances of long-term vegetation damage caused by severe overgrazing.

POPULATION MANAGEMENT

There are several alternatives for managing these deer. None will satisfy all interested groups. The current program, under bucks-only harvest regulations, attempts to maintain a minimum proportion of males in the post-hunt population by restricting tag sales and timing the season to preceed the fall migration. This strategy largely allocates population regulation by default to the weather, and ensures a low harvest from a large, female-biased population subject to large fluctuations in number including periodic die-offs.

However, given the unpredictable nature of precipitation and vegetation growth in the eastern Sierra Nevada, deer management based upon an assumption of density dependence in a stable environment is clearly inappropriate. Many of the following comments are based on ideas expressed in McCullough (1987, 1988). Such a strategy, seeking a fixed annual kill regardless of sex, could result in overharvest, and if continued would drive the population toward extinction (i.e., along the left side of the productivity parabola in McCullough [1987:541]). However, both theory and the present empirical results support the contention that density does have an effect in these herds. Theory predicts that if a population at high density shows a large effect of environmental variation, i.e., fluctuates with environmental conditions, at lower density, with fewer individuals in better condition, such effects should be less. Empirically, even the modest reduction in deer numbers on the SG range was followed by a differential response in reproduction and condition in the SG and BM herds.

This presents an opportunity to manage these herds on an opportunistic or ad hoc basis (McCullough 1988) to lessen the the pattern of population boom-and-bust. With increased precipitation, the deer population should grow again. If a sufficient number of individuals of both sexes were taken at the beginning, or in the middle, of the growth curve, it would decrease the residual population size, maintain better condition in the survivors, and dampen population fluctuations in the future. In addition, it would allow additional people an opportunity to hunt, and would permit human harvest of deer that would otherwise die of malnutrition-related causes in a future population crash.

Further, and of great importance if one is to follow the philosophy of "adaptive management" (Walters 1986), the Round Valley situation presents an opportunity to evaluate such a program, comparing the SG to the BM herd.

The existence of a time lag between precipitation, vegetation response, and deer population growth allows managment activities to be planned ahead. For example, assume the winters of 1988-89 and 1989-90 are wet and produce good forage conditions. The census in January 1990 should show an increase in the deer population. Managers could then plan a hunt for January 1991. This would necessarily be an antlerless hunt. Bucks-only regulations cannot result in the removal of sufficient animals to demonstrate density effects, and in the Round Valley situation, most males remaining in the population after the regular season could be eliminated from the population under such regulations. As in the the hunt in the winter of 1984-85, future antlerless hunts should occur on the winter range, to avoid the possibility of extirpation of local deer populations on the most accessible areas of summer range, and before males begin to cast antlers, so that sex can be readily determined in the field.

To have an effect, a hunt must result in a substantial reduction in numbers. The hunt in 1984-85 took <10% of the SG deer. In the future, I suggest an initial removal of about 30%, which would have a greater effect, and yet would be sufficiently conservative so as not to drive the population to extinction. Again, the best way to measure the effect would be to leave the BM deer as an unmanipulated control, subject to ongoing regulations, and to monitor numbers, condition, and reproductive output in both herds.

The hunt could continue annually for as long as favorable precipitation and forage occur. Numbers of tags issued could be determined as a result of censuses in January. Upon the next drought, the harvest can be suspended if population size reaches some minimum number. Guidelines for this number can come from population size in the current decline, e. g., 1000 deer on the SG range. When this criterion is reached, the hunt is suspended until conditions again are reversed. Evaluation of such a program necessitates a long-term committment to monitor its effects on animal numbers, condition, and reproduction, as well as on vegetation.

There are obstacles to overcome in the management program outlined above. One is a reluctance by many hunters to kill antlerless deer, and the desire by them and animal protectionists to prevent others from doing so. In California, the former is expressed in local county veto power over antlerless proposals, and in Round Valley is complicated by the fact that the SG range straddles Inyo and Mono counties. This socio-political hurdle can only be overcome by educating the various interest groups, and local politicians, about the issues involved. This includes emphasizing the fact that the current management policy necessarily produces starving deer and heavy die-offs during drought.

Another obstacle may be the 5- or 10-year planning horizon necessary in such a scheme, which contrasts with the current year by year decisionmaking process on harvest regulations. Such a medium-term approach is necessary, however, if a goal is to reduce the occasional large die-offs seen in these herds.

HABITAT MANAGEMENT

Winter habitat

An alternative to the management policy of manipulating the population is manipulating its resources, either by improving habitat or by providing supplementary food in poor years. However, in environments with low and variable precipitation, the opportunities for active habitat improvement are limited. The successful use of fire to enhance bitterbrush (Purshia) stands is complex, involving considerations of soil moisture and type, season of burning, plant ages, browsing pressure, and possible genetic differences among plants in different areas (Nord 1965, Martin and Driver 1983, Rice 1983). Seeding and transplanting bitterbrush are also complex and difficult, and success varies widely (see reviews in Tiedemann and Johnson 1983). Nord (1965) used Purshia on the BM range to exemplify the importance of precipitation to seedling establishment. There, at elevations below about 2133 m (7000 ft), he found few seedlings. Above this, up to 3000 m, where moisture was greater, seedlings were abundant. However, most deer winter at the lower elevations. Seeding or transplanting in Round Valley would be further complicated by the lack of roads, the rocky, alluvial soils, and intense herbivory by high populations of large and small mammals.

Supplementary feeding has been frequently suggested as a tactic for saving starving deer, and has been evaluated as successful, if expensive, in avoiding mortalities from severe winter weather in Colorado (Baker and Hobbs 1985). In the present case, however, occasional heavy snowfall causing acute problems of access to covered forage is not the problem. Chronic malnutrition, caused by thousands of animals feeding on vegetation limited by drought, is more common. A program to feed thousands of deer for several months over winters following poor forage production would be enormously expensive and logistically difficult, although not impossible given sufficient resources. If it worked, however, and thereby reduced mortality and increased recruitment, it would just postpone the problem for another year, when even more deer might need to be fed.

Another suggestion locally has been to convert an alfalfa ranch on the SG range to production largely for deer. This would supply a predictable, high quality addition to the winter diet, and could mitigate effects of a drought, i. e., stabilize K. This would lessen population fluctuations, but unless harvest regulations were changed, the eventual result would be the same: a large, female-biased population near or at K, exhibiting heavy mortality in the occasional year with deep snows or extreme temperatures. It would also do little or nothing for the larger

BM herd. Also, esthetic objections to such an artificially maintained population could be raised.

