WEST WALKER DEER HERD STUDY
FINAL REPORT
1992-1995
(Contract No. FG-1230)

Submitted to:

California Department of Fish and Game
Region 5
407 W. Line Street
Bishop, CA 93514
Contact: Bob Schaefer
(909) 584-4616

Submitted by:

Timothy J. Taylor
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June Lake, CA 93529
(760) 648-7227

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# TABLE OF CONTENTS

Chapter 1. Executive Summary

Chapter 2. Migration and Interseasonal Movements
   Introduction
   Study Area
   Methods
   Results
      Spring Migration
         Pattern and Timing of Deer Movement
         Locations of Deer Movement
         Nevada Winter Ranges
         California Winter Ranges
      Fall Migration
         Pattern and Timing of Deer Movement
         Fidelity
            Summer Range
            Winter Range
   Discussion
   Management Recommendations
   Acknowledgments
   Literature Cited

Chapter 3. Condition and Reproduction
   Introduction
   Study Area and Methods
   Results
   Discussion
   Acknowledgments
   Literature Cited

Chapter 4. Diet Composition and Quality
   Introduction
   Study Area and Methods
   Results
      Diet Composition of Feces
         Winter Range
         Summer Range
         Transition Range
      Diet Quality
   Discussion
   Acknowledgments
   Literature Cited
TABLE OF CONTENTS (cont.)

Chapter 5. Winter Home Range and Habitat Use

    Introduction 5-1
    Study Area 5-2
    Methods 5-4
    Results 5-6
        Winter Habitat Use 5-6
    Discussion 5-9
        Management Recommendations 5-13
    Acknowledgments 5-14
    Literature Cited 5-15
CHAPTER 1. EXECUTIVE SUMMARY

From May 1992-June 1995, I used radio-telemetry to determine the seasonal movement and migration patterns of mule deer (Odocoileus hemionus hemionus) from the West Walker (WW) herd. We captured 133 deer and attached radio transmitters to 47 adult females and 10 adult males. Ninety-seven percent of radio-collared deer were migratory with distinct summer and winter ranges. Linear distances traveled between winter and summer range centers of activity (COA’s) varied from 5.7 to 71.3 km. Changes in elevation between winter and summer ranges varied from +550 to +1,425 m. Timing of spring migration from the winter range varied annually by as much as 1 month during the study and was related to winter severity and cool spring temperatures. Deer made extensive use of holding areas during spring migration, the period of delay averaged 20 days following mild winters and 35 days following severe winters.

Deer occupied approximately 2,450 km² of summer range located on both the east and west slopes of the Sierra Nevada. Sixty-four percent of radio-collared deer summered on east slope summer ranges and 36% summered on west slope summer ranges. Deer showed poor fidelity to consecutive summer range COA’s. Distances separating summer range COA’s of females monitored for ≥ two successive years averaged 1.6 km. Timing of fall migration from the summer range varied by as much as two weeks and was related to the severity of fall weather. Deer showed poor fidelity to early winter (November-January) COA’s. Distances separating early winter COA’s of adult females monitored for ≥ two successive years averaged 4.7 km. Deer showed stronger fidelity to late winter (February-April) COA’s. Distances separating late winter COA’s of females monitored for ≥ 2 successive years averaged 1.8 km.

This study revealed that deer from a relatively small area of winter range (800 km²) inhabited a large geographical area of summer range (2,450 km²) on both the east and west slopes of the central Sierra Nevada. This study also revealed that WW deer shared summer range with Rocky Mountain mule deer from two other eastern Sierra Nevada herds and California mule deer (O. h. californicus) from at least three western Sierra Nevada herds. Therefore, habitat management programs designed to increase deer productivity in the WW herd should be conducted on primary winter range sites when deer are concentrated and can be managed on a herd-specific basis. Similarly, any reduction in the amount of area available on primary winter ranges due to habitat loss, human disturbance or other factors, could have broad implications in the occurrence of deer summering over a large portion of central Sierra Nevada.

I determined reproductive performance in relation to age and physical condition of 58 female Rocky Mountain mule deer collected from the WW winter range in northern Mono County, California, and southwestern Douglas County, Nevada, during March 1993 and March 1994. Among adult females, pregnancy and fetal rates were 86% and 1.52 fœtuses/female in 1993 and 88% and 1.56 fœtuses/female in 1994. Bleached carcass weights, eviscerated carcass weights, and kidney fat indices of adult females were greater in 1994, indicating that deer were in
better condition than in 1993. Litter category was not related to age or female body condition. The overall sex ratio of fetauses was 107 males:100 females. Reproductive potential in the West Walker deer herd was comparable to that reported for other nutritionally stressed mule deer populations.

My study suggested that low productivity was in response to drought-induced changes in habitat quality, which was compounded by severe winter conditions in 1992-93. During periods of drought, the first step wildlife managers should take is to increase the quality of the food supply. Therefore, I recommend management practices on WW deer winter ranges and holding areas that promote and ensure access to late season growth of succulent forage on irrigate pasture.

Thirty-two of 57 radio-collared deer died during the course of the study and I determined the proximate source of mortality for 23 of these deer. Predation and anthropogenic causes, including automobiles, capture myopathy, and hunting, each comprised 43% of the fatalities detected; malnutrition accounted for 14% of fatalities. Among predation incidences, mountain lions (Felis concolor) accounted for 100% of fatalities; vehicles and hunting were responsible for 50% and 40% of anthropogenic causes, respectively. Bleich and Taylor (in press) compared cause-specific mortality and survivorship in the WW deer herd with four other populations of mule deer wintering in eastern California and western Nevada.

Microhistological analysis of composited fecal-pellet groups identified 33 plant genera in the winter diets of WW deer, including 10 shrubs, 17 forbs, and 6 grasses. Diets generally contained equal amounts of browse and forbs during early winter (November-December), but forb and grass consumption increased during late winter (February-April) with the emergence of new spring growth. Antelope bitterbrush was the most common shrub in early winter diets, while sagebrush and saltbush were most common during late winter. Lower consumption of antelope bitterbrush during February and March was usually compensated for by higher sagebrush and saltbush use. Lower overall shrub use during April was generally compensated for by higher forb and grass use. Forbs were important to deer, comprising 41% and 52% of early and late winter diets, respectively.

Twenty-nine diet items were identified to genus by microhistological analysis of composited fecal-pellet groups collected from the WW summer range. This included 9 shrubs, 15 forbs, and 5 grasses. Shrub use by deer from east slope summer ranges was greatest in June, declined through July and August, and then increased in September. Shrub use by deer from west slope winter ranges was greatest in August and lowest in September. Sagebrush, bitterbrush, mountain mahogany, and ceanothus were important foods throughout the entire summer. Forbs, especially buckwheat, were used extensively during all summer months.

Levels of fecal nitrogen in monthly diets varied seasonally and generally reflected changes in dietary composition; that is, lower during fall and winter and higher during spring and summer.
From March 1992-April 1995, I determined habitat use patterns on the WW herd winter range based on 429 relocations of 35 radio-collared deer. During early winter (November-January), deer inhabited upper elevation, secondary winter ranges where they used all habitats in proportion to their availability. However, use preference ratings indicated that montane chaparral, aspen forest, mountain mahogany, and big sagebrush were important deer habitats during early winter, comprising approximately 11% of the deer locations. These habitats were important to deer because they occurred in complex mosaics that enhanced forage and cover opportunities, thereby reducing deer concentrations and competition for available resources.

Habitat use during late winter (February-April) appeared to be closely related to the temporal availability and phenological development of succulent, herbaceous forage. Deer preferred the lower elevation low sage, annual grassland, and desert scrub communities that provided an abundance of succulent forage early in the growing season; low sage/annual grassland habitat comprised approximately 18% of the mapped area, but included 34% of late winter locations.

Irrigated pasture habitat was important to deer, especially during early winter when it made up 12% of deer use. Deer used pinyon-juniper woodland in relation to its availability; however, its relative importance was demonstrated by 35% and 32% use during early and later winter, respectively. Most pinyon-juniper stands inhabited by deer were in early and mid-successional phases and supported dense shrub layers where bitterbrush was a conspicuous understory component.

Recommendations to increase carrying-capacity for mule deer on the WW winter range include (i) manipulation of pinyon-juniper forest through prescribed burning to reduce tree dominance before stands close and increase the production of shrubs, grasses, and forbs; (ii) maintaining and enhancing bitterbrush communities to rejuvenate existing older plants and high-cover stands by topping, and replanting and protecting burned stands from grazing to allow recovery to dense stands that were present before fires occurred; and (iii) reseeding burns to decrease invasion of less desirable annual weeds and increase amounts of nutritional perennial forage.
CHAPTER 2. MIGRATION AND INTERSEASONAL MOVEMENTS

INTRODUCTION

Migratory mule deer (Odocoileus hemionus hemionus) in the eastern Sierra Nevada, Inyo and Mono Counties, California, have been studied extensively since 1983 to determine their general population characteristics, seasonal distribution patterns, and the habitats they occupy (Thomas 1985\(^1\), Kucera 1988\(^2\), Taylor 1988\(^3\), 1991\(^4\), Loft et al. 1989). Information from these studies has enabled the California Department of Fish and Game (CDFG) to readjust herd boundaries to reflect the seasonal distribution and movement patterns of each individual deer herd and to prescribe management activities that meet the demands of deer herds in delineated areas. More importantly, this information has enabled wildlife managers to evaluate the potential effects of subdivisions, recreational developments, and other land uses on essential deer habitat and, in many cases, to successfully defend these values in land use planning.

Physical and human disturbances associated with housing and recreational developments constructed on or adjacent to essential mule deer winter and transition range can adversely affect deer use of an area (Mackie and Pac 1980, Smith and Conner 1989). Therefore, it is imperative that detailed data on seasonal distributions, migration habits, and population characteristics be obtained for all deer ranges, particularly those in areas where potential threats to winter ranges and migration corridors exist (Bertram and Remple 1977, Mackie and Pac 1980).

Rocky Mountain mule deer in the intermountain west often migrate long distances between different areas in response to the seasonal availability of resources (Gruell and Papez 1963, Garrott et al. 1987, Pac et al. 1987, Loft et al. 1989, Brown 1992, Kucera 1992). These authors have also demonstrated that individual deer, especially adult females, migrate along traditional travel routes and return to the same seasonal home range area each year. Marked deer residing from a distinct winter range will migrate to the same summer range, indicating that migration routes and seasonal ranges are characteristic of family groups (Gruell and Papez 1963). Deer from the same winter range will also migrate to different summer ranges, while, conversely, those sharing a common summer range will migrate to several distinct winter ranges (Gruell and Papez 1963).

\(^1\)Thomas, R. D. 1985. Management plan for the West Walker deer herd, Calif. Department of Fish and Game, Bishop, California, USA.
\(^2\)Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California, Ph.D. Dissertation, University of California, Berkeley, California, USA.
\(^3\)Taylor, T. J. 1988. Migration and seasonal habitats of the Casa Diablo deer herd, Calif. Department of Fish and Game, Bishop, California, USA.
\(^4\)Taylor, T. J. 1991. Ecology and productivity of two interstate deer herds in the eastern Sierra Nevada: East Walker-Mono Lake deer herd study, Calif. Department of Fish and Game, Bishop, California, USA.
Knowledge of factors that influence deer seasonal movements is important to wildlife managers because disturbance impacts of development projects within migration corridors can often be mitigated by avoiding disruptive activities during this critical period. Garrott et al. (1987) discussed factors influencing the timing and pattern of seasonal migration of mule deer. These authors suggested that mule deer in northwest Colorado migrated in response to the seasonal availability of succulent forage on the year-round range of the animals. Other studies (Kucera 1992, Leopold et al. 1951, Gilbert et al. 1970) have discussed the effects of weather, particular snowstorms, on the timing of fall migration to the winter range.

This chapter reports the results of a 3.5-year study of the seasonal distribution and movements of the West Walker deer herd, a migratory herd of mule deer wintering in the eastern Sierra Nevada, California. It also discusses proximal factors influencing the timing and rate of mule deer migration from seasonal ranges. My objectives were to (i) determine the migration routes and seasonal ranges of deer from the West Walker herd, (ii) determine the timing and pattern of seasonal migration, (iii) the fidelity of deer to specific migration routes and seasonal ranges, and (iv) to provide recommendations to maintain and enhance the WW deer herd and its environment.

**STUDY AREA**

The West Walker deer herd occupied approximately 3,230 km² in the central Sierra Nevada, California (Figure 2-1). Winter range habitat encompassed approximately 800 km² near the western rim of the Great Basin in northern Mono County, California, and southern Douglas County, Nevada. Following Mayer and Laudenslayer (1988), major vegetational communities on the winter range between 1,600-2,500 m elevation included big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), pinyon pine (*Pinus monophylla*)-juniper (*Juniperus occidentalis*) woodland, agricultural meadow, and irrigated pasture. Topography on the winter range was highly variable, ranging from flat in the agricultural valleys to steep and rugged on portions of the Sierra escarpment. Roads were common throughout the winter range, which is bisected by a major interstate highway (U.S. 395) that separates California and Nevada ranges. Water was abundant on California ranges in numerous permanent creeks and streams that flow east from the Sierra crest; Nevada winter ranges were arid, containing fewer sources of permanent water.

Regional climate was semiarid with marked variation in seasonal precipitation and temperature (Figure 2-2). Winter precipitation occurred mostly in the form of snow, which periodically covered lower elevation (1,500-2,000 m) winter ranges from November-February (Figure 2-2).

Within the total winter range were 7 distinct deer concentration areas or primary winter ranges that each support several hundred to several thousand deer annually. These areas were selected to sample wintering deer that, based on previous telemetry studies (Loft et al. 1989, Thomas 1985), migrate in different directions. In California, primary
Figure 2-2. Total Precipitation, Snowfall, and Average Minimum Temperatures Recorded by Month on the West Walker Deer Herd Winter Range, Coleville, California, 1992-1995.
winter ranges were located in Little Antelope Valley (LAV), Slinkard Valley (SV), and along the East Side (ES) of Antelope Valley at the base of the Wellington Hills (Figure 2-1). Nevada primary winter ranges were located near Topaz Lake in the Gray Hills (GH) and on Wild Oat Mountain (WOM), and in the Wellington Hills near Jack Wright Summit (JW) and Boulder Hill (BH) (Figure 2-1). The magnitude and period of deer use on primary winter ranges varied according to winter severity (e.g., depth and duration of snowpack). Also included within the total winter range are secondary winter ranges. Secondary winter ranges encompassed upper elevations (2,000-2,500 m) of the winter range that were used by deer from November-January.

Transition ranges and delay areas occurred between 2,000 and 2,500 m and were dominated by antelope bitterbrush, big sagebrush, mountain mahogany (Cercocarpus ledifolius), pinyon pine forest, and Jeffrey pine forest (Figure 2-1). Meadow and quaking aspen forest (Populus tremuloides) habitats dominated vegetation along drainages that flow east from the Sierra crest. The summer range encompassed some 2,450 km² on both the east and west slopes of the central Sierra Nevada on the Toiyabe National Forest (TNF), Stanislaus National Forest (SNF), and in Yosemite National Park (YNP) in Mono, Alpine, and Tuolumne Counties, California (Figure 2-1). Elevations ranged from 2,200-3,300 m. Major vegetational types on the summer range included big sagebrush, antelope bitterbrush, montane chaparral, pinyon-juniper forest, Jeffrey pine (Pinus jeffreyi) forest, lodgepole pine (Pinus contorta) forest, mixed conifer forest, aspen forest, red fir forest, and whitebark pine (Pinus albicaulis) forest.

METHODS

Capture and Marking
We captured deer on primary winter ranges using drive nets (Beasom et al. 1980) and a Bell Jet Ranger helicopter. Deer were hazed slowly by helicopter into the net which consisted of 15-30 panels, each 25 m long and 2.4 m high. The panels were oriented end to end in the desired size and configuration and propped up by light weight wooden poles. Net size and configuration were based on terrain features and the deer’s anticipated flight path. Net sites were selected by experienced members of the capture team during preliminary aerial reconnaissance. Net sites usually employed natural escape routes such as drainage bottoms where the net was concealed by terrain (Thomas and Novak 1991). Anywhere from 1-10 deer were captured on successive drives until desired numbers were obtained for each capture location.

We captured 133 deer and all were marked with 8-x 8-cm plastic ear tags, consecutively numbered and color coded to capture location. Forty-seven adult does and 10 adult bucks were equipped with radio-collars (Telonics® Inc., Mesa, Ariz.) that weighed 260-270 g and had an operational life of 24-36 months at 35-75 pulses per minute. Radio transmitters fitted on adult males were mounted on expandable collars to allow for neck swell during the rut. All telemetry units were equipped with mortality
sensing circuitry that doubled the pulse rate after 3-5 hours with no movement.

**Radio-telemetry**

Deer were monitored by aircraft once per week, weather permitting, during the spring and fall migrations, and 1-2 times monthly during the summer and winter. All locations were made during daylight hours, usually between 0800 and 1200 hours. Aerial radio-tracking was conducted from a Cessna 185 at air speeds ranging from 80-110 km per hour. Aerial relocation bearings were recorded in longitude and latitude coordinates to 0.01 minute, using a “Loran C” system. The mean error (n = 17, \( \bar{x} = 295 \) m, SE = 50.2) aerial locations was determined during the course of the study by measuring distances between dead radio-collared deer and estimated locations. I used program LATLONG (Kie et al. 1996) to convert location coordinates to Universal Transverse Mecator (UTM) coordinates. I then plotted UTM coordinates on U.S. Geological Survey 7.5-minute maps.

Initial ground locations were made from a vehicle equipped with a Telonics® TR-2 receiver with an attached program/scanner (TS-1) and a base loaded whip antenna. Triangulation bearings were taken with a hand-held, directional “H”antenna (RA-2A; Telonics® Inc., Mesa, Ariz.) and ear phones. Because all radioed animals were marked for visual identification, a visual location was obtained to verify triangulation bearings.

