NEW STRATEGIES FOR PRONGHORN FOOD HABIT STUDIES

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Abstract: A food habits project was conducted on pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionnus*), bighorn sheep (*Ovis canadensis*), feral horses (*Equus caballlus*) and feral burros (*Equus assinus*) on 2 national wildlife refuges, one in Oregon and one in Nevada from 1993 to 1995. We report findings emphasizing pronghorn diet and the relationship with the other 4 ungulates. Diet composition varied considerably among seasons and between years for 3 native ungulates. Digestibility correction factors were employed for the first time in pronghorn diet studies and provided a more accurate assessment of forage consumed. Pronghorn and mule deer primarily alternated use between forbs and shrubs, while bighorn alternated between grass and forbs. Both feral equids foraged on grasses with some seasonal forb use. Diet quality for all ungulate species at both refuges varied seasonally with the highest quality generally during spring when forbs were used most heavily. Lowest quality occurred during winter when forage was generally senescent. Apparent relationships of diet quality indices with weather, particularity temperature and precipitation were noted. Based on results of this project, we recommend future diet studies for pronghorn consider using digestibility correction factors, forage quality indices and correlation of diet composition with weather patterns.

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Literature on pronghorn diets has spanned close to 200 years. During the historic Lewis and Clark expedition across America from 1803 to 1806, Lewis reported anecdotal observations of plants consumed by pronghorn (Moulton 1987). Rouse (1941) documented the earliest quantified diet composition for pronghorn. More than 250 diet studies of pronghorn diet have been conducted during the last 50 years (Sundstrom et al. 1973, Yoakum 1990). Pronghorn food habit studies originally used observation methods, then changed to rumen analyses, and more recently, fecal analyses (Yoakum 1990). Fecal analysis for pronghorn diets has been used since the 1970s (Jacobs 1973, Schwartz and Nagy 1976, Sneva and Vavra 1978). Procedural techniques have been standardized with few changes.

The project was initiated during the development of an Environmental Impact Statement/Comprehensive Management Plan for the Hart Mountain National Antelope Refuge (HMNAR) in Oregon (U.S. Fish and Wildlife Service 1994). Diet composition data for the HMNAR were more than 40 years old for pronghorn, did not exist for other wild and domestic ungulates, and lacked nutritional values for plants. Similar information was needed to meet management objectives on the nearby Sheldon National Wildlife Refuge (SNWR) in Nevada (Yoakum 1992). This study represents the first use of digestibility correction factors for pronghorn diets, as well as forage quality indices and the correlation of diets with weather patterns.

Our paper focuses on the portions of the study (Hansen and Anthony 1999) pertaining to pronghorn diets and diet overlap of pronghorn with other ungulates. Our specific objectives were to:

1. Determine diet composition for all ungulates (corrected for differential digestion for pronghorn), and preference ratios for pronghorn
2. Determine diet quality indices
3. Correlate diet information with weather patterns
4. Calculate dietary overlap between pronghorn and other ungulates.

STUDY AREA

The HMNAR contains approximately 88,000 ha in southcentral Oregon and the nearby SNWR encompasses some 120,000 ha in northwestern Nevada--all within the Great Basin ecoregion (Figure 1). Elevations ranged from 1,400 m on the SNWR to 2,400 m on the HMNAR. Average annual precipitation was 25 to 35 cm with most received as rain and snow during winter and spring. Both refuges are in the shrubsteppe biome with vegetative communities dominated with sagebrush (*Artemisia spp.*), rabbitbrush (*Chrysothamnus spp.*), and western juniper (*Juniperus occidentalis*). Predominate grasses included bluegrass (*Poa secunda*), bluebunch wheatgrass (*Agropyron spicatum*), and at higher elevations, fescue (*Festuca spp.*).