Spring, summer, and migration habitats

Concerns regarding migratory and summer habitats are different from those relevant to winter habitat, and present different opportunities and constraints. Radio-telemetry indicated that most of the Round Valley deer summered on the west side of the Sierra Nevada. Most of these areas were in the Ansel Adams and John Muir wildernesses on the Sierra National Forest, and in Kings Canyon National Park. Thus there is little opportunity for active habitat management on these west side summer ranges.

Eastern Sierra sumer ranges, although more restricted in extent by topography and climate, have more potential for habitat improvements. The most likely techniques involve management of livestock grazing and the use of fire. There is little timber harvesting in the area, and few other land management activities occur that could be designed to produce desired effects on deer habitat. Fire is understandably controversial in such an arid area, but an opportunity exists to study the effects of at least one uncontrolled burn in spring and summer habitat. In the fall of 1987, a fire burned some 3000 ha at the base of Laurel Mountain, and removed much of the shrub cover in the spring holding area just south of Mammoth Lakes. Consequences of this burn on vegetation and herbivores should be evaluated over the next few years to determine the desirability of current fire suppression policies and to guide future practices.

Probably of greatest long-term concern to the deer population is the incremental loss of migration habitat due to human developments in the area (Kucera and McCarthy 1988). Existing and planned residential, commercial, recreational, and energy developments, many of which overlap restricted travel routes of deer, may alter or eliminate migration patterns of deer. The long-term consequences of these developments and increased human presence and vehicular traffic could be greater than drought, livestock, or predator effects combined, but are much more difficult to predict or manage.

LIVESTOCK

One of the interests of the Bureau of Land Management (BLM) in this study was to determine opportunities for livestock use of the winter range, which is largely managed by BLM. Given the fact that the deer are at or exceeding maximum numbers now, with consequent heavy impacts to the vegetation and population crashes, addition of livestock would mean a decrease in forage available for deer. It has been suggested that cattle can alter the columnar growth form of bitterbrush heavily browsed by deer to a more compact form which improves seed production and makes more of the plant available to deer (Hormay 1943). However, heavy stocking rates are necessary to accomplish this, and it has already been tried unsuccessfully on the southern portion of the SG range (BLM files, Bishop, Calif.). If alteration of bitterbrush growth form is desirable, a work crew from the local Conservation Camp, with pruning shears and chain saws, could accomplish the task more quickly and precisely than could cattle. Thus, given the importance of Round Valley as a winter range for deer from a large area of the Sierra Nevada, the current situation of the deer populations fluctuating with precipitation and forage, and the possibility of modulating those fluctuations only by increasing forage resources per capita through density reductions of deer, addition of livestock to the winter range seems unwise.

Many of the migratory and spring holding areas of deer are grazed by livestock in the summer, after deer have moved through. The fact that deer populations can reach high levels concurrent with such grazing argues against a major deleterious effect, at least on migratory deer. Effects of livestock on deer summering on the east slope of the Sierra Nevada, and those on the west side in livestock areas, may be more serious. Heavy grazing by cattle can reduce cover needed to hide fawns (Loft et al. 1987), as well as reduce forage. Domestic sheep can have a similar impact, or in concentrated areas such as bedding grounds, even greater impacts. Livestock impacts on summering deer is another fruitful area of management oriented research.

PREDATORS

It is unlikely that predators, especially mountain lions (Felis concolor), played an important role in the decline of the BM and SG herds. The much more likely cause was drought expressed through poor forage growth and malnutrition. Little is known of mountain lion numbers in the area, although frequent sightings in the Swall Meadows area immediately adjacent to the SG range (Lt. Mike Wolters, CDFG, Bishop, pers. commun.) and the fact that lions killed several deer in traps attest to their presence.

A more legitimate concern involves a potential for predators to inhibit or prevent growth of the deer population when vegetation conditions become favorable. In Alaska, predation by wolves (Canis lupis) was implicated in preventing a recovery of moose (Alces alces) and caribou (Rangifer tarandus) populations which were reduced by causes other than predation (Gasaway et al. 1983). The likelihood of a similar phenomenon in the Eastern Sierra Nevada cannot be known before the fact. However, one approach to the situation would be to reduce the local mountain lion population and eliminate the possibility that they could restrict deer population recovery. Aside from being politically and socially objectionable, this approach would eliminate the possibility of knowing if, in fact, mountain lions can affect deer population recovery. Such knowledge would be important locally, because environmental conditions, and vegetation and herbivore populations, will continue to fluctuate. Knowledge of the role of predators in dampening or altering the herbivore fluctuations, and contributing to the system's "centripetality" (Caughley 1987), would be helpful in guiding management of both herbivores and predators. Such an understanding would also have implications through much of the arid west, where environments and deer populations fluctuate.

A better approach would be to study the predator population through the expected herbivore recovery. Knowledge of how many mountain lions are present, how often they kill deer, how long they are present on the winter range, to what extent they follow the deer in migration, and where they go in summer, combined with knowledge of deer numbers and population growth rate, would allow evaluation the role of predators in this fluctuating environment. Round Valley is an ideal situation for such work because it is compact, relatively accessible, and has a well known deer population presently at low numbers. Such work would have important implications for deer and mountain lion management in many areas of California and the west.

A FINAL COMMENT

The consequence of failing to conduct these studies, and maintaining current practices, is to enter the 21st century with wildlife managers and the public still unsure of why there are so few, or so many, deer, and continuing to argue the relative roles of predators, hunting, and weather. To be a profession, the field of wildlife management should do better.

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Appendix I. Summary of habitat data from transects in summer ranges of mule deer in the central Sierra Nevada, California, 1984 and 1985. Numbers associated with any plant species refer to the number of hits on, or nearest to, that species on 100 toe-points on the transect.