Migration routes between winter and summer ranges were ascertained by tracking radioed deer closely once they departed the winter range. The locations of these routes were mapped on U.S. Geological Survey 7.5 minute maps and the proportions of radio-collared deer using each route was determined. Following Brown (1992), I used the mean UTM of seasonal locations for individual radio-collared deer to determine the geographical center of activity (COA) (Hayne 1949) for summer and winter seasonal use areas. I defined migratory deer as those animals that moved between seasonal use areas with no overlap of winter and summer range COA’s. Seasonal use areas for migrant deer were defined as those areas where deer remained for an extended period of time. Straight-line distances between consecutive year COA’s were calculated to determine fidelity to summer and winter seasonal ranges. Non-migratory deer were defined as those animals that remained on the winter range year-round and had overlapping winter and summer range COA’s. The timing of spring and fall migrations for individual radio-collared deer was estimated as the mid-point date of the interval in which the radio signal was last received and first not received on the winter range (Kucera 1992). Delay areas were defined as sites where deer remained for several days or more along the migration route (Bertram and Remple 1977).

I used standard techniques for statistical testing with \( \alpha = 0.05 \). I tested for differences among 2 means (i.e., sexes, years) with a t-test. Differences among > 2 means (i.e., years, subgroups) were tested using analysis of variance. I used a Spearman rank correlation to examine for relationships between consecutive year periods in the spring departure dates of individual radio-collared deer from the winter range.
RESULTS

From May 1992-June 1995, I made 953 aerial and 1,187 ground radio locations of 57 radio-collared deer (47 females and 10 males). I monitored 25 deer for ≤ 1 year, 15 for 1-2 years, 7 for 2-3 years, and 10 for > 3 years. A total of 34 deer were monitored until their death, 10 until their transmitter batteries failed, and 14 until the study terminated in September 1995.

SPRING MIGRATION

Pattern and Timing of Deer Movements

Spring migration from the winter range was approximately 3 weeks earlier in 1992 and 1994 than in 1993 and 1995. In 1992 and 1994, the first radioed deer left the winter range during mid-April, with most deer migrating by early May (Figure 2-3). The 1993 and 1995 migrations, however, did not begin until the last week of April and the first week of May, respectively, with most deer migrating by the third week in May. Mean departure dates from the winter range during spring migration differed significantly among the 4 years studied (F = 43.9; 3, 86 d.f.; P ≤ 0.000). During the 1992 and 1994 migrations, mean departure dates from the winter range were 24 April and 26 April, respectively. In comparison, mean departure dates during the 1993 and 1995 spring migrations were 6 May and 14 May, respectively.

Rank correlation analysis indicated no relationship between 1992 and 1993 (r_s = -0.063; n = 19; P > 0.05), 1993 and 1994 (r_s = 0.077; n = 13; P > 0.05), and 1994 and 1995 (r_s = -0.194; n = 13; P > 0.05) in the spring departure dates of individual deer monitored for two consecutive years. There were large differences between years in the timing of deer migration from the winter range. For example, in 1994 individual deer departed the winter range as many as 26 days earlier and 11 days later than in 1993 (Table 2-1).

Changes in elevation between winter and summer ranges used by migratory deer varied from approximately +550 to +1,425 m. Mean elevations occupied by deer on specific dates during spring migration differed among the 4 years studied (F = 3.07; 3, 80 d.f.; P = 0.03) (Table 2-3). During the spring migrations of 1992 and 1994, which followed winters of below normal snowfall, deer remained on primary winter ranges at 1,650-1,720 m elevation until mid-April, then gradually drifted to higher elevations (Figure 2-4). In both years, deer delayed migration in Bagley Valley (1,890 m) and in the vicinity of Sonora Junction (2,000-2,300 m) until late May and most deer were on their summer ranges by mid-June. In 1992, a series of spring snow storms during the second week in June caused two deer to reverse their migrations. During a telemetry flight on 5 June, female 515 was located on her summer range COA on White Mountain (3,000 m elev.). On 17 June, however, she was located back in Bagley Valley (2,000 m elev.), some 22 km north of White Mountain. Also on 5 June, male 415 was located at
Figure 2-3. Cumulative Percent of Radio-Collared Deer Migrating from the West Walker Winter Range during Spring Migration, 1992-1995
Table 2-1. Differences in number of days between two consecutive year periods in the departure dates of individual radio-collared deer from the West Walker herd winter range, 1992-1995. Negative numbers indicate that movement was later than the previous year, while positive numbers indicate that movement was earlier.

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Table 2-2. Differences in meters between two consecutive year periods in the mean elevations occupied by radio-collared deer during spring migration, 1992-1995. Negative numbers indicate that elevations occupied were less than the previous year, while positive numbers indicate that elevations occupied were greater than the previous year.

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Figure 2-4. Mean Elevations Occupied by West Walker Radio-Collared Deer during Spring Migration, 1992-1995.
approximately 3,000 m elevation near the headwaters of the West Walker River. During a telemetry flight on 17 June, however, he was located approximately 6 km down river (2,250 m elev.) from his previous location.

In comparison, during the 1993 and 1995 spring migrations, which followed winters of above normal snowfall, deer remained on primary winter ranges until the third week of May, after which they migrated to higher elevation holding areas (Figure 2-4). In both years, cool spring temperatures on the winter range and along migration routes prevented snow from melting rapidly. Minimum temperatures on the winter range in spring 1993 averaged 0.6° C in March and April, while temperatures during spring 1995 averaged -2.1° C in March and 0° C April. During spring 1993 and 1995, deer delayed migration on the Bagley Valley and Sonora Junction holding areas until the first and last weeks of June, respectively, before migrating to the summer range.

Because the 1992 and 1995 spring migrations followed the driest and wettest winters, respectively, I compared these two years to examine for differences in the duration of delay on spring holding areas. In spring 1992, the first deer arrived on the Bagley Valley and Sonora holding areas on 20 April and the last deer departed on 1 June (Figure 2-5). In comparison, in spring 1995, the first deer arrived on the holding areas on 5 May and the last deer departed on approximately 29 June (Figure 2-5). There was a significant difference between 1992 and 1995 in the interval of delay on spring holding areas (t = -3.51; 27 d.f.; P = 0.0016). In 1992, deer delayed migration on holding areas for an average of 20 days (range 13-36 days) (Figure 2-6). In 1995, however, deer delayed migration for an average of 35 days (range 21-46 days).

Locations of Deer Movements

Linear distances traveled between winter and summer range COA’s for 42 migrants varied from 5.7 to 71.3 km (X = 35.9 km, SE = 2.0) (Table 2-3). There was no difference (t = -0.07, 42 df, P = 0.47) between males (n = 7, X = 36.3, SE = 2.1) and females (n = 36, X = 35.5, SE = 3.5) in distances traveled between winter and summer COA’s. Distances traveled between winter and summer range COA’s did not differ among years (F = 0.87; 51, 2 df; P = 0.59). There was, however, a highly significant difference among deer from the 7 primary winter ranges (LAV, SV, WOM, GH, ES, JW, and BH) in the mean distances traveled between winter and summer range COA’s (Table 2-3, F = 3.88; 5, 39 df; P = 0.0043). Deer from BH traveled nearly twice as far to summer ranges (X = 51.8, SE = 4.7) than deer from LAV (X = 27.0, SE = 5.4).

Nevada Winter Ranges

Deer (n = 22) from the Wellington Hills, Nevada, including JW, ES and BH, migrated south to summer ranges located in the central Sierra Nevada, California. The migration route used by deer (n = 17) wintering on the north and west slopes of the
Figure 2-5. Percent of Radio-Collared Deer Arriving on and Departing from the Sonora and Bagley Valley Holding Areas during the 1992 and 1995 Spring Migrations
Figure 2-6. Period of Delay for Individual Radio-Collared Deer on the Sonora and Bagley Valley Holding Areas during the 1992 and 1995 Spring Migrations
Wellington Hills, including ES and JW, went south along the west slope of the Wellington Hills, through Indian Valley and Jackass Flat, and then south along the west slope of the Sweetwater Mountains to the Sonora Junction holding area (Figure 2-7, Table 2-4). The Sonora Junction holding area encompasses approximately 200 km² at elevations ranging from 2,100-2,500 m. It extends from Cottonwood Creek, on the west side of the Sweetwater Mountains, south to Pickle Meadow, and east to Bush Mountain (Figure 2-7, Table 2-4). Within the Sonora holding area, deer from ES and JW delayed migration in the vicinity of Pickle Meadow (2,100-2,250 m). This portion of the holding area was dominated by big sagebrush scrub and wet meadow habitats that provided deer with an abundance of succulent forage. Much of this area, however, was grazed by cattle and had high levels of human disturbance from recreational activity and training maneuvers associated with the U.S. Marine Corp. Mountain Warfare Training Center.

Deer from BH (n = 5), on the east side of the Wellington Hills, migrated south from Smith Valley up the Desert Creek drainage, and then crossed the crest of the Sweetwater Mountains (2,500 m elev.) to the west side of the Sweetwater range and the Sonora holding area (Figure 2-7, Table 2-4). Within the Sonora holding area, deer from BH delayed migration primarily in the vicinity of Fales Hot Springs and Swauger Creek (2,300-2,500 m). This portion of the holding area was relatively free of human disturbance and supported habitats that provided deer with an abundance of cover and high quality forage. After the spring holding period, 12 of the 22 deer that delayed on the holding area migrated south to summer range located within and adjacent to the West Walker River drainage, from Poore Lake south to Emigrant Pass and east to Walker Mountain (Figure 2-7, Table 2-4). Four deer migrated south from the holding area through Leavitt Meadow and over the Sierra Crest to summer range located on the west slope of the Sierra Nevada in the Kennedy Creek drainage (Figure 2-7, Table 2-4). Three deer, 2 from BH and 1 from ES, migrated south down the Swauger Creek drainage and then around Bush Mountain and Sawmill Ridge to the Twin Lakes drainage (Figure 2-7, Table 2-4). From Twin Lakes, 2 of these deer continued south around Monument Ridge and then up the Green Creek drainage and over Virginia Pass (3,300 m elev.) into YNP. Two deer occupied summer home ranges within the holding area and 1 deer died on the holding area before its migration route was determined.

Deer from WOM (n = 5) traveled southwest from the winter range to Bagley Valley where they delayed migration (Figure 2-7, Table 2-4). After the holding period, 3 does migrated south up the Wolf Creek drainage and then went west up the Dixon Creek to summer range near Ebbett’s Pass. One doe traveled south up Silver King Valley to the East Fork of the Carson River, then continued south to her summer range on White Mountain (Figure 2-7, Table 2-4). A fifth doe migrated north down the East Fork of the Carson River to the vicinity of Markleeville, after which she went west up the Hot Springs Creek drainage and then south up Charity Valley Creek to the Blue Lakes Basin.

Of the five deer radioed on the GH, only 1 (doe 315) migrated to the summer range (Figure 2-7, Table 2-4). This doe moved west from GH around the south end of
Table 2-3. Mean distances traveled between winter and summer range COA’s by migratory mule deer from 7 primary winter ranges of the West Walker herd, 1992-1995.

<table>
<thead>
<tr>
<th>Area</th>
<th>n</th>
<th>Mean (km)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAV</td>
<td>9</td>
<td>29.1</td>
<td>6.9</td>
</tr>
<tr>
<td>SV</td>
<td>9</td>
<td>33.4</td>
<td>2.2</td>
</tr>
<tr>
<td>GH</td>
<td>1</td>
<td>23.0</td>
<td>0.0</td>
</tr>
<tr>
<td>WOM</td>
<td>5</td>
<td>31.6</td>
<td>3.0</td>
</tr>
<tr>
<td>ES</td>
<td>11</td>
<td>39.5</td>
<td>2.4</td>
</tr>
<tr>
<td>JW</td>
<td>3</td>
<td>32.6</td>
<td>6.6</td>
</tr>
<tr>
<td>BH</td>
<td>3</td>
<td>56.3</td>
<td>6.9</td>
</tr>
</tbody>
</table>

LAV = Little Antelope Valley, SV = Sinkard Valley, GH = Gray Hills, WOM = Wild Oat Mountain, ES = East Side, JW = Jack Wright, BH = Boulder Hill

Table 2-4. Direction of migration from the winter range, holding area used, and summer range used (east or west slope of the Sierra Nevada) by deer from the 7 primary winter ranges of the West Walker herd, 1992-1995.

<table>
<thead>
<tr>
<th>Wintering Area</th>
<th>Migration Direction</th>
<th>Holding Area Used</th>
<th>Summer Range Used</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>South</td>
<td>West</td>
<td>Sonora</td>
</tr>
<tr>
<td>LAV</td>
<td>7</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>SV</td>
<td>4</td>
<td>4</td>
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</tr>
<tr>
<td>GH</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>WOM</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>ES</td>
<td>14</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>JW</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>BH</td>
<td>5</td>
<td>0</td>
<td>5</td>
</tr>
</tbody>
</table>

LAV = Little Antelope Valley, SV = Sinkard Valley, GH = Gray Hills, WOM = Wild Oat Mountain, ES = East Side, JW = Jack Wright, BH = Boulder Hill
Topaz Lake, crossed SR 395, and then traveled to Slinkard Valley where she delayed migration for 7 days in 1992 and 18 days in 1993. She then migrated to her summer range on Silver Hill approximately 4 km west of Bagley Valley. Two deer (1 male and 1 female) from the GH winter range did not migrate. Both of these deer moved south from the GH a distance of approximately 5 km to summer range on the West Walker River in Antelope Valley. One doe was killed and the transmitter of another failed before their migration routes were determined.

California Winter Ranges

Deer from LAV (n = 10) migrated both south and west to summer range located in the central Sierra Nevada, California (Figure 2-7, Table 2-4). Deer that migrated south from LAV (n = 7) moved up the Mill and Lost Cannon Creek drainages to the Sonora holding area where they delayed in the vicinity of Pickle Meadows (Figure 2-7, Table 2-4). After the spring holding period, 3 of the 7 LAV migrants moved south to summer range located in the West Walker River and Molybdenite Creek drainages (Figure 2-7, Table 2-4). One adult doe traveled south from the holding area up Buckeye Canyon and then crossed over the Sierra Crest at Rock Island Pass (3,000 m elev.) into YNP. She then migrated southeast across Suicide Ridge and Slide Canyon to her summer range in Matterhorn Canyon, YNP. The remaining 3 deer migrated to summer ranges located in proximity to the SHA, in the Wolf Creek, Silver Creek, and Cowcamp Creek drainages (Figure 2-7, Table 2-4).

Deer that migrated west from LAV (n = 3) moved up the Golden Gate Mine drainage and then over Lightening Ridge into the Snodgrass Creek drainage, Alpine County (Figure 2-7, Table 2-4). One doe summered in the Snodgrass Creek drainage, while the other two continued west into Silver King Valley. One of these deer delayed in Silver King Valley and then migrated south up the East Fork of the Carson River to her summer range in Dumonts Meadows, Alpine County. The other deer delayed in Bagley Valley and then migrated northwest to her summer range on the East Fork of the Carson River (Figure 2-7, Table 2-4).

Deer from SV (n = 8) migrated both south and west to central Sierra Nevada summer ranges (Figure 2-7, Table 2-4). Deer that migrated south (n = 4) moved through LAV and then up the Lost Cannon Creek and Mill Creek drainages to the Sonora holding area where they delayed in the vicinity of Pickle Meadows (Figure 2-7, Table 2-4). After the spring holding period, 3 of the 4 migrants moved south up the West Walker River drainage to summer ranges located west of the Sierra Crest in the Emigrant Wilderness; the fourth deer occupied summer range located within the SHA (Figure 2-7, Table 2-4).

Deer that migrated west (n = 4) from SV first delayed migration in Bagley Valley, after which two does migrated north down the East Fork of the Carson River to the vicinity of Markleeville (Figure 2-7, Table 2-4). From Markleeville they continued west up the Hot Springs Creek drainage and then south up Charity Valley Creek to the Blue
Lakes Basin. One doe migrated south from Bagley Valley up the Wolf Creek drainage and then went west up the Dixon Creek to her summer range near Ebbett’s Pass (Figure 2-7, Table 2-4). The fourth doe died on the Bagley Valley holding area before her summer range was determined.

**FALL MIGRATION**

**Pattern and Timing of Deer Movements**

The timing of fall migration from the summer range differed significantly among years ($F = 8.96; 2 \, df; \, P = 0.0004$). In 1992 and 1993, deer migrated from the summer range an average 12 and 14 days earlier, respectively, than in 1994 (Figure 2-8). Differences among years in the timing of fall migration was related to the severity of fall weather. Fall migration in 1994 lasted from approximately 28 September to 21 October and was characterized by two distinct periods of peak migration. The first pulse of activity occurred between 5 and 7 October when 53% of radio-collared deer migrated from the summer range (Figure 2-8). These deer migrated in response to a storm on 4 and 5 October, when 14 cm of snow fell at 2,400 m elevation; snowfall amounts were undoubtedly much greater at higher elevations of the summer range. The remaining deer migrated from the summer range in response to a second storm on 14 and 15 October, when approximately 2.5 cm of snow fell at 2,400 m elevation (Figure 2-8).

In comparison, there were no fall snow storms during 1992 and 1993 (Figure 2-8). As a result, migration was prolonged over several months, from approximately mid-October to mid-November. In 1992, approximately 41% of radioeared deer migrated between 12 and 18 October, despite the absence of fall snow storms. Similarly, in 1993, 47% of deer migrated between 14 and 18 October, also in the absence of snow. In both years, peak migration may have occurred in response to below freezing temperatures in mid-October. Average minimum temperatures of $-4.4^\circ C$ in October of both years may have decreased the quality and quantity of summer range vegetation.

Mean elevations occupied by deer on specific dates during fall migration differed among years ($F = 5.36; 3 \, d.f.; \, P = 0.015$) (Table 2-5). During fall 1992 and 1993, mild weather conditions in October and November enabled deer to delay migration on upper elevation summer and transition ranges. Mean elevations occupied by migratory deer during mid-October were 325 and 400 m higher in 1992 and 1993, respectively, than in 1994 (Figure 2-9). During 1994, mid-October snow storms and below freezing temperatures forced most deer to migrate directly to lower elevation winter ranges.