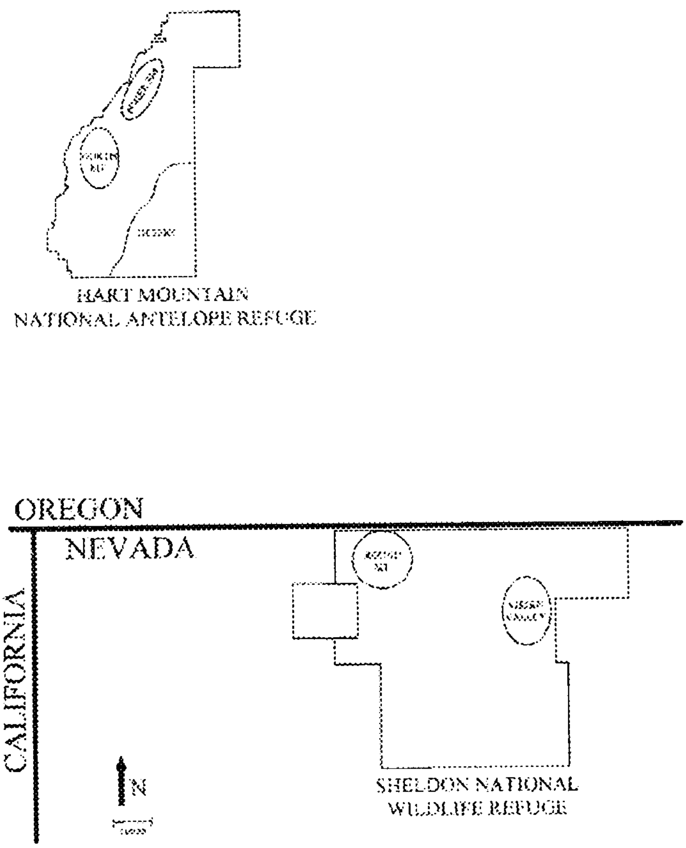


Fig. 1. Map of Hart Mountain National Antelope Refuge and Sheldon National Wildlife Refuge showing study areas.

A large diversity of annual and perennial forbs grow in various vegetative communities on both refuges.

METHODS

The study commenced in October 1993 and terminated in June 1999. Field collections of biological samples were conducted by U.S. Fish and Wildlife personnel between October 1993 and September 1995. Determination of diet composition and quality were accomplished by the Wildlife Habitat Laboratory at Washington State University, Pullman, Washington.

Sample Collections.--Fecal samples were collected from pronghorn, bighorn sheep, mule deer and feral horses on both refuges, and from feral burros on the SNWR. Two sample locations on the SNWR and 3 on the HMNAR (see Figure 1) were established because they represented typical plant communities on each refuge, exhibited maximum species overlap, multi-season use, and presence of feral burros and horses that were of special interest. We attempted to collect fecal samples from all ungulates inhabiting each collection site on each refuge. Thus, during some sample periods, fecal samples were collected from the same ungulate species in up to 3 locations on the HMNAR, but only 1 location for another ungulate species. Occasionally some ungulate species could not be located within designated locations; consequently, samples were collected in the closest adjacent area where animals were found and the vegetative community was similar.

Fecal samples were collected by observing specific animals (or groups of animals) until they defecated. Information on sex and age of the animals was recorded. For pronghorn, fecal samples were predominantly collected from adult females. Sample collection times were concentrated during periods when the diversity of plant species was high and the change in plant phenology was rapid (April, May, June), then equally spaced during the remainder of the year (August, October, and January). Sample sizes were increased when plant species diversity was high (Davitt and Nelson 1984): 15-20 samples/month in the spring and summer and 10 samples/month during the autumn and winter. Two years of diet information were collected in an attempt to establish how diets varied between years with differing weather conditions.

Diet Composition.--Determination of dietary components was done by microhistological analysis. Composite samples were obtained for each refuge, sampling period, and were available for each sample location by compositing 1 gm of fecal material from each individual sample to remove bias due to pellet size (Jenks et. al. 1989). Two hundred microscope fields per composite sample were inspected for identifiable plant species using methods of Davitt and Nelson (1980). However, uncorrected diet composition data does not account for the effect of differential digestibility of the various forage plants consumed, especially forbs (Dearden et al. 1975, Vavra and Holechek 1980, Holechek and Valdez 1985, Hansen 1996). Therefore, concurrent with collection of additional fecal samples in the second year, specimens of important forage plants were collected. *In-vitro* digestion trails on these plants were used to determine correction factors for species with differential digestibility. These factors were then applied to the diet composition data from both years to give a more accurate estimation of the relative quantity of each plant species actually consumed by the animals.