	ANIMAL NO.:	411	285	100	39	221	451	424	236	330	211
	SEX:	F	F	F	F	F	F	F	F	F	F
	EAST or WEST SIDE:	E	E	E	E	W	W	W	W	W	W
	ELEVATION (m):	3139	2499	2377	2957	3139	2256	2926	2347	3109	2396
	% BARE:	30	12	30	13	4	10	31	30	5	5
	% LITTER:	20	63	32	21	32	45	40	35	53	51
Plant	% ROCK:	48	9	8	40	25	15	14	10	3	17
Group/family	Species % PLANT:	2	17	30	26	39	31	15	25	33	17
MOSS:	Moss (unk.)	0	0	0	0	3	0	0	0	0	1
FERN:	Cystopteris fragilis	0	0	0	0	0	0	0	0	0	0
	Fern	0	0	0	0	0	0	0	0	0	0
	Cryptogramma acrostichoides	0	0	0	0	0	0	0	0	0	0
	Onychium densum	0	0	0	0	0	1	0	0	0	0
	Pellaea Bridgesii	0	0	0	0	0	0	0	0	0	0
	Pteridium aquilinum	0	0	0	0	0	5	0	0	0	0
CONIFER:	Abies concolor	0	0	0	0	0	1	0	0	0	0
	A. magnifica	0	0	0	0	0	0	0	0	0	0
	Juniperus occidentalis	0	0	0	1	0	0	0	0	0	0
	Pinus monticola	0	0	0	0	0	0	1	0	0	1
	P. Murrayana	0	0	0	0	0	0	0	0	0	2
	P. albicaulis	2	0	0	0	0	0	0	0	0	0
	P. ponderosa	0	0	0	0	0	0	0	0	0	0
	Tsuga Mertensiana	0	0	0	0	1	0	0	0	0	4
Amaryllidaceae	Allium obtusum	1	0	0	0	0	0	0	0	0	0
	A. validum	0	0	0	0	0	0	0	0	0	1
Cypraceae	Cyperaceae (unk.)	0	0	0	0	0	0	0	0	0	0
	Carex sp.	2	1	0	0	0	0	0	0	0	0
	C. Rossii	0	5	0	0	0	0	0	0	0	0
Gramineae	Grass (unid)	13	42	22	15	63	35	26	2	54	30
	Oryzopsis hymenoides	0	1	2	0	0	0	0	0	0	0
	O. sp.	0	0	0	0	0	1	0	0	0	0
Juncaceae	Juncus Nevadensis	0	0	0	0	7	0	1	1	1	0
Liliaceae	Smilacina stellata	0	0	0	0	0	2	0	0	0	0
	Veratrum Californicum	0	0	0	0	0	0	0	0	0	0
Orchidaceae	Habenaria dilata	0	0	0	0	0	0	0	0	0	0
	Dicot (unk)	0	3	0	0	0	0	0	0	0	0
Aceraceae	Acer glabrum	0	0	0	0	0	1	0	0	0	0
Compositae	Composite (unk.)	0	0	0	0	0	0	0	0	4	0
	Achillea lanulosa	0	0	0	0	0	1	0	0	0	0
	Antennaria rosea	0	0	0	0	0	0	0	0	2	0
	A. ummbrinella	0	0	0	0	6	0	0	0	0	0
	Artemisia sp.	0	0	0	0	0	0	0	0	0	0
	A. ludoviciana	0	0	0	0	0	6	0	0	0	0
	A. tridentata	0	5	20	11	0	0	0	5	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	411	285	100	39	221	451	424	238	330	211
	Aster alpigenus	0	0	0	0	0	0	0	0	4	2
	Chrysopsis Breweri	0	0	0	0	0	0	0	0	0	7
	Chrysothamnus sp.	0	3	0	0	0	0	0	0	0	0
	C. nauseosus	0	0	2	0	0	0	0	0	0	0
	Cirsium sp.	0	0	0	0	0	0	0	0	0	0
	C. Andersonii	0	0	0	0	0	2	0	0	0	0
	Erigeron sp.	0	0	0	0	0	0	0	0	0	0
	E. Breweri	0	0	0	0	0	4	0	0	0	0
	E. compositus	4	0	0	0	0	0	0	0	0	0
	E. linearis	0	0	0	0	0	0	1	0	0	0
	Eupatorium ocidentale	0	0	0	0	0	1	0	0	0	0
	Haplopappus suffruticosus	0	0	0	0	0	0	0	0	0	0
	Helenium Bigelovii	0	0	0	0	0	1	0	0	0	0
	Hieracium gracile	0	0	0	0	0	5	0	3	0	0
	H. horridium	27	0	0	0	0	0	0	0	0	0
	Senecio sp.	0	0	0	0	0	0	0	0	0	0
	S. aronicoides	0	0	0	0	0	0	0	0	0	0
	S. Clarkianus	0	0	0	0	0	0	0	0	0	0
	S. triangularis	0	0	0	0	0	0	0	0	2	0
	Solodago Canedensis	0	0	0	0	0	1	0	3	0	0
	Tetradymia sp.	0	0	0	0	0	0	0	0	0	0
	T. canescens	0	0	1	0	0	0	0	0	0	0
	Anaphalis margaritacea	0	0	0	0	0	0	0	0	0	0
	Taraxacum officinale	0	0	0	0	0	0	0	0	0	0
Betulaceae	Alnus tenuifolia	0	0	0	0	0	3	0	0	0	0
Apocynaceae	Apocynum pumilum	0	0	0	0	0	1	0	0	0	0
Cruciferae	Arabis sp.	16	0	0	0	0	0	0	0	0	0
	A. Lyallii	0	0	0	0	0	0	0	0	0	0
	A. platysperma	0	0	0	0	1	0	8	0	1	0
	Erysimum perenne	0	2	0	0	0	0	0	0	0	0
	Streptanthus cordatue	0	0	0	0	0	0	0	0	0	0
	S. tortuosus	6	0	0	0	0	0	0	0	0	0
Ericaceae	Arctostaphylos mariposa	0	0	0	0	0	0	0	42	0	0
	A. patula	0	0	0	0	0	0	40	0	0	0
	A. Nevadensis	0	0	0	0	0	0	0	0	0	0
	Cassiope Mertensiana	0	0	0	0	0	0	0	0	0	1
	Ledum glandulosum	0	0	0	0	0	0	0	0	0	8
	Phyllodoce Breweri	0	0	0	0	9	0	0	0	1	18
	Vaccinium nivictum	0	0	0	0	0	0	0	0	0	0
	V. occidentale	0	0	0	0	0	0	0	0	0	2
	V. parvifolium	0	0	0	0	0	0	0	0	0	0
Fagaceae	Castanopsis sempervirens	0	0	0	0	0	0	6	0	0	0