Some SV and WO deer delayed migration in Bagley Valley (1,850-2,500 m elev.) before migrating to the winter range. During fall 1992, 3 SV deer and 1 WO deer delayed in Bagley Valley for several days (range = 3-7 days) each between mid-October and early November. In 1993, 1 WO deer and 2 SV deer delayed migration in Bagley Valley for a period of 5-12 days during October. In both years, deer from the Wellington Hills did not

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California Department of Fish and Game
West Walker Deer Herd Study

Chapter 2. Migration
May 1997

Page 2-19
Table 2-5. Differences in meters between two consecutive year periods in the mean elevations occupied by radio-collared deer during fall migration, 1992-1994. Negative numbers indicate that elevations occupied were less than the previous year, while positive numbers indicate that elevations occupied were greater than the previous year.

<table>
<thead>
<tr>
<th>Date</th>
<th>1992</th>
<th>1993</th>
<th>1994</th>
</tr>
</thead>
<tbody>
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<td>9-28</td>
<td>-15</td>
<td>+85</td>
<td>-40</td>
</tr>
<tr>
<td>10-1</td>
<td>-170</td>
<td>+135</td>
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<td>10-5</td>
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<td>+175</td>
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<td>10-7</td>
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<td>-90</td>
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</tr>
<tr>
<td>11-15</td>
<td>-20</td>
<td>+190</td>
<td>-170</td>
</tr>
</tbody>
</table>

delay on the Sonora holding area, but instead migrated directly to secondary winter range located at the northeast end of the Sweetwater Mountains, from Rock Creek north to Jackass Flat (2,100-2500 m) (Figure 2-7).

Fidelity

Summer Range

Distances separating summer range COA’s of females monitored for ≥ two successive years averaged 1.6 km (n = 24, SE = 0.41). Fifty percent of females occupied COA’s ≤ 1 km apart, and 83% occupied COA’s ≤ 2 km apart. There was no difference among years in mean distances separating summer range COA’s (F = 2.3, 2, 43 df, P = 0.11). Distances between summer range COA’s occupied in 1992 and 1993 averaged 2.0 km (n = 23, SE = 0.49), while distances between 1993 and 1994 summer range COA’s averaged 0.73 km (n = 14, SE = 0.2). Distances separating 1992 and 1994 summer range COA’s averaged 1.8 km (n = 9, SE = 0.2).

The 1993 spring migration was preceded by an usually severe winter, with snowfall accumulations on the summer range exceeding 120% of normal. This heavy
Figure 2-9. Mean Elevations Occupied by West Walker Radio-Collared Deer during Fall Migration, 1992-1994
Figure 2-8. Cumulative Percent of Radio-Collared Deer Migrating from the West Walker Summer Range during Fall Migration, 1992-1994
snowpack persisted until early June at lower elevations of the summer range and until mid-August at higher elevations. An aerial survey conducted on the summer range in late-June 1993 indicated that much of the summer range above 2,800 m was snow covered. During this survey, 66% (10 of 15) of the radio-collared deer for which locations were determined remained > 2 km (range = 0.28-14.4 km) from their 1992 COA’s. Two BH females that summered at higher elevations (3,025-3,125 m) on the Sierra Crest in YNP were located east of the Sierra Crest at approximately 2,700 m elevation; these deer did not arrive on their previous year COA’s until mid-August.

Winter Range

Deer showed poor fidelity to early winter (November-January) COA’s. Distances separating early winter COA’s of adult females monitored for ≥ two successive years averaged 4.7 km (n = 11, SE = 1.4). Nineteen percent of females used early winter COA’s ≤ 1 km apart and 36% used COA’s ≤ 2 km apart. Winter weather in 1992-93 was severe, with 180 cm of snow and average minimum temperatures of -16°C in January. In comparison, the winter of 1993-94 was mild, with 81 cm of snow and minimum temperatures averaging -6°C in January. During the 1993-94 winter, 2 migratory females occupied early winter COA’s separated by 11.4 km and 13.9 km. Additionally, because of mild snow conditions, 36% (8 of 22) of radio-collared deer occupied summer and transition ranges until late-January.

Deer showed stronger fidelity to late winter (February-April) COA’s. Distances separating late winter COA’s of females monitored for ≥ two successive years averaged 1.8 km (n = 14, SE = 0.58). Fifty-seven percent of females occupied consecutive late winter COA’s ≤ 1 km apart and 71% occupied COA’s ≤ 2 km apart. The distance between early and late winter COA’s of females averaged 6.1 km (n = 11, SE = 1.8).

DISCUSSION

Timing of spring migration from the winter range varied annually by as much as 1 month during the study and was related to winter severity and cool spring temperatures. The spring migrations of 1993 and 1995 followed extremely wet winters with total snowfall accumulations on the winter range exceeding 120% and 150% of normal, respectively. In both years, a heavy snowpack persisted until early May along migration routes and on holding areas because of cool spring temperatures that prevented snow from melting rapidly. As a result, plant phenology was delayed, and deer remained on winter and spring ranges where high quality forage was readily available.

In comparison, the 1992 and 1994 spring migrations followed extremely mild winters, with total snowfall accumulations in the eastern Sierra averaging approximately 50% of normal, respectively. Consequently, snow melt and vegetation growth along migration routes and holding areas occurred earlier, enabling deer to begin their migration from the winter range in mid-April.
Several authors (Russel 1932, Leopold et al. 1951, Loft et al. 1989) have associated the timing of spring migration from the winter range with the receding snow pack and the availability of spring forage. Loft et al. (1989) reported that differences among years in the timing of spring migration for deer from the WW herd was related to snow depth. Deer from the North Kings herd migrated from the winter range approximately two weeks earlier following dry winters of normal to below normal precipitation (Bertram and Remple 1977). In Colorado, Garrott et al. (1987) reported that the timing of spring migration following a severe winter was approximately 1 month later than after winters that were relatively mild. Garrott et al. (1987) hypothesized that to initiate migration, which requires additional energy demands, deer must first reverse the negative energy balance experienced during the winter. Hence, after more severe winters, deer migration is delayed on lower elevation winter ranges to extend the intake of high quality forage and improve the deer's overall physiological condition. Garrott et al. (1987) also suggested that by delaying migration after a severe winter, deer can avoid the heavier snowpack at upper elevations, which would impede their movements and reduce forage availability at a time when energy demands of pregnant does are high because of the late stage of pregnancy.

Kucera\textsuperscript{2} (1988) reported that deer from two eastern Sierra winter ranges consistently migrated in early April despite extremes in winter severity. He hypothesized that similarities among years in the temporal pattern of spring migration may have been related to nutritional factors, assuming that forage on the winter range in early-April was of poor quality, or in lesser abundance than on the holding area. Deer may have also been attempting to seek thermal relief at upper elevations because maximum daytime temperatures averaged about 22\textdegree C in April and 26\textdegree C in May. Other factors, including relative humidity and insect activity could also influence the timing of spring migration from the winter range (Russel 1932, Leopold et al. 1951, McCullough 1954).

West Walker deer delayed spring migration for 5 to 8 weeks on holding areas, which are characteristic of Sierra Nevada deer herds (Jordon\textsuperscript{4}, Bertram and Remple 1977, Loft et al. 1989). These areas are recognized for their importance in providing deer with nutritious spring forage at a time when adult does have increased energy demands because of late stage pregnancy and migration (Bertram and Remple 1977, Holl et al. 1979, Loft et al. 1989). Holding areas in this study had topographic and vegetative features similar to spring ranges described by Kucera\textsuperscript{2} (1992) and Taylor\textsuperscript{4} 1991 for other eastern Sierra Nevada deer herds. They occurred at intermediate elevations near the base of the Sierra escarpment and were largely dominated by big sagebrush scrub, irrigated pasture and Jeffrey pine forest. These habitats support a wide variety of plant species that provided deer with a diverse, high quality diet (Taylor Unpubl. data). The high nutritive value of this diet is optimal for rapid recovery from overwinter weight loss, and for satisfying productive functions such as antler development and body growth (Short 1981, Garrott et al. 1987).

\textsuperscript{1}Jordon, P. A. 1967. Ecology of migratory deer in the San Joaquin River drainage. Ph.D. Dissertation, University of California, Berkeley, California, USA.
Mean distance migrated between winter and summer ranges averaged 35.9 km and was greater than distances reported by Brown (1992) and Carpenter et al. (1979), but less than distances reported by Taylor (1991) for two eastern Sierra Nevada mule deer populations. Distances traveled between winter and summer ranges did not differ among males and females, which is similar to the findings of Brown (1992), Carpenter et al. (1979), and Garrott et al. (1987) for other Great Basin mule deer populations. There was a significant difference among deer from the seven primary winter ranges in the mean distances migrated between winter and summer range COA’s. Deer from BH migrated nearly twice as far to summer ranges than deer from LAV. The BH winter range is located approximately 15 airline km east of the LAV winter range, which may explain the longer migration observed in BH deer. Thus, spring and fall transition ranges could be particularly important habitats for BH deer because of the higher energy demands associated with a longer migration.

Distances between COA’s occupied in different years is a measure of fidelity (Brown 1992). Mean distances between consecutive year summer ranges of female deer in this study were more than twice that reported by Kucera (1992) for another eastern Sierra mule deer population. These distances were also greater than distances reported by Garrott et al. (1987) and Kufeld et al. (1989) for Colorado mule deer. Brown et al. (1992) reported that distances between consecutive summer range COA’s were ≤ 1 km for 83% and ≤ 2 km for 100% of female deer monitored in Idaho. Ackerman et al. (1984) reported that deer in Idaho occupied consecutive summer range COA’s separated by a mean distance of 0.8 km. Distances separating consecutive summer range COA’s in my study were ≤ 1 km for 50% and ≤ 2 km for 83% of females monitored.

Deer in this study showed poor fidelity (X = 1.6 km) to summer ranges, especially in 1993 when mean distances between COA’s occupied during consecutive summers averaged 2.0 km. During the summer of 1993, 5 radioed females and 1 male did not move to traditional summer ranges, but instead occupied COA’s located ≥ 2 km (range = 2.8-8.4 km) from COA’s occupied in 1992. This poor fidelity may be related to the severe winter of 1992-93, which resulted in a late snowmelt on the summer range that prevented some deer from occupying traditional summer home ranges. A telemetry flight conducted on the summer range in mid-July 1993 indicated that much of the summer range above 2,900 m was still snow covered. This prolonged snow cover may have delayed plant phenology at these higher elevations during a time when the energy demands of females was high because of late stage pregnancy and lactation. Hence, deer remained at lower elevations of the summer range where high quality forage was readily available. Loft et al. (1989) observed that California mule deer (O. h. californicus) on the west slope of the Sierra Nevada dropped their fawns on lower elevation holding areas because traditional summer range was not inhabitable until early July.

Deer in this study showed poor fidelity to consecutive early and late winter COA’s. Nineteen and 57% of females used consecutive early and late winter COA’s ≤ 1 km apart, and 36-71% used COA’s ≤ 2 km apart. In northwest Colorado, Garrott et al. (1987) reported that 56 and 66% of female mule deer used consecutive early and late
winter COA’s ≤ 1 km apart, and 71-82% used COA’s ≤ 2 km apart. Similarly, Brown (1992) found that 53% of mule deer in southeast Idaho used consecutive winter COA’s separated by ≤ 1 km, and 79% by ≤ 2 km.

In southeast Idaho, Brown (1992) found that deer use of winter range was strongly influenced by winter severity and that deer displayed high mobility in response to varying snow conditions, and cover or forage availability. In this study, fidelity to winter range sites was also influenced by winter severity. During the 1993-94 winter, mild snow conditions enabled some deer (36%) to delay migration on summer and transition ranges until late January. In comparison, during the severe 1994-95 winter, heavy snowfall from early to mid-October forced most deer to migrate directly to traditional winter ranges. Deer that delay migration on upper elevation summer and transition ranges during mild winters reduce intraspecific competition by exploiting forage resources that are normally unavailable because of deep snow (Brown 1992). Conversely, intensive and prolonged deer use on traditional winter range areas during severe winters could damage plants through defoliation, which ultimately depletes food reserves for deer (Mackie 1981).

The timing and pattern of the 1994 fall migration was similar to other studies (Russel 1932, Leopold et al. 1951, Bertram and Remple 1977, Kucera 1992) where migration occurred in response to major fall snow storms. Migration in 1994 began in late September and early October when a series of fall storms deposited heavy snow over the highest elevations of the summer range. Because of the severity of these storms, and the effects of snow on forage availability, deer hastily vacated the summer range and migrated en masse to the winter range. Consequently, fall migration to the winter range was completed by mid-October.

In comparison, fall migration in 1992 and 1993 could not have been initiated by fall snow storms because no measurable precipitation occurred during October and November. As a result, deer migrations occurred gradually, lacked any episodes of mass movement, and were extended into mid-November. Garrott et al. (1987) postulated that deer in northwest Colorado migrated not because of snow, but instead in response to photoperiod. By migrating prior to the first heavy snowfall, deer could take advantage of higher quality forage on the winter range before it became senescent and snow covered. However, in this study, I found no evidence to suggest that forage quality was greater on lower elevation holding areas and winter ranges. These areas were also subjected to drought-induced changes in habitat quality and they lacked the diversity of forage and cover types found on the summer range. Therefore, it seems unlikely that differences in forage quality between winter and summer ranges is adequate to fully explain why fall migration occurred well in advance of the first heavy snow.

Possibly, migration in both years was initiated by a combination of occurrences including drought conditions and below freezing temperatures that desiccated forage on the summer range, habitual behavior patterns, differential dispersal of sex and age groups, and hunting pressure. In the absence of snow, deer may habitually migrate at specific
times during fall migration because they learned to do so as fawns following their mothers. This behavior would have originated during years when drought conditions reduced the quantity and quality of summer range forage, thereby stimulating deer to migrate in the absence of snow storms.

Kucera (1992) suggested that females may be constrained in their timing of fall migration because of smaller body size, lactation, and by the inability of fawns to cope with severe fall weather. Therefore, an appropriate migratory strategy would be for females with fawns to leave the summer range before they were forced out by deep snow. Males, however, do not have the same energetic, nutritional, and parental constraints and thus, could afford to remain on the summer range for longer periods. Differential dispersal of sex and age groups during fall migration may also provide another benefit, it increases the amount of area available to individual animals. This could be beneficial to deer during autumn when forage quantity is limited due to plant senescence, drought, or other factors.

Deer from SV and WO delayed in Bagley Valley for 3-12 days during fall migration. Similarly, Loft et al. (1989) reported that WW deer delayed migration in Bagley Valley for approximately 1-2 weeks during the fall. Bagley Valley is comprised mostly of private land having low levels of human disturbance, and therefore, has traditionally provided deer refuge during the hunting season. Deer from the Wellington Hills did not delay on fall holding areas, but instead migrated directly to secondary winter range located largely on public land in a remote and highly inaccessible portion of the Sweetwater Mountains, California. This area of winter range could have provided deer refuge from hunting because it is located just south of Nevada, where hunting occurs during October, November and December.

Management Recommendations

Mule deer from the WW herd are migratory, spending the colder winter period at lower elevations (1,700-2,200 m elev.) in northern Mono County, California and southern Douglas County, Nevada, and the warmer summer months at higher elevations (2,250-3,200 m elev.) in the central Sierra Nevada, California. A small number of deer are year-round residents on the winter range, occupying the cooler river drainages and irrigated valley bottoms during the summer months. This study was similar to studies conducted by Taylor4 (1991) and Kucera (1992) in that deer from a relatively small area of winter range (800 km²) inhabited a large geographical area of summer range (2,450 km²) on both the east and west slopes of the central Sierra Nevada. This study also revealed that WW deer shared summer range with Rocky Mountain mule deer from two other eastern Sierra Nevada herds (Taylor4 1991) and California mule deer (O. h. californicus) from at least three western Sierra Nevada herds, including the Stanislaus, Tuloume (J. Maddox pers. comm.) and Railroad Flat herds (Loft et al. 1989).
Habitat management programs designed to increase deer productivity in the WW herd should be conducted on primary winter range sites where deer are concentrated and can be managed on a herd-specific basis. Winter range enhancement projects, such as reseeding, fertilization, and irrigation programs, livestock reductions, and prescribed burns, would benefit larger numbers of deer than similar projects conducted on the summer range where deer are more widely distributed. Moreover, because of the manner in which WW deer distribute themselves on the summer range, any changes in productivity resulting from winter range improvements would be reflected in a less dramatic but more widespread change in productivity. Similarly, any reduction in the amount of area available on primary winter ranges due to habitat loss, human disturbance or other factors, could have broad implications in the occurrence of deer summering over a large portion of central Sierra Nevada (Mackie and Pac 1980).

Private land subdivisions, both existing and proposed, currently pose the biggest threat to deer habitat on the WW winter range. Approximately 15% of the winter range is comprised of private land, much of which supports essential, high quality habitat for wintering mule deer. In California, areas of essential winter range with greatest potential for development occur along the base of the Sierra escarpment, west of SR 395, from the town of Walker north to the State Line, and near the base of the Wellington Hills, east of East Side Lane, from the County dump south to Walker. These areas are used heavily by deer during severe winters and during the spring because they occur at lower elevations (≤ 1,800 m) and support habitat types providing a diversity of forage and cover. Programs, such as private land acquisition or development of cooperative land use exchanges, should be developed to protect and maintain these important deer areas, if they are to continue to support deer throughout the total herd range. These types of programs are not without precedent on the WW winter range. The CDFG already owns and manages the LAV and SV Wildlife Management Areas, both derived through private land acquisition for the purpose of preserving and maintaining essential deer winter range.