All plant species were grouped into three forage classes (grasses, forbs and shrubs) commonly used in pronghorn food habit studies (Yoakum 1990); consequently, it was possible to compare results of this study with similar studies in the Great Basin, and to calculate dietary overlap for each forage class. Sedges and rushes were included with grasses--moss was listed with forbs.

Forage preference ratings (PR) were calculated as: PR=D/R, where D was the percentage of forage class in diet composition and R was the percentage forage class in vegetative production (Krueger 1972). Plants rating greater than 1.0 were preferred. Vegetative production data were obtained for the low sagebrush community during spring/summer 1993 and 1995 (Crawford and Coggins 1997).

Dietary overlap refers to the degree of similarity in use of food sources among different animal species occupying the same rangeland, whether concurrently or not (Schoener 1970, McCullough 1980). It is high when both animals ingest the same or similar proportions and kinds of forage and nonexistent when none or small quantities are consumed.

Diet Quality.--Fecal nitrogen in forage plants was assessed using the Kjeldahl technique, a simple chemical procedure that measures the percent by weight of nitrogen in a sample. Diaminiopimelic acid (DAPA) was assessed with techniques reported by Davitt and Nelson (1984). Both quality indices were measured on an individual sample basis in which each individual defecation was considered 1 sample, and on an organic matter basis to remove confounding effects of ingestion of soil or other minerals (Wehausen 1995).

Statistical Analysis.--For statistical comparisons of diet composition and quality, we combined monthly values of grass, forb and shrub consumption, FN, and DAPA into a spring season (April, May, June) and a winter season (December, January and February), and applied standard ANOVA techniques. Factors used in ANOVA models for each of the independent variables (shrub, forb, grass, FN, and DAPA) were animal species, refuges, year, and season/month. Seasons used were winter (December, January, and February) when diet quality was at its lowest and spring (April, May, and June) when diet quality peaked for the year.

Standard multiple linear regression techniques were used to explore the relationships between diet quality and weather variables. In these analyses, FN and DAPA were the dependent variables and minimum, maximum, and mean daily temperature and precipitation were the independent variables. All statistical comparisons were performed using SYSTAT software (Wilkinson 1996).

RESULTS

Diet Selection.-- Pronghorn ate 52 plant species on the HMNAR and 51 species on the SNWR (Table I). Before digestibility corrections were made grasses and shrubs made up more of the total diet than forbs (Table, 2, 3: Figure 2, 3). Forb use was greater on HMNAR than on SNWR. However, when correction factors were applied, forbs were selected over shrubs by 17% on HMNAR. On SNWR, where there is less diversity of forbs, pronghorn still consumed a higher percentage (65%) of shrubs than forbs (25%), after digestibility corrections. Pronghorn and mule deer

Table 1. Number of forage taxa consumed by three wild and two feral ungulates on the Hart Mountain National Antelope Refuge (HMNAR) and the Sheldon National Wildlife Refuge (SNWR) from 1993 to 1995.