	Quercus vaccinifolia	0	0	0	0	0	14	0	37	0	0
	Q. dumosa	0	0	0	0	0	0	0	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	411	285	100	39	221	451	424	238	330	211
Scrophulariaceae	Castilleja sp.	0	0	0	0	0	0	0	0	0	0
	C. Breweri	0	0	0	0	0	1	0	0	0	0
	C. Applegatei	0	0	0	0	0	0	0	0	0	0
	Mimulus sp.	0	0	0	0	0	0	0	0	0	0
	M. nasutus	0	0	0	0	0	0	0	0	0	0
	Pedicularis semibarbata	0	0	0	0	0	0	0	0	0	0
	Penstemon sp.	0	1	0	0	0	0	0	0	0	0
	P. Bridgesii	0	0	0	0	2	0	0	0	0	0
	P. Davidsonii	13	0	0	0	0	0	0	0	0	0
	P. heterodoxus	0	0	0	0	0	0	0	0	0	0
	P. Newberryi	0	0	0	0	0	1	16	0	0	1
	P. Rothrockii	0	0	0	0	0	2	0	5	0	0
	Collinsia Torreyi	0	0	0	0	0	0	0	0	0	0
Rhamnaceae	Ceanothus cordulatus	0	0	0	0	0	1	0	0	0	0
	C. velutinus	0	5	30	0	0	0	0	0	0	0
Rosaceae	Amelanchier pallida	0	0	0	0	0	0	0	0	0	0
	Cercocarpus ledifolius	0	3	0	8	0	0	0	0	0	0
	Fragaria platypetala	0	0	0	0	0	0	0	0	8	2
	Holodiscus Boursieri	0	1	0	0	0	0	1	0	0	0
	H. microphyllus	0	0	0	3	0	0	0	0	0	0
	Petrophytum caespitosum	0	0	0	0	0	0	0	1	0	0
	Potentilla sp.	0	0	0	0	0	0	0	0	0	0
	P. Drummondii	0	0	0	0	0	0	0	0	0	0
	Prunus sp.	0	0	0	0	0	0	0	0	0	0
	P. emarginata	0	0	2	0	0	0	0	0	0	0
	Purshia tridentata	0	12	0	0	0	0	0	0	0	0
Boraginaceae	Cryptantha sp.	0	0	0	1	0	0	0	0	0	0
	Hackelia sp.	0	0	0	0	0	1	0	0	0	0
	H. nervosa	0	0	0	0	0	0	0	0	0	0
Polygonaceae	Eriogonum sp.	0	0	0	4	0	0	0	0	0	0
	E. incanum	4	0	0	0	0	0	0	0	0	0
	E. microthecum	0	0	4	0	0	0	0	0	0	0
	Oxyria digyna	0	0	0	0	0	0	0	0	0	0
	Rumex paucifolia	0	0	0	0	0	0	0	0	0	0
Euphorbiaceae	Euphorbia sp.	0	0	0	0	0	1	0	0	0	0
Rubiaceae	Gallium aparine	0	0	0	0	0	0	0	0	0	0
	Epilobium angustifolium	0	0	0	0	0	0	0	0	1	0
	E. Oregonense	0	0	0	0	0	0	0	0	0	0
	E. Pringleanum	0	0	0	0	0	0	0	0	0	0
	Gayophytum sp.	0	0	1	0	0	0	0	0	0	0
Umbelliferae	Heradeum lanatum	0	0	0	0	0	0	0	0	0	0
	Ligusticum Grayi	0	0	0	0	0	0	0	0	0	0
	Osmorhiza occidentalis	0	0	0	0	0	0	0	0	0	0
	Perideridia Bolanderi	0	0	0	0	0	0	0	0	0	0
	Sphenosciadium capitellatum	0	0	0	0	1	0	0	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	411	285	100	39	221	451	424	233	330	311
Saxifragaceae	Heuchera rubesens	0	0	0	3	0	0	0	0	0	0
	Ribes sp.	0	0	0	0	0	0	0	0	0	0
	R. cereum	0	1	0	4	0	0	0	0	0	0
	R. lasianthum	0	0	0	0	0	0	0	0	0	0
	R. montigenum	0	0	0	0	2	0	0	0	9	8
	R. Roezlii	0	0	0	0	0	3	0	0	0	0
	R. velutinum	0	0	0	0	0	0	0	0	0	0
Leguminosae	Lotus crassifolius	0	0	0	0	0	1	0	1	0	0
	Lupinus sp.	0	0	0	0	0	0	0	0	0	0
	L. Culbertsonii	0	0	0	0	0	0	0	0	0	0
	L. latifolius	0	0	0	0	0	1	0	0	0	0
	L. Lobbii	0	0	0	0	1	0	0	0	1	0
	L. Lyallii	0	0	0	0	0	0	0	0	0	0
	Vicia Californica	0	0	0	0	0	1	0	0	0	0
Primulaceae	Dodecatheon alpinum	0	0	0	0	0	0	0	0	0	0
	D. Jeffreyi	0	0	0	0	0	0	0	0	0	0
	D. redolens	0	0	0	0	0	0	0	0	0	0
Labiatae	Monardella odoratissima	1	0	0	14	0	0	0	0	0	0
Hydrophyllacea	Phacelia hastata	3	0	0	0	0	0	0	0	0	0
	P. mutabilis	0	0	0	0	0	1	0	0	0	0
Polemoniaceae	Phlox sp.	0	0	0	0	0	0	0	0	0	0
	P. diffusa	0	0	0	0	0	0	0	0	0	0
	P. Stansburyi	0	6	14	0	0	1	0	0	0	0
Salicaceae	Populus tremuloides	0	0	0	12	0	1	0	0	0	0
	Salix sp.	0	0	0	0	0	0	0	0	0	0
	Salix orestra	0	0	0	0	3	0	0	0	0	0
Caprifoliaceae	Sambucus caerulea	0	0	0	0	0	1	0	0	0	0
	Symphoricarpos sp.	0	0	0	0	0	0	0	0	0	0
	S. Parishii	0	0	0	0	0	8	0	0	0	0
	S. vaccinioides	0	8	2	16	0	1	0	0	0	0
	Lonicera conjugalis	0	0	0	0	0	0	0	0	0	0
Crassulaceae	Sedum obtusatum	0	0	0	0	0	1	0	0	0	0
Ranunculaceae	Thalictrum sp.	0	0	0	0	0	0	0	0	0	0
	T. Fendleri	0	0	0	0	0	0	0	0	0	0
	Aquilegia formosa	0	0	0	0	0	0	0	0	0	0
	Aconitum columbianum	0	0	0	0	0	0	0	0	0	0
Violaceae	Viola purpurea	8	0	0	0	0	0	0	0	0	0
Unknown		0	5	0	8	0	1	0	0	2	12