When disturbance impacts from development projects cannot be avoided, mitigation measures should be developed to minimize potential direct, indirect, and cumulative impacts to areas providing important deer habitat. My study provided only general information on the timing and location of deer movement patterns on the WW winter range, holding areas, and migration routes. Such information can be used to formulate general guidelines for managing residential, commercial, and recreational development on areas of critical deer habitat (Table 2-6). However, it should not be used to fully evaluate potential effects to mule deer resulting from individual proposed projects, such as housing and resort developments. Pursuant to the California Environmental Quality Act (CEQA), these types of projects require the collection of detailed information on the amount, timing, and specific locations of deer use. This site-specific information is vital for complete and accurate assessment of potential project related effects resulting from habitat loss and alteration, human intrusion, and other factors. It is only through such thorough assessment that meaningful mitigation can be developed.
Table 2-6. Recommended mitigation measures developed to minimize potential impacts of residential, commercial, and recreational development on important mule deer range in the eastern Sierra Nevada (Taylor\textsuperscript{5} 1991, Taylor\textsuperscript{6} 1994, Taylor\textsuperscript{7} 1996).

1. Avoid disruptive activities on winter ranges, migration routes, and holding areas during critical deer use periods. For the WW deer herd, this would include the period from 1 October to 30 November and 1 April to 15 May on migration routes, holding areas and secondary winter ranges (> 2,000 m), and 1 December to 15 April on primary winter ranges (<2,000 m).

2. On larger parcels (> 0.81 ha), confine livestock to corral areas to prevent destruction, e.g., trampling and overgrazing, of deer foraging and cover areas.

3. Livestock corrals should incorporate use of poles, pipe, split rails, or other natural, non-wire materials to allow safe passage for deer.

4. Prohibit construction of tall or solid fences (e.g., woven wire fence, chainlink etc.), along property line boundaries.

5. Construct property line fences of 3 single strand wires placed 20, 30 and 42 inches from the ground with the bottom wire a smooth strand.

6. Contain dogs within an enclosed, private yard fenced area.

7. Reiterate Mono County leash laws in project CC&R’s.

8. Prohibit dogs in project areas during construction.

9. Aim, shield, and direct night lighting to provide illumination of target areas with minimal offsite visibility.

10. Control noise emissions during construction by muffling such things as engines and generators.

11. Utilize existing dirt roads to avoid unnecessary disturbance to native vegetation.

12. Use minimum road construction specifications based on projected transportation needs.

\begin{flushright}
\textsuperscript{5}Taylor, T.J. 1991. Arcularius Ranch vegetation and wildlife assessment study, Mono County, California.
\textsuperscript{6}Mono County Planning Department, Bridgeport, California, USA.
\textsuperscript{7}Taylor, T.J. 1994. Inaja Land Company wildlife and vegetation assessment study, Mono County, California. Mono County Planning Department, Bridgeport, California, USA.
\textsuperscript{8}Taylor, T.J. 1996. Deer habitat suitability study for the Meadow Cliff Lodge expansion area, Mono County, California. Mono County Planning Department, Bridgeport, California, USA.
\end{flushright}
Table 2-6 (cont.). Recommended mitigation measures developed to minimize potential impacts of residential, commercial and recreational development on important mule deer range in the eastern Sierra Nevada (Taylor\textsuperscript{5} 1991, Taylor\textsuperscript{6} 1994, Taylor\textsuperscript{7} 1996).

13. Close and rehabilitate roads that are no longer necessary or compatible with range area management.

14. Avoid placing structures (e.g., fences) in drainage corridors, draws, washes, or other areas that may facilitate deer movements through a project area.

15. Establish vegetative screening adjacent to individual homesites, subdivisions, commercial and recreational developments.

16. Establish setbacks between adjacent property line boundaries to facilitate deer movement through housing subdivisions.

17. Control dust generated during site clearing and movement of heavy machinery through watering or other acceptable measures.

18. Conduct refueling of construction equipment in areas away from sensitive wildlife habitat such as perennial or ephemeral streams.

19. Limit vegetation removal to only those areas identified on approved land use plans.

20. Impose restrictions on management of remaining open space on private land parcels, including snag removal, clearing of underbrush, disposal of trash and hazardous materials, and livestock use.

21. Encourage development designers to use techniques to reduce the amount of area altered by pads and drives.

22. Encourage landowners to protect valuable habitat features such as existing trees, brush stands, downed logs, and water sources.

23. Prohibit project proponents from requesting depredation permits for controlling mule deer.

24. Revegetate disturbed areas with native plants grown from seeds and seedlings obtained from local native stock.
Brown (1992) warned that weak fidelity to winter range areas, as shown in this study, could strongly influence both cost and accuracy of deer census data. During this study, mild winter conditions prevailed during 1993-94 and some deer remained on upper elevation secondary winter ranges until late January. If these areas were not included in post-season survey efforts, then underestimates in population size may have occurred. Moreover, differential patterns of migration by particular sex and age groups could significantly influence herd composition estimates (Brown 1992). Therefore, knowledge of areas used by deer during mild winters is essential for obtaining reliable information on population size and sex and age composition.

ACKNOWLEDGMENTS

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LITERATURE CITED


CHAPTER 3. CONDITION AND REPRODUCTION

INTRODUCTION

During 1987-1994, Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) mule deer populations in the eastern Sierra Nevada, California, experienced poor fawn survival and low recruitment. For example, fall fawn ratios for the West Walker (WW) deer herd in northern Mono County, averaged 26 fawns:100 females, while spring ratios averaged 20 fawns:100 adults (R. Thomas, California Department of Fish and Game, pers. comm.). This low recruitment was concomitant with 7 consecutive years of drought, which subjected this deer population to repeated episodes of nutritional stress.

Nutrition is an important factor influencing productivity of deer populations (Verme 1967, McCullough 1979), because it affects the proportion of females that become pregnant, as well as ovulation rates (Sadler 1987, Folk and Klimstra 1991). These effects are well documented for free-ranging (Morton and Cheatum 1946, Julander et al. 1961, Kucera 1988) and captive deer (Verme 1965, 1967, Ozoga and Verme 1982). Research consistently has shown that deer on good quality ranges have higher rates of ovulation, conception, and pregnancy than deer on poor ranges.

An understanding of the relationships between body condition and reproductive performance of wild ungulate populations is necessary for their management (Saltz et al. 1992). Therefore, a high priority in any deer herd where fawn production is suboptimal should be to evaluate the physical condition of females during breeding and pregnancy (Connolly 1981, Saltz et al. 1992).

Body fat is the component most often associated with animal condition, and can be used to index animal response to nutritional and climatic stressors (Robbins et al. 1974, Torbit et al. 1985). Various fat indices have been developed to estimate body condition, including bone marrow fat (Cheatum 1949; Riney 1955; Ransom 1965, 1967), kidney fat (Riney 1965; Ransom 1965, 1967, Batcheler and Clark 1970; Van Vuren and Coblenz 1985), and visual scoring methods (Ransom 1965, Kistner 1976). I used kidney fat indices and reproductive tracts to determine the physical condition and reproductive potential of adult female mule deer collected from the West Walker deer herd during March 1993 and March 1994. My objectives were to (i) assess the effects of a prolonged drought, followed by an unusually severe winter, on the spring condition of female mule deer and (ii) compare the effects of an unusually severe and an unusually mild winter on deer condition and productivity. This descriptive study is intended to provide information on mule deer condition and reproduction in order to facilitate a better understanding of interactions that occur between the WW deer herd and its environment.

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STUDY AREA AND METHODS

During 18-19 March 1993 and 15-16 March 1994, free-ranging female mule deer were collected from WW winter ranges in northern Mono County, California, and southwestern Douglas County, Nevada (Fig. 1). Winter range of the WW herd encompasses approximately 780 km² at elevations from 1,530 to 2,550 m. Dominant plant communities (following Mayer and Laudenslayer 1988) on the winter range include bitterbrush (Purshia sp.), sagebrush (Artemisia sp.), and pinyon pine (Pinus monophylla). Descriptions of WW herd ecology, winter range vegetation, climate, and topography have been reported by Thomas³ (1985), Loft et al. (1989), and Taylor⁴ (1993).

Deer were collected by two-person teams that shot the first identifiable adult or yearling female in each group of deer encountered, regardless of the animal’s apparent body condition. Animals were shot in the head, neck, or thorax with a high-powered rifle. Carcasses were transported to a field processing station where they were weighed to the nearest kilogram (bled carcass weight, BCW) using a spring scale. External body measurements (chest girth, left hindfoot length, and contour length) to the nearest centimeter were recorded. Animals were eviscerated and reproductive tracts (uterus and ovaries), right kidneys, right femurs, and lower jaws were extracted. Ages were estimated by tooth wear and replacement (Larson and Taber 1980). After field necropsies were completed, deer were weighed to the nearest kilogram to determine eviscerated carcass weights (ECW). The kidney fat index (KFI, Riney 1955), was calculated by dividing the fresh weight of kidney fat by the fresh weight of the fat-free kidney, multiplied by 100.

Ovaries were sectioned at 5-mm intervals and examined macroscopically for corpora lutea of pregnancy (CLP), which were used to estimate ovulation rates. I used a fetus scale (Forestry Suppliers Inc., Jackson, Mississippi, USA) to determine forehead-rump lengths of fetuses in order to estimate fetal age (Hudson and Brownman 1959) and conception and fawning dates. Conception date was back-calculated from estimated fetal age. Approximate date of parturition was determined by adding 204 d (Anderson 1981) to conception date. Weather data were obtained from the National Oceanic and Atmospheric Administration weather station in Coleville, California.

I used standard techniques for statistical testing with α = 0.05. Analysis of variance (ANOVA) was used to test for differences in mean reproductive characteristics and condition indices between years and among collection areas and to examine the relationship between “litter category” (number and sex composition of litters, i.e., single female, twin females, single male, etc.) and BCW, ECW, and KFI; kidney fat indices were log-transformed to normalize these data prior to analysis. I tested for deviations from the expected 1:1 sex ratio among fetuses with a binomial test (Siegel 1956); deviations from the expected distribution of sex ratios among litter categories were tested using chi-

³Thomas, R. D. 1985. Management plan for the West Walker deer herd, Calif. Dep. Fish and Game, Bishop, California, USA.
square analyses. I also used chi-square tests to examine differences in fetal sex ratio between years and among collection areas. Means and standard errors were calculated from untransformed data.

RESULTS

Deer (29 each year) were collected from three primary areas within the range that supported deer concentrations during all winters. A total of 20 deer (10 each year) were collected from Little Antelope Valley (LAV), California; 20 deer (10 each year) were collected from the east side (ES) of Antelope Valley near the base of the Wellington Hills, Nevada; and 18 deer (9 each year) were collected from the vicinity of Topaz Lake (TL), Nevada (Fig. 1).

Winter weather in 1992-93 was severe, with 180 cm of snow and average minimum temperatures of -16°C in January. In comparison, the winter of 1993-94 was mild, with 81 cm of snow and minimum temperatures averaging -6°C in January.

Pregnancy and fetal rates were similar in 1993 and 1994. Mean age (4.9 yr in 1993 and 5.2 yr in 1994) of adult females did not differ significantly between years (F = 0.227; 1, 54 df; P = 0.972). Among adult females examined, 25 of 29 (86%) were pregnant in 1993 and 24 of 27 (88%) were pregnant in 1994 (Table 1). Mean fetal rates of 1.52 fetuses per adult female in 1993 and 1.56 fetuses in 1994 did not differ between years (F = 0.357; 1, 54 df; P = 0.553), and mean fetal rates did not differ among collection areas (F = 0.001; 2, 53 df; P = 0.999) (Table 1). Of the 29 adult females collected in 1993 for which ovaries were examined, 46 CLP resulted in 44 viable, implanted fetuses. Of the 27 adults collected in 1994, 45 CLP resulted in 43 viable, implanted fetuses.

Estimated breeding and parturition dates were similar in both years. Ages of fetuses in 1993 indicate that breeding occurred between 23 November and 30 December, with a median date of 6 December. In 1994, breeding occurred between 28 November and 14 December, with a median date 7 December. Predicted parturition for deer examined in 1993 ranged from mid-June to mid-July; the median date was 2 July. In 1994, predicted parturition ranged from 20 June to 7 July; the median date was 28 June.

Deer were in better condition in 1994 than in 1993 (Table 2). Mean BCW of adult females (44.5 kg in 1993 and 50.9 kg in 1994) differed between years (F = 13.79; 1, 54 df; P = 0.001); however, mean BCW did not differ among collection areas (F = 0.170; 2, 53 df; P = 0.193), and the year by area interaction was not significant (F = 0.360; 1, 54 df; P = 0.700). Eviscerated carcass weights of adult females followed a similar trend, differing between years (F = 25.57; 1, 54 df; P = 0.000), but not among collection areas (F = 2.05; 2, 53 df; P = 0.141); year by area interaction also was not significant (F = 0.095; 1, 54 df; P = 0.910). Mean KFI was significantly lower in 1993 (9.3%) than in 1994 (36.0%) (F = 29.53; 1, 54 df; P < 0.001), but did not differ among the three collection areas (F = 0.939; 2, 53 df; P = 0.399); year by area interaction was not significant (F = 0.124; 1, 54 df;
Table 1. Frequency of fetuses in adult mule deer collected from the West Walker deer herd winter range in March 1993 and March 1994, Mono County, California, and Douglas County, Nevada.

<table>
<thead>
<tr>
<th>Location</th>
<th>0 No.</th>
<th>Litter Size</th>
<th>Total No. of Fetuses</th>
<th>Total No. of Does</th>
<th>Ave. No. Fetuses per Doe</th>
<th>Ave. No. Fetuses Pregnant Doe</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LAV</td>
<td>0</td>
<td>4</td>
<td>6</td>
<td>0</td>
<td>16</td>
<td>10</td>
</tr>
<tr>
<td>ES</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>14</td>
<td>10</td>
</tr>
<tr>
<td>TL</td>
<td>1</td>
<td>2</td>
<td>6</td>
<td>0</td>
<td>14</td>
<td>9</td>
</tr>
<tr>
<td>1994</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LAV</td>
<td>0</td>
<td>2</td>
<td>7</td>
<td>0</td>
<td>16</td>
<td>9</td>
</tr>
<tr>
<td>ES</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>0</td>
<td>12</td>
<td>9</td>
</tr>
<tr>
<td>TL</td>
<td>1</td>
<td>1</td>
<td>7</td>
<td>0</td>
<td>15</td>
<td>9</td>
</tr>
</tbody>
</table>

LAV = Little Antelope Valley; ES = East Side; TL = Topaz Lake

Table 2. Mean bled carcass weight (BCW), eviscerated carcass weight (ECW), and kidney fat index (KFI) for 56 adult female Rocky Mountain mule deer collected on the West Walker deer herd winter range in March 1993 and March 1994, Mono County, California, and Douglas County, Nevada.

<table>
<thead>
<tr>
<th>Location</th>
<th>n</th>
<th>BCW (kg)</th>
<th>ECW (kg)</th>
<th>KFI (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X</td>
<td>SD</td>
<td>X</td>
<td>SD</td>
</tr>
<tr>
<td>1993</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LAV</td>
<td>10</td>
<td>44.1</td>
<td>4.52</td>
<td>31.0</td>
</tr>
<tr>
<td>ES</td>
<td>10</td>
<td>42.6</td>
<td>5.07</td>
<td>30.2</td>
</tr>
<tr>
<td>TL</td>
<td>9</td>
<td>47.1</td>
<td>7.57</td>
<td>34.1</td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>44.5</td>
<td>5.90</td>
<td>31.7</td>
</tr>
<tr>
<td>1994</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LAV</td>
<td>9</td>
<td>49.7</td>
<td>3.82</td>
<td>35.7</td>
</tr>
<tr>
<td>ES</td>
<td>9</td>
<td>51.0</td>
<td>6.16</td>
<td>36.8</td>
</tr>
<tr>
<td>TL</td>
<td>9</td>
<td>52.1</td>
<td>4.39</td>
<td>38.6</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>50.9</td>
<td>4.75</td>
<td>37.0</td>
</tr>
</tbody>
</table>

LAV = Little Antelope Valley; ES = East Side; TL = Topaz Lake
West Walker females produced more male than female fetuses. However, the overall sex ratio of fetuses, 1.07:1.00 in favor of males 45 males:42 females) was not significantly different from unity (Z = -0.21, P = 0.83) (Table 3). Single fetuses were present in 12 of 49 pregnant females; 36 carried twins, and one had triplets (Table 1). Among the 12 litters of singletons, four fetuses were male and eight were female. Among the 36 sets of twins, 18 were of mixed sex, 9 were twin females, and 9 were twin males. These frequencies of sex ratio categories were not different from random expectation (χ² = 4.5; 2 df; P = 0.105). Sex ratios of fetuses in 1993 and 1994 did not differ (χ² = 0.57; 1 df; P = 0.451). Overall, sex ratio categories did not differ among collection areas (χ² = 5.28; 2 df; P = 0.072), but in 1994 LAV and TL females produced significantly more males than ES females (χ² = 11.3; 2 df; P 0.004) (Table 3). I found no relationship between litter category and maternal age (F = 1.55; 5, 43 df; P = 0.208), nor between litter category and BCW (F = 1.61; 5, 43 df; P = 0.178), ECW (F = 0.846; 5, 43 df; P = 0.52) and KFI (F = 1.63; 5, 43 df; P = 0.173).

DISCUSSION

Reproductive rates observed during this study were similar to those reported by Bischoff (1958), Jordan (1967), and Kucera (1988) for other central Sierra Nevada mule deer populations. I detected no significant differences in measures of reproduction between years, despite significant increases in measures of body condition in 1994. Fetal rates during this study were 1.52 fetuses/doe in 1993 and 1.56 fetuses/doe in 1994; mean KFI’s increased from 9% in 1993 to 36% in 1994. In the eastern Sierra Nevada, Taylor (1991) documented reproductive rates on two mule deer winter ranges of 1.88 and 1.93 fetuses/doe when KFI’s averaged 32% and 25%, respectively. Kucera (1988) found low reproductive rates (1.06-1.42 fetuses/female) among mule deer when mean KFI’s averaged 10%-27%; a higher reproductive rate (1.88 fetuses/female) was observed with mean KFI > 60%. Taylor (1988) reported that mule deer from the Casa Diablo herd had reproductive rates of 1.74 and 1.70 fetuses/doe when KFI’s averaged 41% and 37%, respectively. These incongruous data suggest that KFI may not be an accurate basis for determining the effects of nutritional status on deer productivity when comparing disparate populations.