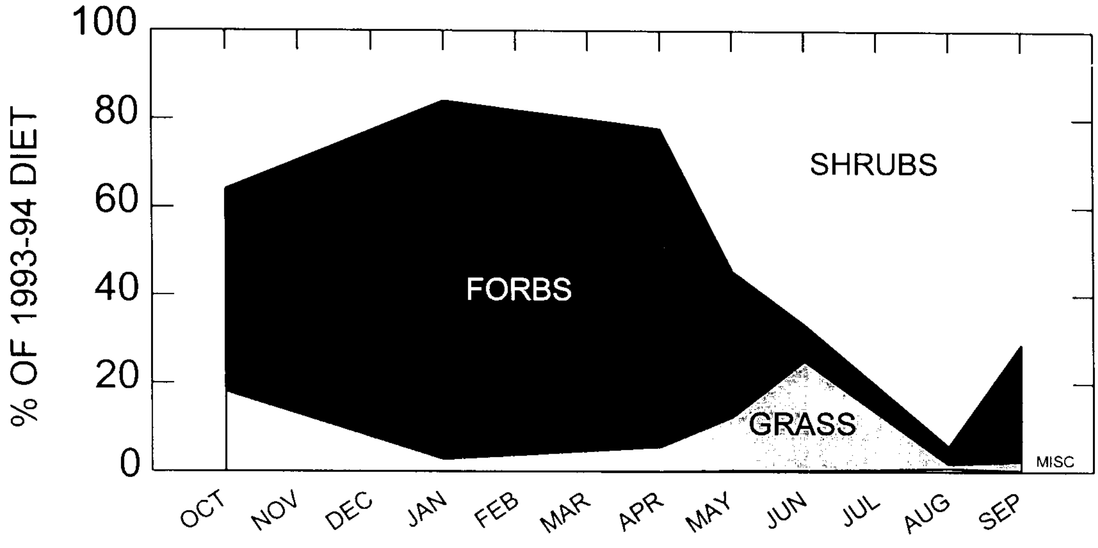
Forage Class	Number of Plant Taxa in Forage consumed								
	Pronghorn		Mule Deer		Bighorn Sheep		Feral Horses		Feral Burros
	HMNAR	SNWR	HMNAR	SNWR	HMNAR	SNWR	HMNAR	SNWR	SNWR
Grass	13	13	16	13	15	18	17	23	15
Forb	27	27	29	31	34	32	10	9	11
Shrub	12	11	14	13	12	7	11	10	7
Total	52	51	59	57	61	57	38	42	33

Table 2. Diet composition of pronghorn by microhistological analyses of feces from the Hart Mountain National Antelope Refuge, Oregon from October 1993 to September 1995.

Forage	Percent Diet Composition									
Class	Uncorrected					Corrected				
	Spring	Summer	Autumn	Winter	Annual	Spring	Summer	Autumn	Winter	Annual
Grass	21.8	3.9	12.6	11.8	12.5	14.0	2.2	10.2	5.5	8.0
Forb	38.4	30.6	28.8	49.0	36.7	47.8	31.1	47.2	71.0	49.3
Shrub	39.8	65.5	58.6	39.2	50.8	38.2	66.7	42.8	23.5	42.8
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.2	100.0	100.1

Table 3. Diet composition of pronghorn by microhistological analyses of feces from the Sheldon National Wildlife Refuge, Nevada from October 1993 to September 1995.

Forage	Percent Diet Composition									
Class	Uncorrected					Corrected				
	Spring	Summer	Autumn	Winter	Annual	Spring	Summer	Autumn	Winter	Annual
Grass	6.5	6.4	9.0	21.7	10.9	3.0	4.6	8.2	24.1	10.0
Forb	33.2	17.2	20.4	13.2	21.0	38.5	14.8	28.1	17.4	24.7
Shrub	60.3	76.4	70.6	65.1	68.1	57.5	80.6	63.7	58.5	65.1
Total	100.0	100.0	100.0	100.0	100.0	99.0	100.0	100.0	100.0	99.8