Appendix I. Cont.

Plant Group/family	Species										
		ANIMAL NO.:	245	311	11	129	350	375	462	211	1	391
		SEX:	F	F	F	F	F	F	F	F	F	F
		EAST or WEST SIDE:	W	W	W	W	W	W	W	W	W	W
		ELEVATION (m):	2682	2347	2714	2682	2499	2713	2347	3109	3109	2195
		% BARE:	6	8	0	19	21	14	11	19	1	2
		% LITTER:	71	45	45	73	67	12	32	34	13	56
		% ROCK:	12	29	43	1	3	40	16	29	6	30
		% PLANT:	11	18	12	7	8	34	41	18	79	2
MOSS:	Moss (unk.)		0	0	0	0	3	27	0	6	2	0
FERN:	Cystopteris fragilis		0	0	0	0	0	0	0	0	0	0
	Fern		0	0	0	0	0	0	0	0	0	0
	Cryptogramma acrostichoides		0	0	0	0	0	2	0	0	0	0
	Onychium densum		0	0	0	0	0	0	0	0	0	0
	Pellaea Bridgesii		0	0	0	0	0	0	0	0	0	0
	Pteridium aquilinum		0	0	0	0	0	0	0	0	0	0
CONIFER:	Abies concolor		0	0	0	0	0	0	0	0	0	0
	A. magnifica		0	0	0	0	24	0	0	0	0	0
	Juniperus occidentalis		0	0	0	0	0	0	2	0	0	0
	Pinus monticola		0	0	0	0	0	0	0	0	0	0
	P. Murrayana		1	0	0	0	2	2	0	1	0	0
	P. albicaulis		0	0	0	0	0	0	0	0	0	0
	P. ponderosa		0	0	0	0	0	0	0	0	0	0
	Tsuga Mertensiana		0	0	0	0	0	0	0	0	0	0
Amaryllidaceae	Allium obtusum		0	0	0	0	0	0	0	0	0	0
	A. validum		0	0	0	0	0	0	0	0	19	0
Cypraceae	Cyperaceae (unk.)		0	0	0	0	0	0	0	0	0	0
	Carex sp.		0	0	0	0	0	0	0	10	5	0
	C. Rossii		0	0	0	0	0	0	0	0	0	0
Gramineae	Grass (unid)		37	33	4	40	20	10	14	17	30	54
	Oryzopsis hymenoides		0	0	0	0	0	0	0	0	0	0
	O. sp.		0	0	0	0	0	13	0	10	2	0
Juncaceae	Juncus Nevadensis		0	0	0	0	0	0	0	0	0	0
Liliaceae	Smilacina stellata		0	0	0	0	0	0	0	0	0	0
	Veratrum Californicum		0	0	0	0	0	0	0	0	0	0
Orchidaceae	Habenaria dilata		0	0	0	0	0	0	0	0	2	0
	Dicot (unk)		0	0	0	0	0	0	0	0	0	0
Aceraceae	Acer glabrum		0	0	0	0	0	0	0	0	0	0
Compositae	Composite (unk.)		0	0	0	0	0	0	0	0	0	0
	Achillea lanulosa		0	1	0	0	0	3	2	0	0	0
	Antennaria rosea		0	2	0	0	0	4	0	0	0	0
	A. ummbrinella		0	0	0	0	0	0	0	0	0	0
	Artemisia sp.		0	0	0	0	0	0	0	0	0	0
	A. ludoviciana		0	12	50	0	0	0	0	0	0	0
	A. tridentata		0	2	3	0	0	3	9	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	245	311	11	129	350	375	462	211	1	391
	Aster alpigenus	2	0	0	0	0	0	0	0	0	0
	Chrysopsis Breweri	16	0	0	0	2	0	0	0	0	0
	Chrysothamnus sp.	0	0	0	0	0	0	0	0	0	0
	C. nauseosus	0	0	0	0	0	0	0	0	0	0
	Cirsium sp.	0	0	0	0	0	0	0	0	0	0
	C. Andersonii	0	4	3	0	0	0	0	0	0	0
	Erigeron sp.	3	0	15	0	0	0	0	0	0	0
	E. Breweri	0	1	0	0	0	0	0	0	0	0
	E. compositus	0	0	0	0	0	0	0	0	0	0
	E. linearis	0	0	0	0	0	0	0	0	0	0
	Eupatorium ocidentale	0	0	0	0	0	0	0	0	0	0
	Haplopappus suffruticosus	1	0	0	0	0	0	0	0	0	0
	Helenium Bigelovii	0	0	0	0	0	0	0	0	0	0
	Hieracium gracile	0	0	0	0	0	0	0	0	0	0
	H. horridium	0	0	0	0	0	0	0	0	0	0
	Senecio sp.	0	0	0	0	0	0	0	0	0	0
	S. aronicoides	0	0	0	0	3	0	0	0	0	0
	S. Clarkianus	0	0	0	0	0	0	0	0	4	0
	S. triangularis	0	0	0	0	0	0	0	0	0	0
	Solodago Canadensis	0	0	0	0	0	0	0	0	0	0
	Tetradymia sp.	6	0	0	0	0	0	0	0	0	0
	T. canescens	0	0	0	0	0	0	0	0	0	0
	Anaphalis margaritacea	0	0	0	0	0	0	0	4	0	0
	Taraxacum officinale	0	0	0	6	0	0	0	0	0	0
Betulaceae	Alnus tenuifolia	0	3	0	0	0	0	9	0	19	0
Apocynaceae	Apocynum pumilum	0	0	0	0	0	0	0	0	0	0
Cruciferae	Arabis sp.	0	0	0	0	0	2	2	0	0	0
	A. Lyallii	0	0	0	0	4	0	0	0	0	0
	A. platysperma	0	1	0	1	0	0	0	0	0	0
	Erysimum perenne	0	0	0	0	1	0	0	0	0	0
	Streptanthus cordatus	0	0	0	0	0	0	0	0	0	0
	S. tortuosus	0	0	0	0	1	0	0	0	0	0
Ericaceae	Arctostaphylos mariposa	0	6	0	0	0	0	0	0	0	0
	A. patula	0	0	0	0	0	0	0	0	0	0
	A. Nevadensis	0	0	0	0	0	15	0	0	0	0
	Cassiope Mertensiana	0	0	0	0	0	0	0	0	0	0
	Ledum glandulosum	0	0	0	0	0	0	0	0	0	0
	Phyllodoce Breweri	0	0	0	0	0	0	0	29	0	0
	Vaccinium nivictum	0	0	0	0	0	0	0	0	0	0
	V. occidentale	0	0	0	0	0	0	0	0	0	0
	V. parvifolium	0	0	0	0	0	0	0	0	0	6