I surmise that increases in deer condition during 1994 were largely due to the wet

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6Taylor, T.J. 1991. Ecology and productivity of two interstate deer herds in the eastern Sierra Nevada: East Walker-Mono Lake deer herd study, Calif. Department of Fish and Game, Bishop, California, USA.

Table 3. Sex of fetuses from 49 adult female Rocky Mountain mule deer collected on the West Walker deer herd winter range in March 1993 and March 1994, Mono County, California, and Douglas County, Nevada.

<table>
<thead>
<tr>
<th>Location</th>
<th>Male (N)</th>
<th>Female (N)</th>
<th>% Male</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1993</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LAV</td>
<td>7</td>
<td>9</td>
<td>43.7</td>
</tr>
<tr>
<td>ES</td>
<td>7</td>
<td>7</td>
<td>50</td>
</tr>
<tr>
<td>TL</td>
<td>7</td>
<td>7</td>
<td>50</td>
</tr>
<tr>
<td>Total</td>
<td>21</td>
<td>23</td>
<td>47.7</td>
</tr>
<tr>
<td><strong>1994</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LAV</td>
<td>10</td>
<td>6</td>
<td>62.5</td>
</tr>
<tr>
<td>ES</td>
<td>2</td>
<td>10</td>
<td>16.6</td>
</tr>
<tr>
<td>TL</td>
<td>12</td>
<td>3</td>
<td>80</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>19</td>
<td>55.8</td>
</tr>
</tbody>
</table>
winter of 1992-93, which enhanced forage production during the spring and summer of 1993, and increased forage availability during the winter of 1993-94. Kucera (1988) reported large increases in forage production on two mule deer winter ranges in the eastern Sierra Nevada following winters of heavy precipitation, which in turn were mirrored by high measures of condition and reproduction. In contrast, my findings indicate that deer productivity in 1994 was not measurably affected by significant increases in body condition. Following the winter of 1992-93, deer may have so exhausted their body reserves that they were not able to attain the threshold of body condition necessary to enhance their reproductive potential, despite greater forage availability during the spring and summer 1993. In years of high forage availability that follow extreme winters, it may not be possible for some deer to achieve enhanced reproductive performance.

The cumulative effects of the drought on summer range forage production presumably had a major influence on deer reproduction in 1993. Of 29 adult females, three were without corpora lutea and seven had one corpus luteum each for an ovulation rate of 1.59 CLP per female. This low ovulation rate indicated that summer ranges occupied by WW deer were of poor nutritional quality and, presumably, were inadequate to allow female deer to achieve peak body condition prior to the breeding season. Short (1981) surmised that when summer ranges provide low quality forage because of drought or other factors, the high metabolic requirements of females are not met and requirements for reproduction are not satisfied. Bertram (1984) reported a pronounced decline in reproductive potential among female mule deer collected from the North Kings herd following the dry spring, summer, and fall of 1977. Several other researchers (Robinette et al. 1955, Swank 1958, Taber and Dasmann 1958, Julander et al. 1961) determined that summer forage nutrition influenced ovulation rates and the number of fetuses produced per female.

Mean KFI of 9% observed in March 1993 is similar to values reported by Kucera (1988) and Anderson et al. (1972) for other nutritionally stressed mule deer populations. KFI values < 15% indicate essentially no fat, and represent the point when animals begin to mobilize femur marrow fat for energy (Ransom 1965, Pojar and Reed 1974, Kie et al. 1983). Animal condition, as indexed by KFI and BCW, was lowest following the severe winter of 1992-93, when snow accumulations on primary winter ranges (1,700 m elevation) totaled 180 cm and lasted from 7 December-3 March. This prolonged snow cover buried sources of forage and, when coupled with persistent low temperatures, resulted in widespread starvation (T. J. Taylor, unpubl. data) and decreased maternal nutrition and productivity among surviving females. Severe winters have been associated with declines in deer condition and productivity (Leach 1956, Gilbert et al. 1970, Gill 1972, Hall 1973, Wallmo et al. 1977). During a severe winter, net productivity is influenced not only by deer lost to starvation, but also because surviving females are in poor condition, a situation that results in high postnatal fawn losses (Robinette 1976).

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8Bertram, R.C. 1984. The North Kings deer herd study, California Department of Fish and Game, Fresno, California, USA.
The preponderance of males produced by ES and TL deer sampled in 1994 may be the result of small sample sizes that typically result in unusual sex ratios (Thomas et al. 1989). Although Robinette et al. (1957) found that mule deer on poor range produced more male fawns, my results do not suggest a male-biased sex ratio in the nutritionally stressed WW mule deer herd.

Reproductive potential in the WW deer herd during 1993 and 1994 was comparable to that reported for other nutritionally stressed mule deer populations throughout the west (Anderson et al. 1972, Kucera 1988). This low productivity was likely in response to drought-induced changes in habitat quality, which was compounded by severe winter conditions in 1992-93. During periods of drought, the first step managers should take to maintain deer herd productivity is to increase the quality of the food supply. Therefore, I recommend management practices on WW herd winter ranges and holding areas that promote and ensure access to late season growth of succulent forage on irrigated pasture. Garrott et al. (1987) found that mule deer in northwest Colorado made extensive use of agricultural meadows during autumn; such areas provided deer with succulent forage at a time when the nutritional quality of summer and winter range vegetation was declining because of plant senescence. Hence, Garrott et al. (1987) recommended irrigation and fertilization programs designed to retain succulent forage late into the growing season, and restrictions on livestock grazing to avoid competition during periods of heavy deer use. Similar management of pastureland occurring on WW herd winter ranges and holding areas might enhance deer productivity by sustaining animal condition during periods of drought.

ACKNOWLEDGMENTS

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LITERATURE CITED


CHAPTER 4. DIET COMPOSITION AND QUALITY

INTRODUCTION

Habitat loss and vegetational change on seasonal ranges occupied by migratory Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) can adversely effect populations (Mackie and Pac 1980, Smith and Conner 1989). Therefore, knowledge of the botanical composition and nutritional quality of mule deer diets is important because mitigation for disturbance impacts associated with development is often viewed as some form of habitat improvement. However, reliable determination of forage species consumed by wild ungulates can be problematic. Direct observations of forage choices and esophageal fistulation are often impractical for large, free-ranging herbivores (Lewis 1994). Estimates of forage quality from hand-collected forages are considered to be generally unreliable because they may not accurately reflect dietary quality (Swift 1948, Schwartz and Hobbs 1985). Direct measures of nutritional status, including nutrient analysis of rumen content and blood samples, require either death or restraint of the animals and may be socially objectionable (Cook et al. 1994). Fecal analysis, however, does not require killing animals and enables acquisition of large sample sizes necessary for studies of free-ranging animals in their natural environments (Lewis 1994). Moreover, fecal indices are considered a feasible alternative to other more costly and time-intensive methods of determining the nutritional content of diets (Leslie et al. 1984). Examination of feces may, however, bias estimates because of the effects of differential digestibility on fragment discernibility (Anthony and Smith 1974).

Nutrition has long been recognized as a critical factor affecting productivity of ungulate populations (Julander 1972, Diemo 1977, Short 1981, Hobbs and Swift 1985). Low diet quality on Rocky Mountain mule deer summer and winter ranges has been associated with nutritional deprivation and low productivity in ungulates (Julander et al. 1961, Pederson and Harper 1978, Kucera 1988). Nutritional deprivation inhibits growth and development in juvenile ungulates (Sadler 1980, Verme and Ozoga 1980) and may increase the risk of disease (Ogra 1984). Therefore, developing a reliable index to seasonal variations in dietary quality for ungulates could explain relationships between nutritional status and population dynamics.

Fecal nitrogen (FN) may be a useful measure of nutritional status in ungulates because it has been correlated with dietary nitrogen (Holechek et al. 1982, Leslie and Starkey 1985) and dietary digestible dry matter (Leslie and Starkey 1985). However, Mould and Robbins (1981) and Robbins et al. (1987) warned that high concentrations of tannins in diets could increase the nitrogen content of feces, thereby producing elevated FN in diets that are normally of low quality.

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In this study, I used composited fecal samples collected from undisturbed habitats to determine year-round patterns of food use by migratory mule deer from the West Walker (WW) herd. My objectives were to (i) identify major forage species in year-round diets, and (ii) estimate the quality of those diets using fecal indices, specifically fecal nitrogen.

**STUDY AREA AND METHODS**

Mule deer feces were collected monthly between November 1993 and April 1994 from WW herd winter ranges in the Wellington Hills, Douglas County, Nevada, and along the Sierra front, Mono County, California; between June 1994 and September 1994 from WW herd summer ranges on the east and west slopes of the Sierra Nevada in Mono and Alpine Counties, California, respectively; and during May 1994 and October 1994 from WW herd transition ranges in Mono County, California (Figure 4-1). The total winter range of the WW herd encompasses approximately 780 km² at elevations ranging from 1,530-2,550 m. Dominant plant communities (following Mayer and Laudenslayer 1988) on the winter range include bitterbrush (*Purshia* spp.), sagebrush (*Artemisia* spp.), low sagebrush (*Artemisia arbuscula*), perennial grassland (*Bromus tectorum, Stipa* spp.), pinyon (*Pinus monophylla*)-juniper (*Juniperus occidentalis*) woodland, and irrigated pasture. In open areas of *Artemisia*, where other vegetation does not occur, buckwheat (*Eriogonum* spp.) may dominate the terrain. Transition ranges occur between 2,000 and 2,500 m and are dominated by antelope bitterbrush, big sagebrush, mountain mahogany (*Cercocarpus ledifolius*), pinyon-juniper forest, and Jeffrey pine (*Pinus jeffreyi*) forest. Meadow and quaking aspen riparian (*Populus tremuloides*) habitats dominate vegetation along drainages that flow east from the Sierra crest. East and west slope Sierra summer ranges are located at elevations ranging from 2,200-3,300 m. Major vegetational types on the summer range include big sagebrush, antelope bitterbrush, montane chaparral, pinyon-juniper forest, Jeffrey pine forest; lodgepole pine (*Pinus contorta*) forest; mixed conifer forest, quaking aspen riparian; and whitebark pine (*Pinus albicaulis*) forest.

During the middle of each month, a minimum of 5 g of fecal material was sampled from 20-30 “fresh” or “recent” defecations, and after being laid out in the sun to dry, was stored in sealed paper bags for subsequent laboratory analysis. Fecal material was pooled by month on winter and summer ranges and, on transition ranges, by herd, and then sent to the Forage Analysis Laboratory, University of Arizona, Tucson.

In the laboratory composite samples were ground to uniform particle size in a blender and then poured through a 140-mesh screen and rinsed thoroughly to remove the digested material. The material left on the screen was undigested plant particles of uniform size. A small amount of this material was placed on a microscopic slide and mixed with a drop of heated Hertwig solution, which consisted of chloral hydrate, hydrochloric acid, and glycerin. The slide was then heated until the mixture boiled and then placed in an oven at 55°C for approximately 1 week to dry and harden.
Figure 4-1. Locations of Deer Fecal-Pellet Group Collection Areas on the West Walker Deer Herd Winter Range, Mono County, California, and Douglas County, Nevada, November 1993-October 1994.
Slides of fecal material were placed under a microscope at a magnification of 100x and examined for species composition by identifying and quantifying fragments of plant epidermis (Sparks and Malachek 1968). All epidermal plant fragments visible in the field of vision were recorded and the slide was then moved to a new field of vision where the fragments were identified again. This process was completed for a total of 20 fields per slide. I categorized plants into 3 major forage classes: (i) browse or shrubs, which included both shrub and tree material; (ii) graminoids, which included sedges (Carex) and rushes (Juncus); and (iii) forbs, which also included lower plant forms such as mosses and lichens. Fecal nitrogen (FN) in composited monthly samples was determined by the Kjeldahl procedure (Horwitz 1980) at the Wildlife Habitat Laboratory, Washington State University.

RESULTS

Diet Composition of Feces

Winter Range. Thirty-three diet items were identified to genera by microhistological analyses of composited fecal-pellet groups collected from the WW winter range from November 1993-April 1994. This included 10 shrubs, 17 forbs, and 6 grasses. Browse and forbs comprised consistently high proportions of deer diets during all winter months (Figure 4-2). For deer wintering in the Wellington Hills, Nevada, shrubs comprised 55 and 47 of early (November-January) and late (February-April) winter diets, respectively. Sagebrush (Artemisia spp.) and saltbush (Atriplex spp.) were the most frequent shrubs, followed by antelope bitterbrush (Purshia tridentata) and Mormon tea (Ephedra nevadensis) (Table 4-1). Relative amounts of Purshia in winter diets was highest during November and December, declined sharply in January, and then increased in April. Lower Purshia consumption during February and March was usually compensated for by higher Artemisia, Atriplex, and Ephedra use. Lower overall shrub use during April (36.5%) was compensated for by higher forb use. Other shrubs that were important to deer during winter included willow (Salix spp.), spiny hopsage (Garyia spinosa), ceanothus (Ceanothus spp.) and curlleaf mountain mahogany (Cercocarpus ledifolius) in descending order of importance.

Forbs were eaten during all winter months by deer from the Wellington Hills, ranging from a low of 22% in January to a high of 54% in April (Table 4-1). Buckwheat (Eriogonum spp.) was the most important forb, comprising between 10%-35% (x = 18.2%, SD = 7.9) of diets, followed by larkspur (Delphinium spp.), cinquefoil (Potentilla spp.), and Indian paintbrush (Castilleja spp.) (Table 4-1). Grasses and sedges comprised 12.9% of January diets, but averaged < 10% of diets during other winter months; grasses were essentially unused in November and February.

Early and late winter diets of deer wintering along the Sierra front were comprised of 51% and 37% shrubs, respectively. Antelope bitterbrush was the most frequent shrub during all winter months, followed by sagebrush and saltbush (Table 4-1). Bitterbrush
Figure 4-3. Percentages of major forage classes in mule deer diets collected from West Walker deer herd summer ranges, June 1993-September 1993.
Table 4-1. Monthly forage species composition of mule deer diets from West Walker deer herd primary winter ranges in the Wellington Hills, Douglas County, Nevada, and along the Sierra Front, Mono County, California, November 1993-April 1994.

<table>
<thead>
<tr>
<th>Forage</th>
<th>Wellington Hills</th>
<th>Sierra Front</th>
<th>Area and Collection Period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nov</td>
<td>Dec</td>
<td>Jan</td>
</tr>
<tr>
<td><strong>Grasses</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mat Mulhy.</td>
<td>5.7</td>
<td>5.2</td>
<td></td>
</tr>
<tr>
<td>Stinkgrass</td>
<td>6.5</td>
<td>5.5</td>
<td></td>
</tr>
<tr>
<td>Great Basin</td>
<td>4.2</td>
<td>2.7</td>
<td></td>
</tr>
<tr>
<td>Wildrye</td>
<td>7.8</td>
<td>6.4</td>
<td></td>
</tr>
<tr>
<td>Cheatgrass</td>
<td>9.5</td>
<td>9.5</td>
<td></td>
</tr>
<tr>
<td>Wiregrass rush</td>
<td>8.7</td>
<td>5.2</td>
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<td>Total Grasses</td>
<td>0.0</td>
<td>9.9</td>
<td>12.9</td>
</tr>
<tr>
<td><strong>Forbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Astragalus spp.</td>
<td>2.2</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td>Lupine</td>
<td>1.9</td>
<td>1.9</td>
<td></td>
</tr>
<tr>
<td>Buckwheat</td>
<td>8.0</td>
<td>8.0</td>
<td></td>
</tr>
<tr>
<td>Storksbill filarec</td>
<td>4.5</td>
<td>4.2</td>
<td></td>
</tr>
<tr>
<td>Monkey flower</td>
<td>10.1</td>
<td>3.1</td>
<td></td>
</tr>
<tr>
<td>Phlox</td>
<td>12.5</td>
<td>3.1</td>
<td></td>
</tr>
<tr>
<td>Penstemon</td>
<td>6.9</td>
<td>3.8</td>
<td></td>
</tr>
<tr>
<td>Avens</td>
<td>8.1</td>
<td>2.0</td>
<td></td>
</tr>
<tr>
<td>Indian paintbrush</td>
<td>6.3</td>
<td>8.2</td>
<td></td>
</tr>
<tr>
<td>Larkspur</td>
<td>3.7</td>
<td>4.7</td>
<td></td>
</tr>
<tr>
<td>Rock-cress</td>
<td>4.7</td>
<td>5.2</td>
<td></td>
</tr>
<tr>
<td>Popcorn Flower</td>
<td>3.9</td>
<td>4.3</td>
<td></td>
</tr>
<tr>
<td>Total Forbs</td>
<td>3.5</td>
<td>4.6</td>
<td></td>
</tr>
<tr>
<td>Shrubs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sagebrush</td>
<td>4.6</td>
<td>10.3</td>
<td>9.5</td>
</tr>
<tr>
<td>Bitterbrush</td>
<td>31.1</td>
<td>17.9</td>
<td>7.9</td>
</tr>
<tr>
<td>Mormon tea</td>
<td>2.2</td>
<td>5.0</td>
<td>3.1</td>
</tr>
<tr>
<td>Saltbush spp.</td>
<td>23.7</td>
<td>27.2</td>
<td>25.3</td>
</tr>
<tr>
<td>Wood rose</td>
<td>3.1</td>
<td>3.1</td>
<td>3.1</td>
</tr>
<tr>
<td>Willow</td>
<td>8.7</td>
<td>8.7</td>
<td>8.7</td>
</tr>
<tr>
<td>Ceanothus</td>
<td>7.9</td>
<td>5.2</td>
<td>2.1</td>
</tr>
<tr>
<td>Curleaf mountain mahogany</td>
<td>7.9</td>
<td>5.2</td>
<td>2.1</td>
</tr>
<tr>
<td>Spiny hopsage</td>
<td>4.6</td>
<td>4.6</td>
<td>4.6</td>
</tr>
<tr>
<td>Gooseberry</td>
<td>1.4</td>
<td>1.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Total Shrubs</td>
<td>3.5</td>
<td>3.5</td>
<td>3.5</td>
</tr>
</tbody>
</table>

* genera averaging less than 1% of the diet (trace amounts).
consumption peaked in December, declined sharply in January and then increased sporadically through April (Table 4-1). In January, decreased bitterbrush consumption was compensated for by higher Atriplex use. During February-April, decreased bitterbrush use was compensated for by higher Artemisia or forb use. Buckwheat and cinquefoil (Potentilla spp.) were the most-used forbs, comprising 21% and 11% of winter diets, respectively. Stinkgrass (Eragrostis cilianensis) and cheatgrass (Bromus tectorum) were the most-used grasses during winter; during February, grasses were essentially unused.