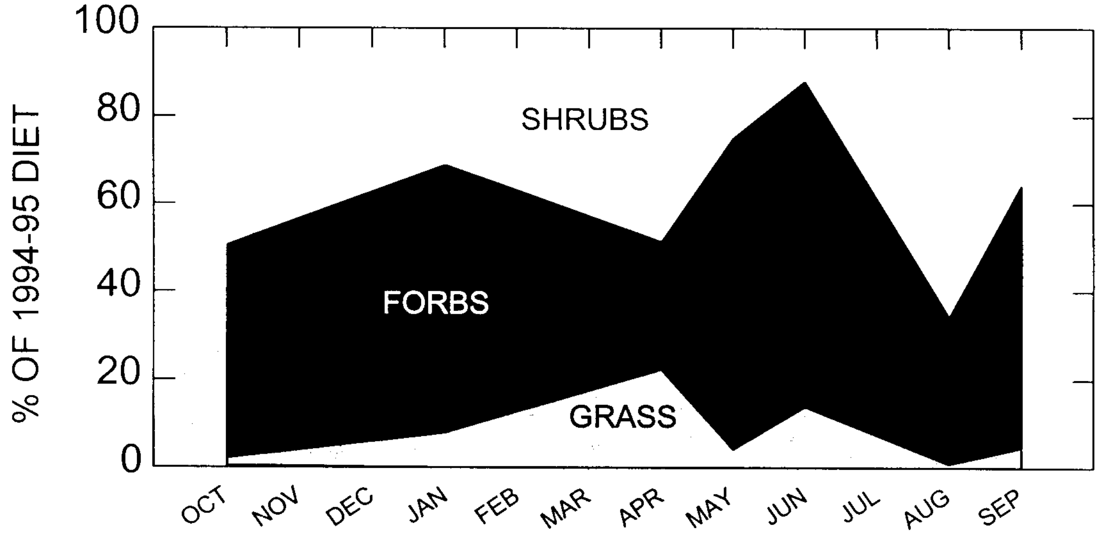


Fig. 2. Corrected plant composition of pronghorn diets measured by microhystological analysis of feces from HMNAR from October 1993 to September 1995.

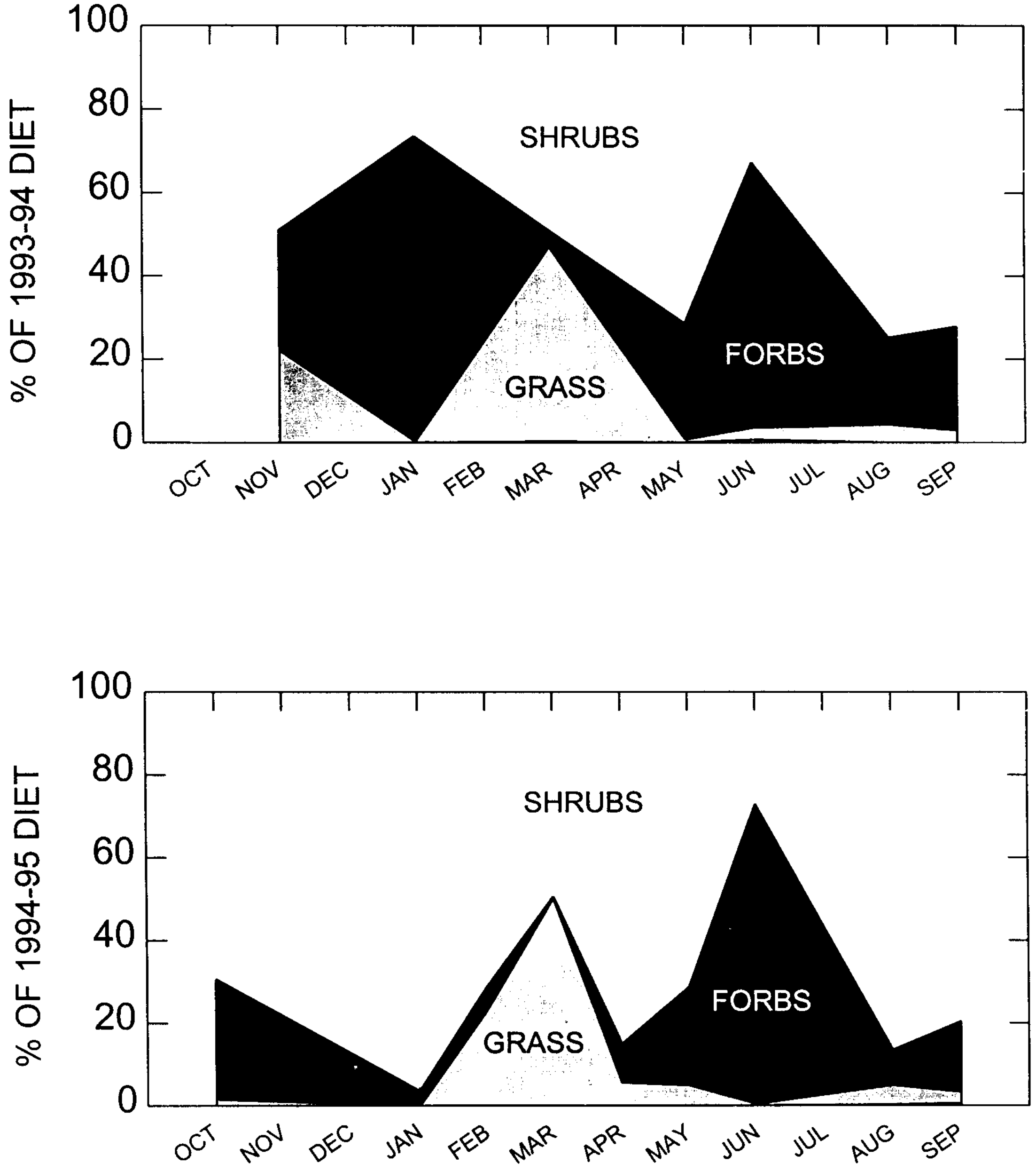


Fig. 3. Corrected plant composition of pronghorn diets measured by microhystological analysis of feces from SNWR from October 1993 to September 1995.