Fagaceae	Castanopsis sempervirens	6	0	0	0	0	0	0	0	0	0
	Quercus vaccinifolia	0	0	0	0	0	0	0	0	0	0
	Q. dumosa	0	0	0	0	0	0	0	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	245	311	11	129	350	375	462	211	1	391
Scrophulariacea	Castilleja sp.	0	4	0	0	0	0	0	0	0	0
	C. Breweri	0	0	0	0	0	0	0	0	0	0
	C. Applegatei	0	0	1	0	0	0	0	0	0	0
	Mimulus sp.	0	0	0	0	0	0	0	0	0	0
	M. nasutus	0	0	0	0	0	0	0	0	2	0
	Pedicularis semibarbata	0	0	0	0	8	0	0	3	0	0
	Penstemon sp.	0	0	0	0	1	0	0	0	0	0
	P. Bridgesii	0	0	0	0	0	0	0	0	0	0
	P. Davidsonii	0	0	0	0	0	0	0	0	0	0
	P. heterodoxus	0	0	0	0	0	0	0	0	0	0
	P. Newberryi	0	7	0	0	0	3	5	0	0	0
	P. Rothrockii	0	0	0	0	0	0	0	0	0	0
	Collinsia Torreyi	0	0	0	0	4	0	0	0	0	0
Rhamnaceae	Ceanothus cordulatus	0	0	0	0	0	0	0	0	0	0
	C. velutinus	0	0	0	0	0	0	0	0	0	0
Rosaceae	Amelanchier pallida	0	0	0	0	0	0	0	0	0	0
	Cercocarpus ledifolius	0	0	0	0	0	0	0	0	0	0
	Fragaria platypetala	10	0	0	15	0	0	0	0	0	0
	Holodiscus Boursieri	0	1	0	0	0	3	2	0	0	0
	H. microphyllus	0	0	0	0	0	0	0	0	0	0
	Petrophytum caespitosum	0	2	0	0	0	0	0	0	0	0
	Potentilla sp.	0	0	0	0	0	0	0	0	0	0
	P. Drummondii	0	0	0	0	0	0	0	0	0	0
	Prunus sp.	0	0	0	0	0	0	0	0	0	0
	P. emarginata	0	0	0	0	0	0	0	0	0	0
	Purshia tridentata	0	0	0	0	0	0	0	0	0	0
Boraginaceae	Cryptantha sp.	0	0	0	0	0	0	0	0	0	0
	Hackelia sp.	0	0	0	0	0	0	0	0	0	0
	H. nervosa	0	0	0	0	0	0	7	0	0	0
Polygonaceae	Eriogonum sp.	0	0	0	11	15	0	0	0	0	0
	E. incanum	0	0	0	0	0	0	0	0	0	0
	E. microthecum	0	0	0	0	0	0	0	0	0	12
	Oxyria digyna	0	0	0	0	0	0	0	0	2	0
	Rumex paucifolia	0	0	0	0	0	0	0	4	0	0
Euphorbiaceae	Euphorbia sp.	0	0	0	0	0	0	0	0	0	0
Rubiaceae	Gallium aparine	0	4	0	0	0	0	0	0	0	0
	Epilobium angustifolium	0	0	0	0	0	0	7	5	0	0
	E. Oregonense	0	0	0	0	0	0	0	0	1	0
	E. Pringleanum	0	0	0	0	0	0	0	0	0	0
	Gayophytum sp.	0	0	0	0	0	0	0	0	0	0
Umbelliferae	Heradeum lanatum	0	2	0	0	0	0	0	0	0	0
	Ligusticum Grayi	0	0	0	0	0	0	0	0	0	0
	Osmorhiza occidentalis	0	0	0	0	0	0	2	0	0	0
	Perideridia Bolanderi	0	0	0	0	1	0	0	0	2	0
	Sphenosciadium capitellatum	0	0	0	0	0	0	0	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	245	311	11	129	350	375	462	211	1	391
Saxifragaceae	Heuchera rubesens	0	1	0	0	0	2	0	0	0	0
	Ribes sp.	0	0	0	0	0	0	11	0	0	0
	R. cereum	0	0	3	0	0	0	0	0	0	0
	R. lasianthum	0	0	1	0	0	0	0	0	0	0
	R. montigenum	5	0	0	11	0	0	0	0	0	0
	R. Roezlii	0	0	0	0	0	0	0	0	0	0
	R. velutinum	0	0	0	0	0	0	0	0	0	0
Leguminoseae	Lotus crassifolius	0	0	0	0	0	0	0	0	0	0
	Lupinus sp.	0	0	0	0	1	0	0	1	0	0
	L. Culbertsonii	0	0	0	0	0	0	0	0	0	0
	L. latifolius	0	0	0	0	0	0	0	0	0	0
	L. Lobbii	3	0	0	0	0	0	0	0	0	0
	L. Lyallii	0	0	0	0	0	0	0	7	0	0
	Vicia Californica	0	0	0	0	0	0	0	0	0	0
Primulaceae	Dodecatheon alpinum	0	0	0	0	0	0	0	0	0	0
	D. Jeffreyi	0	0	0	0	0	0	0	0	1	0
	D. redolens	0	0	0	0	0	0	0	0	0	0
Labiatae	Monardella odoratissima	1	0	0	0	1	0	0	0	0	0
Hydrophyllacee	Phacelia hastata	0	0	0	0	0	0	0	0	0	0
	P. mutabilis	0	0	0	0	0	0	0	0	0	0
Polemoniaceae	Phlox sp.	0	0	0	6	0	2	0	0	0	16
	P. diffusa	0	2	0	0	0	0	0	0	0	0
	P. Stansburyi	0	0	0	0	0	0	0	0	0	0
Salicaceae	Populus tremuloides	0	0	0	0	0	0	0	0	0	0
	Salix sp.	0	0	1	0	0	0	2	1	0	0
	Salix oreatra	0	0	0	0	0	0	0	0	0	0
Caprifoliaceae	Sambucus caerulea	0	0	0	0	0	0	0	0	0	0
	Symphoricarpos sp.	0	0	0	0	0	0	2	0	0	0
	S. Parishii	6	3	0	0	0	0	0	0	0	0
	S. vaccinioides	0	0	9	0	0	0	14	0	0	0
	Lonicera conjugalis	0	0	0	0	0	0	0	0	0	0
Crassulaceae	Sedum obtusatum	0	2	0	0	0	5	0	0	0	0
Ranunculaceae	Thalictrum sp.	1	0	10	0	0	0	0	0	0	0
	T. Fendleri	0	6	0	1	0	1	2	0	2	0
	Aquilegia formosa	0	0	0	0	0	0	0	0	1	0
	Aconitum columbianum	0	0	0	0	0	0	0	0	5	0
Violaceae	Viola purpurea	0	0	0	0	0	0	0	0	0	0
Unknown		2	1	0	9	7	3	7	2	1	12