**Summer Range.** Twenty-nine diet items were identified to genus by microhistological analyses of composited fecal-pellet groups collected from the WW summer range from June-September, 1993. This included 9 shrubs, 15 forbs, and 5 grasses. The cell fragment of several species of grasses were indistinguishable so they were combined into a single category (other grasses and sedges). There was no consistent pattern of similarity of forage class use between deer from east and west side summer ranges (Figure 4-3). Shrub use by deer from east slope summer ranges was greatest in June, declined through July and August, and then increased in September (Table 4-2). Sagebrush, bitterbrush, mountain mahogany, and ceanothus were important foods throughout the entire summer. In September, gooseberry (Ribes spp.) and willow (Salix spp.) were also important. Lower shrub use in July and August was compensated for by higher forb use. Forbs were used extensively during all summer months, especially July and August when they comprised between 62% and 70% of diets. Buckwheat was the most frequent forb in June-July and September, comprising between 10-30% (\(\bar{x} = 22.6\%), SD = 5.7\) of diets. In August, cinquefoil was most common, followed by buckwheat and fiddleneck (Amsinkia spp.). Other important forbs consumed by east slope deer included bush mallow (Sphaeralcea spp.) and lupine (Lupinus spp.) (Table 4-2). Use of grasses and sedges was highest during July, but averaged < 5% of diets during all months.

In comparison, shrub use by deer from west slope winter ranges was greatest in August and lowest in September (Figure 4-3). Sagebrush, bitterbrush, mountain mahogany, and ceanothus were important foods throughout the entire summer (Table 4-2). Willow was important during June-August and gooseberry was important during August. Forbs were used extensively during all months, especially in July and September when they comprised 68% and 75% of diets, respectively. Buckwheat was the most heavily used and consistently eaten forb throughout the summer. In June, bush mallow was most important, followed by buckwheat and cinquefoil. Grasses were lightly used during all months, comprising between 0% and 4% of epidermal fragments.

**Transition Range.** Thirteen plant items were identified to genus by microhistological analyses of composited fecal-pellet groups collected from the WW herd transition ranges during spring migration. May diets were comprised of 59% shrubs, 35% forbs, 3% grasses, and 3% sedges. Sagebrush and bitterbrush were the most important shrubs, comprising 30% and 16% of diets, respectively. Cinquefoil was the most important forb (18%), followed by popcorn flower (6%) and buckwheat (5%). During fall
Figure 4-2. Percentages of major forage classes in mule deer diets collected from the West Walker deer herd winter range, November 1993-April 1994.
Table 4-2. Monthly forage species composition of mule deer diets collected from West Walker deer herd summer ranges on the east and west slopes of the Sierra Nevada, Mono and Alpine Counties, California, June-September 1993.

<table>
<thead>
<tr>
<th>Forage</th>
<th>June Eastern Sierra</th>
<th>July Eastern Sierra</th>
<th>Aug Eastern Sierra</th>
<th>Sept Eastern Sierra</th>
<th>June Western Sierra</th>
<th>July Western Sierra</th>
<th>Aug Western Sierra</th>
<th>Sept Western Sierra</th>
</tr>
</thead>
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<tr>
<td>Grasses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other Grasses and Sedges</td>
<td>2.0</td>
<td></td>
<td></td>
<td></td>
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<td>2.0</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Great Basin wildrye</td>
<td>4.4</td>
<td></td>
<td></td>
<td>1.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Muhly</td>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.0</td>
</tr>
<tr>
<td>Indian ricegrass</td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stinkgrass</td>
<td>2.6</td>
<td>4.0</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Total Grasses</td>
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<td>2.6</td>
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<td>4.0</td>
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<tr>
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<td>6.8</td>
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<td>18.4</td>
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<tr>
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<td>9.3</td>
<td>11.2</td>
<td>10.4</td>
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<td>10.0</td>
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<td>4.1</td>
<td>26.7</td>
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</tr>
<tr>
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<td>1.0</td>
<td>1.8</td>
<td>3.7</td>
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<td></td>
<td></td>
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* genera averaging less than 1% of the diet (trace amounts).
migration, shrubs, mainly bitterbrush and sagebrush, comprised approximately 59% of diets, while forbs, mainly buckwheat, comprised the remainder.

Diet Quality

Winter range. Monthly fluctuations in the level of FN in the feces were similar for deer wintering in the Wellington Hills, Nevada, and along the Sierra front, California. In general, percent FN in winter diets was lowest from December through February, and highest during April (Figure 4-4). In the Wellington Hills, FN ranged from a low of 1.53% in February to a high of 2.52% in April. In comparison, along the Sierra front, FN ranged from 1.52% in December to 2.85% in April (Figure 4-4). During spring migration in May, the nitrogen content of feces collected from transition ranges was about 2.9%.

For deer from the Wellington Hills, I found no correlation between FN and both percent Purshia ($R^2 = 0.014$, $P = 0.46$) and Artemisia ($R^2 = 0.024$, $P = 0.76$) in composite winter samples. I also found no correlation between percent FN and both percent Purshia ($R^2 = 0.043$, $P = 0.69$) and Artemisia ($R^2 = 0.043$, $P = 0.65$) for deer from the Sierra front.

Summer range. Fecal nitrogen in mule deer diets from west slope summer ranges reached a higher level earlier and was maintained longer than diets from east side summer ranges (Figure 4-5). On east side summer ranges, FN peaked in August at 3.6% and then rapidly declined to 2.1% in September (Figure 4-5). On west slope summer ranges, the nitrogen content of feces peaked in July at about 3.5% and then subsequently declined through September. During fall migration in October, the nitrogen content of feces collected from transition ranges was about 1.9% FN.

DISCUSSION

Diet species composition data for each wintering area was obtained from single samples consisting of a minimum of 20 defecations which were composited by month. This precluded the use of statistical tests to determine differences in the relative proportions of species at monthly intervals or between areas. However, species composition data was useful in determining temporal differences in diet composition of the WW herd.

Early and late winter diets of deer from the Sierra front and Wellington Hills were similar, despite many obvious vegetational differences between these two areas. The Wellington Hills is the least diverse vegetationally, supporting pinyon-juniper woodland, big sagebrush, antelope bitterbrush, low sagebrush, and perennial grassland habitats. The Sierra Front has the same plant communities as the Wellington Hills, but also comprises montane chaparral, irrigated pasturland, and woodland riparian habitat, all of which are
Figure 4-5. Percent fecal nitrogen in winter diets of mule deer from West Walker herd summer ranges on the east and west slopes of the Sierra Nevada, Mono and Alpine Counties, California, June-September 1993.
Figure 4-4. Percent fecal nitrogen in winter diets of mule deer from the West Walker herd winter range, Mono County, California, and Douglas County, Nevada, November 1993-April 1994.
limited in the Wellington Hills. In both areas, monthly deer diets during winter mirrored patterns of plant growth on the winter range.

I identified 34 plant genera in diets of mule deer wintering in the Wellington Hills and on the Sierra front. Food habits on both wintering areas appear strongly influenced by the relative abundance of different species as well as phenological changes in forages. In general, the composition of deer diets on the WW winter range were different from those of other eastern Sierra Nevada winter ranges described by Kucera\(^1\) (1988) and Taylor\(^2\) (1991) in that diets contained less browse and more forbs.

Taylor\(^2\) (1991) found that forbs comprised between 3.8-4.9\% and 1.1-1.7\% of early and late winter deer diets, respectively, from the East Walker and Mono Lake herd winter ranges. Kucera\(^1\) (1988) reported that forbs averaged < 1\% of early winter diets and approximately 2.1\% of late winter diets from the Buttermilk herd winter range in Inyo County, California. Similarly, Kucera\(^1\) (1988) found that forbs averaged < 1\% of both early and late winter deer diets from the Sherwin Grade winter range. In this study, forbs accounted for 40\% and 52\% of early and late winter deer diets, respectively, from the Wellington Hills. Early and late winter deer diets from the Sierra front were similarly comprised of 40\% and 52\% forbs, respectively. Most forb use during early winter occurred at higher elevations (> 2,200 m) of the winter range in open big sagebrush habitat (See Chapter 2). Forb use during late winter occurred at lower elevations (1,550-2,000 m), primarily on south aspect slopes in low sagebrush, annual grassland, alkali desert scrub and irrigated pasture habitat (T. J. Taylor, unpubl. obs.).

Buckwheat was the most important forb, comprising approximately 18\% and 21\% of winter diets from the Wellington Hills and Sierra front, respectively. The high amount of winter forb use by deer in this study may be related to the abundance of buckwheat and the relative scarcity of browse (because of a prolonged drought). In studies of Rocky Mountain mule deer (Urnness 1973) and desert mule deer (Gill and Wallmo 1973), Wright buckwheat (\textit{E. wrightii}) and sulphur buckwheat (\textit{E. umbellatum}), respectively, were highly preferred forages, even though they were very low in nutritional quality (Wallmo and Regelin 1981). Milchunas\(^3\) (1977) found that because the lignin content of sulphur buckwheat is high, it is apparently more brittle and therefore, more highly digestible, which may increase amounts of digestible and metabolized energy. This suggests that lignin can enhance opportunities for deer to obtain maximum benefits from forages that are otherwise low in nutritional quality (Wallmo and Regelin 1980).

Shrub consumption by deer in this study was higher during early winter than late winter. Early winter diets were generally characterized by higher amounts of \textit{Purshia} and

\(^2\)Taylor, T.J. 1991. Ecology and productivity of two interstate deer herds in the eastern Sierra Nevada: East Walker-Mono Lake deer herd study, Calif. Department of Fish and Game, Bishop, California, USA.

lower amounts of *Artemisia* and *Atriplex*, compared to late winter diets. For example, in the Wellington Hills, amounts of bitterbrush in early winter diets ranged from a high of about 31% in November to a low of 8% in January. During late winter, however, bitterbrush use remained <3.5% in February and March, while consumption of sagebrush, saltbush and forbs increased. Bitterbrush consumption increased again during April, which reflects the beginning of spring growth.

Similar patterns of *Purshia* use have been reported for other Great Basin mule deer populations. In eastern Washington, Burell (1982) found that amounts of *Purshia* in mule deer diets decreased as winter progressed. This decrease, however, did not effect winter survival because deer had access to alternative foods, primarily buckwheat. In the Piceance Basin, Colorado, Bartmann (1983) using a bite-count technique, found that antelope bitterbrush (*P. tridentata*) comprised 19% of October diets, but only 6% of November and ≤1% January-February diets. As consumption of antelope bitterbrush declined, use of other shrubs, primarily big sagebrush (*A. tridentata*), shadscale (*Atriplex confertifolia*), and rubber rabbitbrush (*Chrysothamnus nauseosus*), increased. Leach (1956) examined the stomach contents of deer from various locations in northeastern California and reported that bitterbrush was more common during winter and spring, while sagebrush was used more heavily in winter. In the eastern Sierra Nevada, Taylor (1991) reported that *Purshia* consumption by deer from the East Walker and Mono Lake herds declined steadily through January and reached its lowest level in March. Lower amounts of *Purshia* during late winter was compensated for by higher amounts of *Artemisia*.

Kucera (1988) determined that *Purshia* use by deer in the eastern Sierra Nevada was most common during early winter and spring, while *Artemisia* was predominant in mid- and late winter.

The role of *Artemisia* in deer diets is poorly understood and as a result, many questions have been raised regarding its nutritional value (Wallmo and Regelin 1981). A potential problem with consumption of sagebrush is the inhibition of bacterial activity in the rumen by volatile oils (Bissell et al. 1955, Nagy et al. 1964). Carpenter (1976) documented physical deterioration in tame deer when levels of sagebrush in the diet approached 30% and Longhurst et al. (1968) reported heavy mortality in wild deer with extensive use of sagebrush. In the eastern Sierra Nevada of California, Kucera (1988) related heavy use of *Artemisia* by deer to extreme nutritional stress as determined by poor body condition, poor reproduction, and a declining deer population.

In this study, diet quality, as reflected by FN, was not correlated with increased sagebrush use during winter. For example, on the Sierra front, winter FN values were lowest from December-February (range = 1.52-1.57%) when sagebrush consumption was also lowest (range = 2.6-9.4). During March, however, both percent sagebrush and FN in diets increased sharply to 33.1 and 1.81%, respectively. These findings are opposite what would be predicted in light of current information pertaining to the effects of *Artemisia* on

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on ruminant digestion. One would predict that a diet high in *Artemisia* would be low in quality and therefore low in FN, which is indicative of a reduced nutritional plane. Kucera\(^1\) (1988) and Taylor\(^2\) (1991) found weak negative correlations between FN and percent *Artemisia* in composite winter diets of eastern Sierra mule deer, thus indicating diet quality in the direction expected. The relatively high FN concentrations of March diets in this study indicate that sagebrush did not have an adverse affect on diet quality. This is perhaps due to the effects of increased levels of herbaceous forages, primarily forbs, in the diet. Grasses and forbs, with high cellulose and high digestibility may serve to increase the digestibility of shrubs with lower digestibility, but higher protein levels (Wallmo and Regelin 1981).

The seasonal pattern of FN in this study was similar to that reported by Kucera\(^1\) (1988) and Taylor\(^2\) (1991) for other eastern Sierra Nevada mule deer populations. FN was highest during August, declined rapidly through the fall and early winter, reached its lowest point during mid-winter, and then increased sharply with the onset of spring. In this study, however, winter FN values were generally higher than those reported for other studies. Kucera\(^1\) (1988) and Taylor\(^2\) (1991) reported minimum FN levels of 0.9 and 1.18, respectively, which is much lower than the minimum of 1.52 for this study. Data from this study was collected during a mild winter (1993-94) when snowfall accumulations on the winter range averaged 50% of normal (See Chapter 3, Condition and Reproduction). These mild conditions permitted deer access to foraging sites that are usually not available because of deep snow. As a result, diet quality was higher than during more severe winters, thus enabling deer to maintain a higher nutritional plane and overwinter in better physiological condition.

Deer summering on both the east and west slopes of the Sierra Nevada consumed many forage species during summer. On both summer ranges, forbs and shrubs were the predominant forage classes used; grasses and grass-like plants were used < 5%. Taylor\(^2\) (1991) reported a much different pattern of shrub and forb use during summer by two other eastern Sierra mule deer populations that, in some locations, share summer range with WW deer. During June-September, shrubs accounted for > 61% of the diet, while use of forbs and grass-like plants comprised between 1-37% and 2-26% of diets, respectively.

In this study, both diet species composition and patterns of forage class use varied between east and west slope Sierra summer ranges. I recorded use of 8 species of shrubs, 13 forbs, and 2 grasses by deer residing on east side summer ranges. In comparison, deer diets from west side summer ranges were comprised of 7 species of shrubs, 15 forbs, and 5 grasses. In June and September, deer from east side summer ranges consumed more shrubs and less forbs. Conversely, during August, deer from west side summer ranges consumed more shrubs and less forbs. Most of the variation between summer diets occurred because of differences between the two areas in plant phenology, plant species diversity, and habitat type.
The range of summer FN values in this study (2.92% in May to 3.59% in August) approximate those reported by Kucera\textsuperscript{1} (1988) and Taylor\textsuperscript{2} (1991) for other eastern Sierra mule deer population. These values, along with the high diversity of summer diets, appear to indicate that forage quality and quantity are not limited on the summer range. Therefore, management of deer habitat on the summer range should focus on maintaining and enhancing important deer habitats by controlling livestock use patterns and altering the timing of grazing to avoid critical deer use periods.

Ensuring adequate forage quality and availability on winter ranges is a major concern of deer managers. Therefore, a clear understanding of important winter diet components is necessary for management. Although browse consumption in this study was less than reported for other eastern Sierra mule deer populations, the importance of browse in winter diets should not be underestimated. Browse is critical to winter survival of deer because it is the most available forage in deep snow. Moreover, browse has nutritional advantages over grasses and forbs because it is a better source of crude protein (Diemo 1977, Bartmann 1983). In the fall, shrubs transfer nitrogenous and mineral compounds, from which proteins are synthesized, from leaves to twigs and stems, thus making these compounds available to deer during the winter (Deitz 1972). Conversely, grasses and forbs store nitrogenous compounds in their roots which are unavailable to deer. Thus, it is imperative that deer have access to areas of high quality browse, especially during periods of drought or heavy snow accumulation.

Bitterbrush was the most important browse species during early winter. Therefore, areas of winter range supporting bitterbrush cover should receive the most management attention. Without proper management, bitterbrush conversion from productive stands providing nutritional browse to senescent stands offering minimal regeneration could reduce the value of this forage type for mule deer (Clements and Young, 1997). Griffith and Peak (1989) found that mule deer in the Columbia River Canyon of northcentral Washington consistently used bitterbrush stands with the highest canopy cover because of increased bitterbrush forage, greater visual concealment, and increased cover of herbaceous forage plants in the understory. These authors recommended several options for maintaining and enhancing bitterbrush communities including rejuvenating existing older plants and high-cover stands by topping, and replanting and protecting burned stands from grazing to allow recovery to dense stands that were present before fires occurred. Similar management of mid- to late seral bitterbrush stands on the WW winter range could increase bitterbrush abundance. However, any practices with this potential should first be tested with species and conditions that exist on the WW winter range and be applied on a large enough scale to be meaningful.