Table 4. Annual diet composition for wild and feral ungulates on the Hart Mountain National Antelope Refuge and the Sheldon National Wildlife Refuge from October 1993 to 1995.

Species	Forage Class	Hart Mt. National Antelope Refuge		Sheldon National Wildlife Refuge	
		Uncorrected Percentages	Corrected Percentages	Uncorrected Percentages	Corrected Percentages
Pronghorn	Grass	12.5	7.9	10.9	9.9
	Forb	36.7	49.3	21.0	25.0
	Shrub	50.8	42.8	68.1	65.1
Mule Deer	Grass	12.9	9.4	10.8	11.8
	Forb	46.0	50.1	24.9	34.0
	Shrub	41.1	40.5	64.3	54.2
Bighorn Sheep	Grass	70.5	59.0	74.4	70.0
	Forb	21.9	32.4	20.8	26.5
	Shrub	7.6	8.6	4.8	3.5
Feral Horse	Grass	88.9	83.7	91.5	90.6
	Forb	8.3	13.0	6.0	7.1
	Shrub	2.8	3.3	2.5	2.3
Feral Burro	Grass	No burros on Refuge	No burros on Refuge	88.8	84.4
	Forb			4.8	6.8
	Shrub			6.4	8.8

foraging percentages were similar, but depicted some variability seasonally (Table 4). For equids on both refuges, the corrected diets showed greater use of forbs than did uncorrected diets. Horses consumed 13% forbs during winter on the HMNAR.

Dietary overlap was calculated for all ungulates on both refuges. Overlap was the highest (about 95%) with mule deer because both species consumed approximately equal percentages of forbs and shrubs (Table 5). Overlap of pronghorn with bighorn sheep was close to 50% with the greatest overlap on forbs. Yearlong dietary overlap with feral horses averaged 20% and feral burros 25%. Forage preference ratings (Figure 6) for pronghorn on the HMNAR indicate that they preferred forbs (1.6) over shrubs (.9), while grasses are nonpreferred (.3).

Diet Quality Indices,--The general ANOVA models relating FN and DAPA to various factors indicated that ungulate species, season, and the interaction between species and season had the greatest effects on diet quality. The overall effects of year and refuge, as well as interactions were not significant ($P > 0.05$) for this analysis.

For pronghorn, the lowest fecal nitrogen (FN) occurred in winter ($\bar{x}$ =1.52%, SD=0.11), and the highest occurred in spring ($\bar{x}$ =3.12%, SD=0.34). Similarly, DAPA values were low in winter ($\bar{x}$ = 0.51 mg/g, SD=0.10) and highest in spring ($\bar{x}$ + 0.94 mg/g, SD=0.16), Fecal nitrogen values for pronghorn were similar at the 2 refuges during spring (df=1, F=1.782, P=0.185) and winter (df= 1, F=0.259, P=0.612) (Figure 4).

Effect of Weather.-- Monthly weather data available for HMNAR (Oregon Climate Service 1995) indicated the 1994-95 season was colder than in 1993-94, but there were only small differences in precipitation between these 2 years (Figure 5). Multiple regression analyses indicated that mean daily temperature and precipitation during the current month explained 84% of the variation in pronghorn FN ($P<0.0001$) and 81% of the variation in DAPA ($P<0.001$) (Table 6).