Appendix I. Cont.

Plant Group/family	Species										
	ANIMAL NO.:	472	32	270	121	51	31	139	320	71	51
	SEX:	F	F	F	M	M	M	M	M	M	M
	EAST or WEST SIDE:	W	W	W	W	W	W	W	W	W	W
	ELEVATION (m):	2682	2957	3018	2804	3018	3170	2316	3010	3353	3200
	% BARE:	23	11	5	15	11	2	3	19	13	13
	% LITTER:	54	8	25	17	21	1	62	34	5	3
	% ROCK:	1	3	17	19	39	52	12	9	39	46
	% PLANT:	22	78	53	49	25	45	23	39	43	28
MOSS:	Moss (unk.)	0	0	6	12	3	1	1	0	0	2
FERN:	Cystopteris fragilis	0	0	0	0	0	0	0	0	1	0
	Fern	0	0	0	0	0	0	6	0	0	0
	Cryptogramma acrostichoides	0	0	0	0	0	0	0	1	0	0
	Onychium densum	0	0	0	0	0	0	0	0	0	0
	Pellaea Bridgesii	0	0	0	0	0	1	0	0	0	0
	Pteridium aquilinum	0	0	0	0	0	0	0	0	0	0
CONIFER:	Abies concolor	0	0	0	0	0	0	0	0	0	0
	A. magnifica	17	0	0	0	0	0	0	0	0	0
	Juniperus occidentalis	0	0	0	0	0	0	0	0	0	0
	Pinus monticola	0	0	1	0	0	0	0	0	0	0
	P. Murrayana	2	1	0	0	1	0	0	2	0	1
	P. albicaulis	0	0	0	0	2	0	0	0	0	9
	P. ponderosa	0	0	0	0	0	0	1	0	0	0
	Tsuga Mertensiana	0	0	9	11	0	0	0	2	0	0
Amaryllidaceae	Allium obtusum	0	0	0	0	0	0	0	0	0	0
	A. validum	0	0	0	0	0	0	0	0	0	0
Cypraceae	Cyperaceae (unk.)	0	0	0	0	0	0	0	0	1	0
	Carex sp.	0	0	10	4	0	0	0	0	2	12
	C. Rossii	0	0	0	0	0	0	0	0	0	0
Gramineae	Grass (unid)	16	46	19	29	16	50	2	27	33	11
	Oryzopsis hymenoides	0	0	0	0	0	0	0	0	0	0
	O. sp.	0	5	0	4	14	0	0	8	1	13
Juncaceae	Juncus Nevadensis	0	0	0	0	0	0	0	0	0	0
Liliaceae	Smilacina stellata	0	0	0	0	0	0	0	0	0	0
	Veratrum Californicum	0	6	0	0	0	0	0	2	0	0
Orchidaceae	Habenaria dilata	0	0	0	0	0	0	0	0	0	0
	Dicot (unk)	0	0	0	0	0	0	0	0	0	0
Aceraceae	Acer glabrum	0	0	0	0	0	0	0	0	0	0
Compositae	Composite (unk.)	0	0	0	0	0	0	0	0	0	0
	Achillea lanulosa	0	0	0	0	2	0	0	0	0	0
	Antennaria rosea	0	3	4	15	0	5	0	0	0	2
	A. umbrinella	0	0	0	0	0	0	0	0	0	0
	Artemisia sp.	0	0	0	0	0	0	14	0	0	0
	A. ludoviciana	0	0	0	0	0	0	0	0	0	0
	A. tridentata	0	8	0	0	2	0	0	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	472	32	270	121	51	31	139	320	71	81
	Aster alpigenus	0	0	0	0	0	0	0	0	0	0
	Chrysopsis Breweri	2	0	0	0	0	0	0	2	0	0
	Chrysothamnus sp.	0	0	0	0	0	0	0	0	0	0
	C. nauseosus	0	0	0	0	0	0	0	0	0	0
	Cirsium sp.	4	0	0	0	0	0	0	0	0	0
	C. Andersonii	0	0	0	0	0	0	0	1	0	0
	Erigeron sp.	2	0	0	2	0	0	0	0	0	0
	E. Breweri	0	0	1	0	0	0	0	1	0	0
	E. compositus	0	0	0	0	0	0	0	0	0	0
	E. linearis	0	0	0	0	0	0	0	0	0	0
	Eupatorium ocidentale	0	0	0	0	0	0	0	0	0	0
	Haplopappus suffruticosus	0	1	0	0	0	0	0	0	0	0
	Helenium Bigelovii	0	0	0	0	0	0	0	0	0	0
	Hieracium gracile	0	0	0	0	0	0	0	0	0	0
	H. horridium	0	0	0	0	0	0	0	1	0	0
	Senecio sp.	0	7	0	0	0	6	0	0	0	0
	S. aronicoides	0	0	5	1	0	0	0	0	0	0
	S. Clarkianus	0	0	0	0	0	0	0	0	0	0
	S. triangularis	0	0	2	0	0	0	0	1	0	0
	Solodago Canadensis	0	0	0	0	0	0	0	0	0	0
	Tetradymia sp.	0	0	0	0	0	0	0	0	0	0
	T. canescens	0	0	0	0	0	0	0	0	0	0
	Anephalis margaritacea	0	0	0	0	0	0	0	0	0	0
	Taraxacum officinale	0	0	0	0	0	0	0	0	0	0
Betulaceae	Alnus tenuifolia	0	0	0	0	0	0	0	0	0	0
Apocynaceae	Apocynum pumilum	0	0	0	0	0	0	0	0	0	0
Cruciferae	Arabis sp.	0	0	0	0	0	0	0	0	0	0
	A. Lyallii	0	0	0	0	0	0	0	0	0	0
	A. platysperma	0	0	0	0	0	1	0	0	0	0
	Erysimum perenne	0	0	0	0	0	0	0	0	0	0
	Streptanthus cordatus	0	0	0	0	0	1	0	0	0	0
	S. tortuosus	0	0	0	0	0	0	0	0	0	0
Ericaceae	Arctostaphylos mariposa	0	0	0	0	0	0	0	0	0	0
	A. patula	3	0	0	0	0	0	0	0	0	0
	A. Nevadensis	0	0	0	0	26	0	0	0	0	0
	Cassiope Mertensiana	0	0	0	0	0	0	0	0	0	0
	Ledum glandulosum	0	0	5	0	1	0	0	0	0	0
	Phyllodoce Breweri	0	0	21	13	5	6	0	25	18	11
	Vaccinium nivictum	0	0	0	4	0	0	0	0	0	10
	V. occidentale	0	0	0	0	0	0	0	7	15	0
	V. parvifolium	0	0	0	0	0	0	0	0	0	0
Fagaceae	Castanopsis sempervirens	0	0	0	0	0	0	0	0	0	0
	Quercus vaccinifolia	0	0	0	0	0	0	28	0	0	0
	Q. dumosa	0	0	0	0	0	0	3	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	472	32	270	121	51	31	139	320	71	31
Scrophulariacea	Castilleja sp.	0	0	0	0	2	0	0	0	0	0
	C. Breweri	0	0	0	0	0	0	0	0	0	0
	C. Applegatei	0	0	0	0	0	0	0	0	0	0
	Mimulus sp.	0	3	0	0	0	1	0	1	0	0
	M. nasutus	0	0	0	0	0	0	0	0	0	0
	Pedicularis semibarbata	0	0	0	0	0	0	0	0	0	0
	Penstemon sp.	0	1	0	0	0	17	0	0	0	0
	P. Bridgesii	0	0	0	0	0	2	0	0	0	0
	P. Davidsonii	0	0	0	0	0	0	0	0	0	0
	P. heterodoxus	0	0	0	0	0	0	0	0	1	0
	P. Newberryi	0	0	0	0	13	0	0	1	5	3
	P. Rothrockii	0	0	0	0	0	0	0	0	0	0
	Collinsia Torreyi	0	0	0	0	0	0	0	0	0	0
Rhamnaceae	Ceanothus cordulatus	0	0	0	0	0	0	5	0	0	0
	C. velutinus	0	0	0	0	0	0	0	0	0	0
Rosaceae	Amelanchier pallida	2	0	0	0	0	0	0	0	0	0
	Cercocarpus ledifolius	0	0	0	0	0	0	0	0	0	0
	Fragaria platypetala	0	0	0	0	0	0	0	0	0	0
	Holodiscus Boursieri	0	0	0	0	0	0	0	1	0	0
	H. microphyllus	0	0	0	0	4	0	1	0	0	0
	Petrophytum caespitosum	0	0	0	0	0	0	0	0	0	0
	Potentilla sp.	0	0	0	0	0	0	0	1	0	0
	P. Drummondii	0	0	0	0	0	0	0	0	0	1
	Prunus sp.	0	0	0	0	0	0	4	0	0	0
	P. emarginata	4	0	0	0	0	0	7	0	0	0
	Purshia tridentata	0	0	0	0	0	0	0	0	0	0
Boraginaceae	Cryptantha sp.	0	0	0	0	0	0	0	0	0	0
	Hackelia sp.	0	0	0	0	0	0	0	0	0	0
	H. nervosa	0	0	0	0	0	0	0	0	0	0
Polygonaceae	Eriogonum sp.	0	0	0	0	0	1	0	1	0	0
	E. incanum	0	0	0	0	0	0	0	0	2	0
	E. microthecum	0	0	0	0	0	0	0	0	0	0
	Oxyria digyna	0	0	0	0	0	0	0	0	0	2
	Rumex paucifolia	0	0	0	0	0	0	0	0	0	0
Euphorbiaceae	Euphorbia sp.	0	0	0	0	0	0	0	0	0	0
Rubiaceae	Gallium aparine	0	0	0	0	0	0	0	0	0	0
	Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0
	E. Oregonense	0	0	0	0	0	0	0	0	0	0
	E. Pringleanum	0	2	0	0	0	0	0	0	0	0
	Gayophytum sp.	0	0	0	0	0	0	0	0	0	0
Umbelliferae	Heradeum lanatum	0	0	0	0	0	0	0	0	0	0
	Ligusticum Grayi	1	0	0	0	0	0	0	0	0	0
	Osmorhiza occidentalis	12	0	0	0	0	0	0	0	0	0
	Perideridia Bolanderi	0	1	4	0	0	0	0	0	0	0
	Sphenosciadium capitellatum	0	0	0	0	0	0	0	0	0	0