Over the past century, the amount of area occupied by pinyon-juniper woodland throughout the Great Basin has reportedly increased (Urness 1976, Wallmo and Carpenter 1981). On the WW winter range, this forest type comprises approximately 34% of vegetation (See Chapter 5, Winter Home Range and Habitat Use). Initially, tree and shrub
invasion of grasslands likely produced favorable cover and forage conditions for mule deer (Urnell 1976, Clements and Young 1997). However, in the absence of fire and mechanical intervention, much of the pinyon-juniper forest has become dense and sterile, thus eliminating understory vegetation (Taylor pers. obs.). When this occurs, woodlands become essentially fire proof, except where severe conditions make fire suppression impossible (Clements and Young 1997). For this reason, partial or complete removal of pinyon-juniper trees before stands close could increase production of shrubs, grasses, and forbs, thereby increasing winter range carrying capacity (Wallmo and Carpenter 1981).

Some of the more common methods used to eradicate pinyon-juniper trees include prescribed burning, individual tree felling, bulldozing, and chaining (Wallmo and Carpenter 1981). However, Clary et al. (1974), in an economic evaluation of pinyon-juniper control projects, determined mechanical treatment to be impractical and suggested that future research projects consider the feasibility of fire as a control agent. Prescribed burning can reduce pinyon-juniper dominance before stand closure occurs (Clements and Young 1997).

Several fires have recently occurred in pinyon-juniper communities along the Sierra front, from Antelope Valley north to Slinkard Valley. Unfortunately, these burns have become dominated by cheatgrass and other invader species, thereby reducing habitat potential for mule deer (T. J. Taylor pers. obs). According to Clements and Young (1997), cheatgrass truncates secondary succession by inhibiting the growth of perennial seedlings through competition for moisture. Therefore, these authors recommended seeding a burn during the first fall following the fire, just before onset of the first snowfall, to lessen the amount of seeds consumed by birds and rodents. Fall seeding has another advantage, it enables birds and rodents to cache seeds before the onset of winter, a process required for successful germination. When seeding is delayed past the first fall, then cheatgrass and other invader species become established, thereby out competing more desirable forage species. Similar fire management on the WW deer herd winter range could be beneficial to mule deer by increasing amounts of nutritional perennial forage, while at the same time decreasing the invasion of less desirable annual weeds that quickly develop into fuel rich environments.

ACKNOWLEDGMENTS

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CHAPTER 5. WINTER HOME RANGE AND HABITAT USE

INTRODUCTION

Throughout the western Great Basin, mule deer (Odocoileus hemionus hemionus) occupy a variety of habitats during winter, including sagebrush steppe, pinyon-juniper woodland, mountain mahogany scrub, perennial bunchgrass, and irrigated meadow (Kucera 1988, Taylor 1988, Taylor 1991, Clements and Young 1997). Until recently, the widespread availability and remote nature of these habitats has enabled wildlife managers to successfully maintain viable deer populations. However, encroachment by a number of land uses, such as agricultural development, livestock grazing, mineral exploration, roads and highways, water development, housing subdivisions, and recreation has altered or removed considerable portions of these habitats (Wallmo et al. 1976, Reed 1981). On some deer winter ranges, these activities may impose significant constraints on herd size and productivity. The West Walker (WW) deer herd winter range in northern Mono County, California, and southern Douglas County, Nevada, provides a case in point.

The WW deer herd winter range is located at lower elevations in the rain shadow of the Sierra Nevada. As a result, it has an arid climate, with hot-dry summers and cold-dry winters. Topographically, the winter range is characterized by extensive valleys and lowlands dissected by numerous isolated mountain ranges that mainly assume a north-south orientation. Vegetation on the winter range is dominated by sagebrush-steppe, irrigated meadows and pinyon-juniper woodland; the latter which occurs mainly on higher elevation slopes and ridges. The lower elevation sagebrush-steppe and irrigated meadow habitats provide essential habitat during severe winters because they accumulate less snow, support a diversity of forage types, and are the first to green-up in the spring. However, the same qualities that make these low-lying areas attractive to deer, also make them attractive to humans. Consequently, large tracts of winter range once providing critical habitat for deer are now primary sites of human occupation and activity. The majority of encroachment has occurred from roads and subdivisions; however, mining, and agricultural and water developments have also displaced considerable amounts of essential habitat. The effects of rural subdivisions on the quantity and quality of deer habitat is most evident in Nevada, where widespread growth and development has virtually gone unchecked; Nevada has few if any state provisions that consider significant environmental effects of development projects on wildlife habitat. Development on California portions of the WW winter range has occurred at a much slower rate; however, numerous projects,

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2Taylor, T.J. 1988. Migration and seasonal habitats of the Casa Diablo deer herd, Calif. Department of Fish and Game, Bishop, California, USA.
3Taylor, T.J. 1991. Ecology and productivity of two interstate deer herds in the eastern Sierra Nevada: East Walker-Mono Lake deer herd study, Calif. Department of Fish and Game, Bishop, California, USA.
both existing and proposed, currently threaten areas of essential habitat.

In addition to development, large areas of essential winter range once supporting antelope bitterbrush, sagebrush steppe and perennial bunchgrass communities have been replaced by dense pinyon-juniper forests (R. Thomas, California Department of Fish and Game, pers. comm.). The encroachment of pinyon-juniper woodland on shrub/grass sites apparently began in the late 1800’s, eventually resulting in sterile, closed stands of trees (Barney and Frischknecht 1974, Urness 1976, Clements and Young 1997). Wildfire is considered the major stand renewal process in Great Basin mule deer winter ranges, and is critical to providing habitat necessary for maintaining productive mule deer populations. (Clements and Young 1997). However, its suppression has permitted the expansion of pinyon-juniper woodland at the expense of palatable shrubs and forbs (Julander 1962). Pinyon is considered unpalatable to deer, but deer will consume juniper when more palatable forages are in short supply (Longhurst et al. 1981).

Clements and Young (1997) emphasized the need for suppression of catastrophic fires prone to invasion of cheatgrass (Bromus tectorum). Cheatgrass is considered undesirable because it forms dense stands that crowd out perennial seedlings through competition for moisture (Longhurst et al. 1981). It also truncates secondary succession by providing an early maturing fuel that increases the susceptibility to fire. This type conversion has negatively effected expansive portions of the WW winter range.

Antelope bitterbrush (Purshia tridentata) is one of the most palatable and nutritious mule deer forages in western North America (Smith and Hubbard 1954, Nord 1965, Kufeld et al. 1973), and is an important component in the diets of wintering WW deer (See Chapter 4, Food Habits and Nutrition). However, natural succession and disturbance from fire and other factors, has led to declines in bitterbrush production and alteration of understory composition throughout its range (Ferguson and Medin 1983).

Because of these habitat changes, and expanding demands for multiple use of mule deer winter ranges, wildlife managers need to consider the habitat needs of individual deer herds. My objectives were to document patterns of habitat use by mule deer on the WW winter range and to use the information to formulate guidelines for winter range management. This information is also important for designing habitat reclamation plans necessary to mitigate vegetational disturbances associated with various land use practices.

**STUDY AREA**

This study was conducted from March 1992 through September 1995 on the WW deer herd winter range in northern Mono County, California, and southern Douglas County, Nevada (Figure 5-1). Winter range boundaries, physiographic features, climate, and the locations of deer concentration areas were described previously (See Chapter 2, Migration and Interseasonal Movements).
Thirteen distinct habitat types were identified on the winter range following Mayer and Laudenslayer (1988): low sage (LS), annual grassland (AG), pinyon (Pinus monophylla)/juniper (Juniperus occidentalis) woodland (PJ), riparian forest (MR), desert scrub (DS), agricultural valley (AV), irrigated pasture (IP), aspen forest (AF), mixed conifer forest (MCF), big sagebrush (Artemisia tridentata) (BS), montane chaparral (MC), antelope bitterbrush (Purshia tridentata) (AB), and mountain mahogany (Cercocarpus ledifolius) (MM).

The low sagebrush (LS) community is generally restricted to basins with alkaline soils and to terraces and rolling hills with hardpan or heavy clay conditions (U.S. Forest Service 1981). It occurred in the Gray Hills, on Wild Oat Mountain, and in Wellington Hills, at elevations ranging from 1,550-1,800 m (Figure 5-1). In addition to low sagebrush (A. arbuscula), common shrub species included black sage (A. nova), Mormon tea (Ephedra nevadensis), and spiny hopsage (Garyia spinosa). Dominant herbs included cheatgrass (Bromus tectorum), larkspur (Delphinium spp.), popcorn flower (Cryptantha spp.), indiana paintbrush (Castilleja spp.), buckwheat (Eriogonum spp.), storksbill filaree (Erodium cicutarium), fiddleneck (Amsinkia intermedia), Indian ricegrass (Achnatherum hymenoides), needlegrass (Hesperostipa spp.), and squirreltail (Elymus elymoides).

Annual grassland (AG) occurred throughout lower elevations (<1,800 m) of the winter range, mainly on Wild Oat Mountain, in the Gray Hills, and on the western slope of the Wellington Hills, from about Blackwell Canyon north to Wellington. This community, dominated by cheatgrass and buckwheat (E. umbellatum), usually occupied openings created as a direct result of fire. In many locations, the AG community occurred in a patchwork association with the LS and the two habitat types were not readily discernible. Therefore, LS and AG were combined into a single category, LSAG. The LSAG community often occurred in association with AB; with LSAG occupying sites having shallow, poorly drained soils, and antelope bitterbrush on the deeper areas.

The DS community, on which spiny saltbush (Atriplex confertifolia), four-wing saltbush (A. canescens), Mormon tea, big sagebrush, bitterbrush, rabbitbrush (Chrysothamnus spp.), and spiny hopsage predominate, occurred on desert flats, alkali basins, and drier slopes east of Topaz Lake. Herbaceous cover in the DS community was dominated by cheatgrass, squirreltail, and Iodine bush (Allenrolfea occidentalis).

MR habitat occurred throughout the entire winter range, but was most common along the West Walker River and the numerous drainages that flow east from the Sierra Nevada. Common species include willow (Salix spp.), black cottonwood (Populus trichocarpa), water birch (Betula occidentalis), aspen, and Wood’s rose (Rosa woodsii). AV occurred mainly along the floodplain of the West Walker River, which flowed north through Antelope Valley from the east slope of the Sierra Nevada. Principal crops included sugar beets, alfalfa, onions, and small grains. Untilled portions of the floodplain with yearlong water availability were classified as IP. This community, which is composed primarily of sedges (Carex spp.) and rushes (Juncus spp.), also dominated habitats on the
Little Antelope Valley (LAV) and Slinkard Valley State Wildlife Areas. Nearly all IP habitat was grazed by livestock, primarily during spring, summer, and fall. However, during mild winters, IP in Antelope Valley was grazed through the entire winter.

The BS community occurred throughout the entire winter range, but was most prevalent on mesic alluvial fans and in drainages located along the east slope of the Sierra Nevada and the west slope of the Wellington Hills. This community was characterized by big sagebrush, with antelope bitterbrush often occurring as a codominant. Other common shrubs included rabbitbrush, desert peach, and Mormon tea. Some of the more common grasses included Indian ricegrass, needle-and-thread grass, and squirreltail; dominant forbs included fiddleneck, storksbill filaree, and lupine (*Lupinus spp.*). The AB community occurred in pure stands dominated by antelope bitterbrush. This habitat type occurred primarily on alluvial fans and north aspect slopes in the Wellington Hills and on Wild Oat Mountain; in Slinkard Valley and Little Antelope Valley; along the west shore of Topaz Lake; and adjacent to the West Walker River, near the communities of Walker and Coleville, California, and Topaz Lake, Nevada.

The MC community occurred on higher elevation (2,000-2,500 m) secondary winter ranges located along the east slope of the Sierra Nevada. Common associates included Jeffrey pine (*Pinus jeffreyi*), tobacco brush (*Ceanothus velutinus*), greenleaf manzanita (*Arctostaphylos patula*), curlleaf mountain mahogany, antelope bitterbrush, and big sagebrush. Some of the more common herbs included squirreltail, Indian ricegrass, and Idaho fescue (*Festuca idahoensis*). MM habitat occurred in isolated patches within the MC community on secondary winter ranges in the Wellington Hills and on the east slope of the Sierra Nevada. It typically occupied steep northerly aspects and ridgetops at elevations ranging from 2,000-2,500 m. Curlleaf mountain mahogany typically occurred as the dominant species, usually in association with western juniper, squirreltail, and Idaho fescue. On more mesic sites, mountain mahogany occurred in association with big sagebrush in dense stands where individual shrubs assumed a tree-like form.

PJ woodland dominated vegetation on the east slope of the Sierra Nevada, in the Wellington Hills, and in the Sweetwater Mountains. Codominance in this community is shared by pinyon pine, Jeffrey pine, and white fir (*Abies concolor*). AF occurred in association with mixed conifer forest in numerous small groves at elevations > 2,000 m.

**METHODS**

Between March-April 1992 and November-April 1993-1995, I monitored 57 radio-collared deer (47 females and 10 males) on the WW winter range. I located deer at 2-5 day intervals by triangulating from the ground, and 1-2 times/month from a fixed-wing aircraft. All locations were made during daylight hours, from approximately 0600 to 1730 hours. Initial ground locations were made from a vehicle equipped with a Telonics® TR-2 receiver with an attached program/scanner (TS-1) and a base loaded whip antenna. Triangulation was accomplished by 1 observer with a hand-held, directional “H” antenna.
(RA-2A; Telonics® Inc., Mesa, Ariz.) and ear phones obtaining ≥3 compass bearings with an intersecting angle of > 60 and <160°; the maximum time between locations was ten minutes. The mean error of ground locations was determined throughout the course of the study from 17 field test transmitters placed at locations unknown to the principal investigator. All locations were triangulated from surveyed points along roads at distances ≤ 1 km from the truck. Ninety percent of telemetry fixes on field test transmitters were accurate to ≤ 125 m (x̄ = 97.0, SE = 12.3) of the actual location. Because all radiocollared animals were marked for visual identification, attempts were made to verify triangulation bearings by moving toward the signal until the deer was visually located; >95% of triangulations were followed by an observation. All relocations were plotted in the field on U.S. Geological Survey 7.5 minute topographic maps and the Universal Transverse Mercator (UTM) coordinates for the positions were recorded to the nearest 50 m.

Aerial radio-tracking was conducted from a Cessna 185 at air speeds ranging from 80-110 km per hour. A directional “H” antenna was attached to each wing strut and these were attached to a switch box for selecting between right, left, or both antennas. Aerial relocation bearings were recorded in longitude and latitude coordinates to 0.01 minute, using a “Loran C” system. I used program LATLONG (Kie et al. 1996) to convert location coordinates to UTM coordinates. The mean error (n = 17, x̄ = 295 m, SE = 50.2) of aerial locations was determined during the course of the study by measuring distances between dead radio-collared deer and estimated locations. This level of accuracy was considered sufficient because most vegetation types, with the exception of MR, occupied large, homogenous areas.

I used the program CALHOME (Kie et al. 1996) to estimate home-range sizes of radio-collared deer. Program CALHOME performs utilization, distribution, or home-range estimates based on data sets consisting of X and Y coordinates for successive locations of a single animal. CALHOME provides home-range estimates using several different methods. For comparative purpose, I selected the minimum convex polygon (MCP) (Mohr 1947) and the adaptive kernel (ADK) (Worton 1989) methods. Because of small sample sizes, I pooled relocation data for all individuals across years to reduce the sample size bias associated with this method and to delineate a 95% composite home range (Andelt and Andelt 1981, Jenkins and Starkey 1984); the 95% estimator was used to eliminate the influence of outlier locations. Areas of concentrated deer use within the composite home-range were defined as core areas (Samuel et al. 1985). Core areas were identified as the largest areas within the composite home range where observed use (based on 75% ADK values) exceeded a uniform distribution (Samuel and Green 1988).

I determined winter range habitat characteristics of deer radio locations from a digital database developed with GIS, specifically ARC/INFO data analysis software (Environmental Systems Research Institute, Inc. Redlands, Calif.). I classified habitat types within the composite winter range from interpretation of 1:24,000 color stereo aerial photographs obtained from the Bureau of Land Management, and these data were verified using ground truthing and knowledge of the area. Using a stereoplotter, I then transferred the photo interpreted data to 1:24,000 black-and-white orthophoto quadrangle maps.
From these orthophoto maps, I digitized and classified for use in the GIS, all visible habitat polygons >2 ha² within the composite home range. I then used GIS procedures (ARC/INFO) to compute area and frequency calculations for each habitat type identified. Finally, UTM coordinates of radio locations were uploaded into ARC/INFO and then overlaid on the GIS file containing the habitat polygons.

Following Neu et al. (1974) and Byers et al. (1984), I used a Chi-square goodness-of-fit test to evaluate the null hypothesis that the use of habitat categories equaled availability. A Bonferroni Z-test (Marcum and Loftsgaarden 1980) was used to determine which habitats on the winter range deviated from expected use. For analysis, locations were grouped by year and by winter season, including early winter (November-January) and late winter (February-April). I based seasonal periods on major shifts in diet species composition.

I evaluated habitat use of disturbed sites associated with development. Disturbed sites included areas in and around housing tracts, subdivisions, commercial and agricultural developments, and other projects where significant alteration (>2 ha²) of winter range had occurred. I included a 200 m buffer around each area of disturbance to account for a project’s zone of influence (Mackie Pac 1980, Smith and Conner 1989), created as a result of the human activity associated with development. Throughout this paper, the terms “use” and “avoidance” are used to denote habitat use greater than and less than availability at the 0.05 experiment-wise level, respectively.

RESULTS

I used 492 telemetry locations of 35 radio-collared deer taken from May 1992-June 1995 to estimate a 95% composite winter home range. After combining data points for all individuals, I estimated a MCP composite winter home range size of 80,500 ha (805 km²) (Figure 5-1). In comparison, the calculated isopleth of the 95% ADK for pooled observations obtained from May 1992-June 1995 was 109,000 ha (1,090 km²). Annual MCP composite winter home ranges averaged 52,970 ha (range = 38,800-70,070 ha). Isopleths of the ADK using 75% of pooled locations identified 3 core areas comprising 18,800 ha (Figure 5-2).

Winter Habitat Use

Analysis of winter habitat use by WW deer was confined primarily to 46,707 ha of primary winter range surrounding Antelope Valley in Mono County, California, and Douglas County, Nevada; it excluded portions of secondary winter range located at the south end of the Pine Nut Mountains, in the Wellington Hills, and at the north end of the Sweetwater Mountains. It also excluded primary winter range located in Smith Valley, Nevada, on the east side of the Wellington Hills (Figure 5-1). These areas were not included in the analysis of habitat use because 1:24,000 orthophoto quadrangle maps, necessary for digitizing habitat polygons, were unavailable from BLM or the U.S. Geological Survey (USGS).
Figure 5-1. Locations of the 95% MCP Composite Winter Home Range and the 46,707 ha Mapped Area Used in Analysis of Habitat Use on the West Walker Deer Herd Winter Range, Mono County, California, and Douglas County, Nevada, 1992-1995.
Figure 5-2. Locations of the 75% ADK Composite Winter Home Range Defining Core Areas on the West Walker Deer Herd Winter Range, Mono County, California, and Douglas County, Nevada, 1992-1995.
I determined winter habitat preference based on 429 locations of 35 radio-collared deer. There was no significant difference in habitat use between early and late winter periods ($\chi^2 = 2.0$, 12 df, $P > 0.05$) (Table 5-1). During early winter, all habitats were used equal to their availability and developed areas were avoided ($\chi^2 = 67.0$, 12 df, $P = 0.000$). During late winter, deer preferred LSAG and DS habitats; MCF, BS, MC, MM, and developed areas were avoided ($\chi^2 = 97.2$, 12 df, $P = 0.000$).

Small sample sizes precluded annual comparisons of habitat use during early winter. There was a significant difference between years in habitat use during late winter ($\chi^2 = 39.5$, 24 df, $P < 0.05$). During late winter 1993, deer preferred LSAG and DS and avoided PJ, MCF, BS, MC, MM, and developed areas ($\chi^2 = 79.9$, 12 df, $P = 0.000$) (Table 5-2). During 1994, deer avoided MR, AF, MCF, MC, AB, MM, and developed areas ($\chi^2 = 29.2$, 12 df, $P = 0.0037$). In 1995, deer avoided MR, AF, MCF, BS, AB, MM, and developed areas ($\chi^2 = 24.0$, 12 df, $P = 0.02$), and used other habitats in proportion to their availability.

**DISCUSSION**

Beginning in mid-November, after completing fall migration from the summer range, deer typically occupied secondary winter ranges until late December, although the duration of use on secondary winter ranges varied according to winter severity (See Chapter 2, Migration and Interseasonal Movements). Secondary winter ranges encompassed a broad area of steep, rugged terrain located in the mountainous areas surrounding Antelope Valley, including the Pine Nut Mountains, the Sierra Front, the Wellington Hills, and the Sweetwater Mountains. However, because of insufficient map coverage, my analysis of habitat use on secondary winter ranges was confined to about 10,000 ha$^2$ that included the northwest portion of the Wellington Hills, from about Blackwell Canyon south to Spring Canyon, and east to Jackass Flat; and to the steeper slopes and ridges located to the north and west of Little Antelope Valley and Slinkard Valley (Figure 5-1).

During late winter (February-April), heavy snow accumulations typically precluded deer occupancy on secondary winter ranges, which could explain why deer avoided MM, AF, MC, and BS. However, use preference ratings indicated that these upper elevation habitats were important to deer during early winter. For example, MM comprised only a small proportion (0.5%) of the total mapped area, but accounted for 4% of deer locations (curleaf mountain mahogany comprised between 4.7-7% of November diets; see Chapter 4, Food Habits and Nutrition). Similarly, AF, MC, and SB made up 12% of the mapped area, but accounted for 9% of deer locations. These habitats were important during early winter because they occurred in complex mosaics that enhanced forage and cover opportunities, thereby reducing deer concentrations and competition for available resources (Brown 1992).
### Table 5-1. Percent mule deer use of available habitats on the West Walker winter range during early November-January) and late (February-April) winter, 1992-1995.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Total Area (Ha)</th>
<th>Availability (%)</th>
<th>No. of Polygons</th>
<th>Ave. Area (ha)</th>
<th>Early Winter (145)</th>
<th>Late Winter (284)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Sage/Annual Grassland</td>
<td>8765</td>
<td>19</td>
<td>15</td>
<td>1473</td>
<td>15</td>
<td>34+</td>
</tr>
<tr>
<td>Montane Riparian</td>
<td>775</td>
<td>2</td>
<td>9</td>
<td>86</td>
<td>0-</td>
<td>1</td>
</tr>
<tr>
<td>Agricultural Valley</td>
<td>1727</td>
<td>4</td>
<td>5</td>
<td>345</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Pinyon-Juniper Forest</td>
<td>15783</td>
<td>34</td>
<td>199</td>
<td>82</td>
<td>35</td>
<td>32</td>
</tr>
<tr>
<td>Irrigated Pasture</td>
<td>5227</td>
<td>11</td>
<td>12</td>
<td>435</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>Desert Scrub</td>
<td>5398</td>
<td>11</td>
<td>39</td>
<td>138</td>
<td>22</td>
<td>19+</td>
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<tr>
<td>Aspen Forest</td>
<td>652</td>
<td>1</td>
<td>11</td>
<td>22</td>
<td>2</td>
<td>0.5</td>
</tr>
<tr>
<td>Mixed Conifer Forest</td>
<td>1877</td>
<td>4</td>
<td>18</td>
<td>104</td>
<td>1</td>
<td>0-</td>
</tr>
<tr>
<td>Big Sagebrush</td>
<td>3890</td>
<td>8</td>
<td>22</td>
<td>176</td>
<td>5</td>
<td>1-</td>
</tr>
<tr>
<td>Montane Chaparral</td>
<td>1227</td>
<td>3</td>
<td>13</td>
<td>94</td>
<td>2</td>
<td>1-</td>
</tr>
<tr>
<td>Bitterbrush</td>
<td>155</td>
<td>0.5</td>
<td>4</td>
<td>38</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mountain Mahogany</td>
<td>326</td>
<td>0.5</td>
<td>12</td>
<td>27</td>
<td>4</td>
<td>0-</td>
</tr>
<tr>
<td>Developed/Disturbed</td>
<td>1014</td>
<td>2</td>
<td>20</td>
<td>50</td>
<td>0-</td>
<td>0.5-</td>
</tr>
</tbody>
</table>

* a No. of locations shown in parentheses.
+ Indicates use > availability and - indicates use < availability (P < 0.05).

### Table 5-2. Percent mule deer use of available habitats on the West Walker winter range during late winter (February-April), 1992-1995.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Total Area (Ha)</th>
<th>Availability (%)</th>
<th>1993</th>
<th>1994</th>
<th>1995</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Sage/Annual Grassland</td>
<td>8765</td>
<td>19</td>
<td>39+</td>
<td>33</td>
<td>29</td>
</tr>
<tr>
<td>Montane Riparian</td>
<td>775</td>
<td>2</td>
<td>0.5</td>
<td>0-</td>
<td>3-</td>
</tr>
<tr>
<td>Agricultural Valley</td>
<td>1727</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>0-</td>
</tr>
<tr>
<td>Pinyon-Juniper Forest</td>
<td>15783</td>
<td>34</td>
<td>20-</td>
<td>42</td>
<td>40</td>
</tr>
<tr>
<td>Irrigated Pasture</td>
<td>5227</td>
<td>11</td>
<td>9</td>
<td>3-</td>
<td>10</td>
</tr>
<tr>
<td>Desert Scrub</td>
<td>5398</td>
<td>11</td>
<td>23+</td>
<td>18</td>
<td>17</td>
</tr>
<tr>
<td>Aspen Forest</td>
<td>652</td>
<td>1</td>
<td>0.5</td>
<td>0-</td>
<td>0-</td>
</tr>
<tr>
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<td>4</td>
<td>0-</td>
<td>0-</td>
<td>0-</td>
</tr>
<tr>
<td>Big Sagebrush</td>
<td>3890</td>
<td>8</td>
<td>2-</td>
<td>2</td>
<td>0-</td>
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<tr>
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<td>0-</td>
<td>0-</td>
<td>1</td>
</tr>
<tr>
<td>Bitterbrush</td>
<td>155</td>
<td>0.5</td>
<td>3</td>
<td>0-</td>
<td>0-</td>
</tr>
<tr>
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<td>326</td>
<td>0.5</td>
<td>0-</td>
<td>0-</td>
<td>0-</td>
</tr>
<tr>
<td>Developed/Disturbed</td>
<td>1014</td>
<td>2</td>
<td>0-</td>
<td>0-</td>
<td>0-</td>
</tr>
</tbody>
</table>

* a No. of locations shown in parentheses.
+ Indicates use > availability and - indicates use < availability (P < 0.05).
A diverse, high quality diet is essential to deer for production of fat reserves necessary for winter survival (Garrott et al. 1987, Short 1981, Clements and Young 1997). Deer with limited fat reserves, such as animals from poor quality summer and fall ranges, will rapidly deplete fat stores and succumb when sufficient energy is no longer available for maintaining body temperatures and normal bodily functions (Short 1981).

During late winter, habitat use appeared to be closely related to the temporal availability and phenological development of succulent, herbaceous forage in the LSAG community. LSAG habitat comprised approximately 18% of the mapped area and included 34% of late winter locations. This habitat type occurred primarily on lower elevation, south aspect slopes, which were the first areas to become snow free. South slopes received more sunlight, accumulated less snow, and thus, provided a microclimate that supported winter sprouting of grasses and forbs (Carpenter and Wallmo 1981). Microhistological analyses of deer fecal pellets indicated that forbs alone comprised between 39-67% of late winter diets; buckwheat was the most important forb, averaging 18% of late winter diets (See Chapter 4, Diet Composition and Quality). Certain species of buckwheat, including sulphur buckwheat (E. umbellatum), may have nutritional benefits over other forages because they have a high lignin content. Plants having high lignin are often brittle, enabling them to break down and pass more quickly. This could actually enhance opportunities for deer to obtain maximum benefits from forages that are otherwise of limited digestibility (Milchunas 1977). Buckwheat was readily available to deer during late winter because it dominated many openings within the low sagebrush and annual grassland communities.

Preference for LSAG habitat during late winter could be associated with deer use of dwarf sagebrush as forage. Some species of dwarf sagebrush, such as low sagebrush (A. arbuscula) and black sagebrush (A. nova), are considered preferred browse by mule deer during winter (Tueller 1970). In this study, sagebrush (Ariemisia spp.) was an important forage component, comprising between 14-34% of late winter diets (See Chapter 4, Diet Composition and Quality).

Saltbush (Atriplex spp.) was the dominate shrub in the DS community, and was readily consumed by deer from December-March. Consumption of saltbush was especially high during January and February, when it comprised between 25% and 35% of diets, respectively (See Chapter 4, Diet Composition and Quality). DS use may have been overestimated in areas that bordered IP habitat. Deer frequently foraged in IP after dark (Taylors, pers. obs.) and bedded in nearby DS during daylight periods when the majority of radio locations were obtained. Similarly, the importance of IP as a critical source of late winter forage was likely underestimated. Nevertheless, IP appears important to deer, as indicated by 12% and 8% use during early and late winter, respectively.

Deer used PJ habitat in relation to its availability; however, its relative importance

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was demonstrated by the 35% and 32% use during early and late winter, respectively. Most PJ stands inhabited by deer were in early and mid-successional phases (T. J. Taylor, pers. obs.). These open stands supported dense shrub layers that provided valuable thermal and escape cover for deer, as well as palatable forage; bitterbrush was often a conspicuous understory component. During the severe winter of 1992-93, however, deer occupied shrub zones among open canopied PJ forests until approximately 6 January, after which heavy snows (>60 cm) forced animals to take refuge in densely forested areas that provided more trafficable snow conditions and shelter from inclement weather (Taylor 1994). During warmer weather, deer foraged in open LSG and IP habitats during the early morning and the evening hours, and bedded in nearby PJ stands during the daytime.

Deer used AB habitat in proportion to its availability, although its relative importance was probably underestimated. There were many smaller bitterbrush stands interspersed within BS and PJ that were mapped as part of these communities and not included in the analysis of bitterbrush use.

Deer showed avoidance for disturbed areas associated with residential, commercial, and agricultural developments. These areas comprised 2% of the mapped area, yet received <0.5% use. Many areas of mapped disturbance included housing subdivisions where individual land owners had retained small islands of big sagebrush, bitterbrush, or pinyon-juniper vegetation, interspersed with driveways, lawns, horse corrals, and private yard fenced areas.

During late winter 1993, LSG and DS were preferred by deer and PJ was avoided. In comparison, these habitats, although important to deer, were used in proportion to their availability during late winter 1994 and 1995. Differences among years in late winter habitat use could be related to the effects of weather on plant phenology. The winter of 1992-93 was severe, with 180 cm of snow and average minimum temperatures of -16°C in January. Snow depths on lower elevation primary winter ranges exceeded 47 cm (range = 41-65 cm) in mid-January, which drastically reduced the amount of forage available to deer. As a result, deer condition deteriorated rapidly and large numbers of carcasses were observed on these ranges by early February. Beginning in mid-February, deer exhibited intense daytime feeding on snow free southerly aspects in LSG and DS habitats (e.g., on 17 February, approximately 75 deer were observed foraging in on a south-facing clearing <2 ha in size; T. J. Taylor pers. obs.). These openings supported winter sprouting of grasses and forbs and provided deer the first opportunity to reverse the negative energy balance acquired over the winter and to regain their overall physiological condition (Garrott et al. 1987). Following heavy winters, deer extended their use of LSG and DS habitats until mid-May because cool spring temperatures along migration routes and holding areas prevented the snowpack from melting (See Chapter 2, Migration and Interseasonal Movements).

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Management Recommendations

Habitat management programs designed to increase deer productivity in the WW herd would be most effective if conducted on core area habitats where deer form the greatest concentrations. Winter range enhancement projects, such as reseeding, fertilization, irrigation programs, livestock reductions, and prescribed burns, would benefit larger numbers of deer than similar projects conducted on summer and transition ranges when deer are more widely distributed. However, the relative importance of secondary winter ranges to deer during early winter also suggests a need to focus management attention on these higher elevation habitats. If deer are divested of intermediate winter ranges, where they first concentrate after fall migration is completed, stresses of severe winters will be increased (Carpenter and Wallmo 1981). Pockets of mixed conifer and aspen forest interspersed with montane chaparral and mountain mahogany, can provide important forage and shelter to deer during early winter.

Diet composition analyses indicated that antelope bitterbrush is a critical browse species for wintering WW mule deer. Therefore, wildlife managers need to assess the current condition of antelope bitterbrush stands to determine their overall vigor and the potential for stimulating growth in less productive stands. Some stands of antelope bitterbrush appeared to be comprised mostly of older plants and were experiencing low seedling recruitment (Taylor pers. obs.). Older bitterbrush plants are less vigorous and do not provide the nutritional browse of younger plants (McConnel and Smith 1977). Wildlife managers have long since recognized that to maintain high carrying-capacities on mule deer winter ranges, they need to maintain subclimax plant communities through deliberate manipulation of plant succession (Reed 1981, Clements and Young 1997).

Griffith and Peak (1989) reported that mule deer in the Columbia River Canyon of northcentral Washington consistently used bitterbrush stands with the highest canopy cover because of increased bitterbrush forage, greater visual concealment, and increased cover of herbaceous forage plants in the understory. These authors recommended several options for maintaining and enhancing bitterbrush communities including rejuvenating existing older plants and high-cover stands by topping, and replanting and protecting burned stands from grazing to allow recovery to dense stands that were present before fires occurred. Similar management of mid- to late seral bitterbrush stands on the WW winter range could increase bitterbrush abundance. However, any practices with this potential should first be tested with species and conditions that exist on the WW winter range and be applied on a large enough scale to be meaningful.

Deliberate manipulation of pinyon-juniper forests before stands close could increase production of shrubs, grasses, and forbs, thereby increasing winter range carrying capacity (Wallmo and Carpenter 1981). Some of the more common methods used to control invasion of pinyon-juniper trees include prescribed burning, individual tree felling, bulldozing, and chaining (Wallmo and Carpenter 1981). However, Clary et al. (1974), in an economic evaluation of pinyon-juniper control projects, determined mechanical treatment to be impractical and suggested that future research projects consider the
feasibility of fire as a control agent. Prescribed burning can reduce pinyon-juniper dominance before stand closure occurs (Clements and Young 1997).

Clements and Young (1997) recommended seeding a burn during the first fall following the fire, just before onset of the first snowfall, to lessen the amount of seeds consumed by birds and rodents. Fall seeding has the advantage of enabling birds and rodents to cache seeds before the onset of winter, a process required for successful germination. When seeding is delayed past the first fall, then cheatgrass and other invader species become established, thereby out competing more desirable forage species. Similar fire management on the WW deer herd winter range could be beneficial to mule deer by increasing amounts of nutritional perennial forage, while at the same time decreasing the invasion of less desirable annual weeds that quickly develop into fuel rich environments.

IP habitat was important to deer, especially during early winter when it made up 12% of deer use. Therefore, management practices should be developed on winter ranges that promote and ensure access to late season growth of succulent forage on irrigated pasture. Mule deer in northwest Colorado made extensive use of agricultural meadows during autumn; such areas provided deer with succulent forage at a time when the nutritional quality of summer and winter range vegetation was declining because of plant senescence (Garrott et al. 1987). Hence, these authors recommended irrigation and fertilization programs designed to retain succulent forage late into the growing season, and restrictions on livestock grazing to avoid competition during periods of heavy deer use. Similar management of pastureland occurring on WW herd winter ranges might enhance deer productivity by sustaining animal condition during periods of drought.

Throughout the WW winter range, there is continued pressure for diversion of deer ranges to other uses. Therefore, programs such as government acquisition of privately owned lands or development of cooperative land use exchanges, should be considered to protect and maintain essential winter habitats.

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LITERATURE CITED