Appendix I. Cont.

	ANIMAL NUMBER:	472	32	270	121	51	31	139	320	71	31
Saxifragaceae	Heuchera rubesens	0	0	0	0	0	0	0	1	0	0
	Ribes sp.	1	0	2	0	0	1	5	0	0	0
	R. cereum	0	0	0	0-	0	0	0	0	0	0
	R. lasianthum	0	0	0	0	0	0	0	0	0	0
	R. montigenum	2	3	4	2	0	0	0	4	0	0
	R. Roezlii	0	0	0	0	0	0	0	0	0	0
	R. velutinum	0	0	0	0	0	0	0	3	0	0
Leguminoseae	Lotus crassifolius	0	0	0	0	0	0	0	0	0	0
	Lupinus sp.	0	4	0	0	0	0	3	0	0	0
	L. Culbertsonii	12	0	0	0	0	0	0	0	0	0
	L. latifolius	0	0	0	0	0	0	0	0	0	0
	L. Lobbii	0	5	0	0	0	3	0	0	0	0
	L. Lyallii	0	0	0	0	0	0	0	0	0	0
	Vicia Californica	0	0	0	0	0	0	0	0	0	0
Primulaceae	Dodecatheon alpinum	0	0	0	0	0	0	0	0	4	0
	D. Jeffreyi	0	0	0	0	0	0	0	0	0	0
	D. redolens	0	0	0	0	0	2	0	0	0	0
Labiatae	Monardella odoratissima	0	0	0	0	0	0	0	0	0	0
Hydrophyllacee	Phacelia hastata	0	0	0	0	0	0	0	0	0	0
	P. mutabilis	0	0	0	0	0	0	0	0	0	0
Polemoniaceae	Phlox sp.	0	0	0	0	0	0	0	0	0	0
	P. diffusa	0	0	0	0	0	0	0	0	1	0
	P. Stansburyi	0	0	0	0	0	0	0	0	0	0
Salicaceae	Populus tremuloides	2	0	0	0	0	0	0	0	0	0
	Salix sp.	0	2	4	0	1	1	2	2	16	8
	Salix orestra	0	0	0	0	0	0	0	0	0	0
Caprifoliaceae	Sambucus caerulea	0	0	0	0	0	0	0	0	0	0
	Symphoricarpos sp.	0	0	0	0	0	0	0	0	0	0
	S. Parishii	0	0	0	0	0	0	0	0	0	0
	S. vaccinioides	2	0	0	0	0	0	0	0	0	0
	Lonicera conjugalis	4	0	0	0	0	0	0	0	0	0
Crassulaceae	Sedum obtusatum	0	0	0	0	0	0	0	0	0	0
Ranunculaceae	Thalictrum sp.	0	0	0	0	0	0	0	0	0	0
	T. Fendleri	1	0	0	0	0	0	0	0	0	0
	Aquilegia formosa	0	0	0	0	0	0	0	0	0	0
	Aconitum columbianum	0	0	0	0	0	0	0	0	0	0
Violaceae	Viola purpurea	0	0	0	0	0	0	0	0	0	0
Unknown		11	2	4	3	4	1	17	10	0	10