DISCUSSION

Diet Composition.-- Our data document that forbs and shrubs were a staple for pronghorn during most seasons of the year. When succulent forbs and grasses were available, together they made up 80-90% of pronghorn diets. *Phlox* and/or *Leptodactylon*, low growing perennial forbs, were apparently selected in winter over the ubiquitous and taller sagebrush when not covered by snow. Grasses were usually the earliest plants to green-up in spring, which explains their appearance in pronghorn diets in February, March and April. Other investigators are consistent in showing that forbs are highest, shrubs intermediate, and grasses lowest in concentrations of crude protein, phosphorus, and cell solubles (Houston et al, 1981, Krysl et al. 1984, Holechek et al. 1998). Although forb selection was yearlong, it was more pronounced when more available during spring and summer.

Table 5. Dietary overlap determined by diet composition studies using digestibility factors for pronghorn and sympatric wild and domestic ungulates on the HMNAR and SNWR, 1993-1995.

Refuge and Ungulate	Forage Class			
	Grass	Forb	Shrub	Total
Hart Mountain National Antelope Refuge				
Mule deer	7.9	49.3	40.5	97.7
Bighorn sheep	7.9	32.4	8.6	48.9
Horses, feral	7.9	13.0	3.3	24.2
Sheldon National Wildlife Refuge				
Mule deer	9.9	25.0	54.2	89.1
Bighorn sheep	9.9	25.0	3.5	38.9
Horses, feral	9.9	7.1	2.3	19.3
Burros, feral	9.9	6.8	8.8	25.5

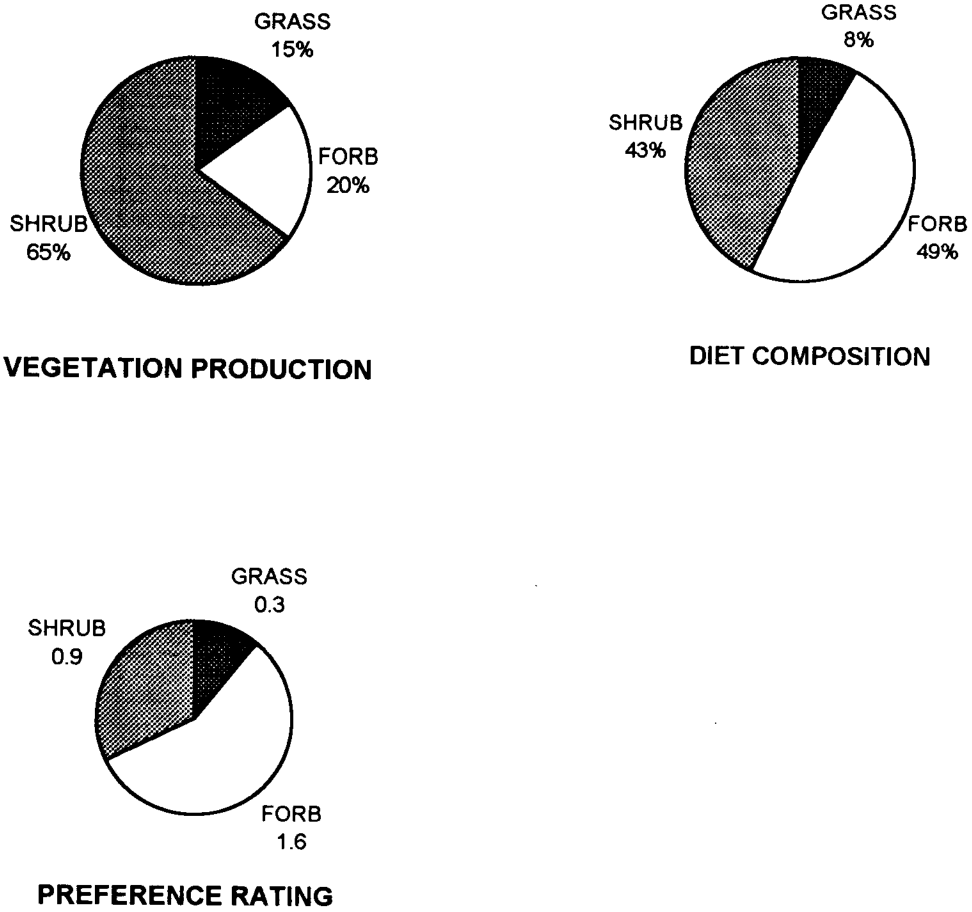


Fig.4. Percent composition of vegetation production, pronghorn diet composition corrected for differential digestibility, and preference rating.

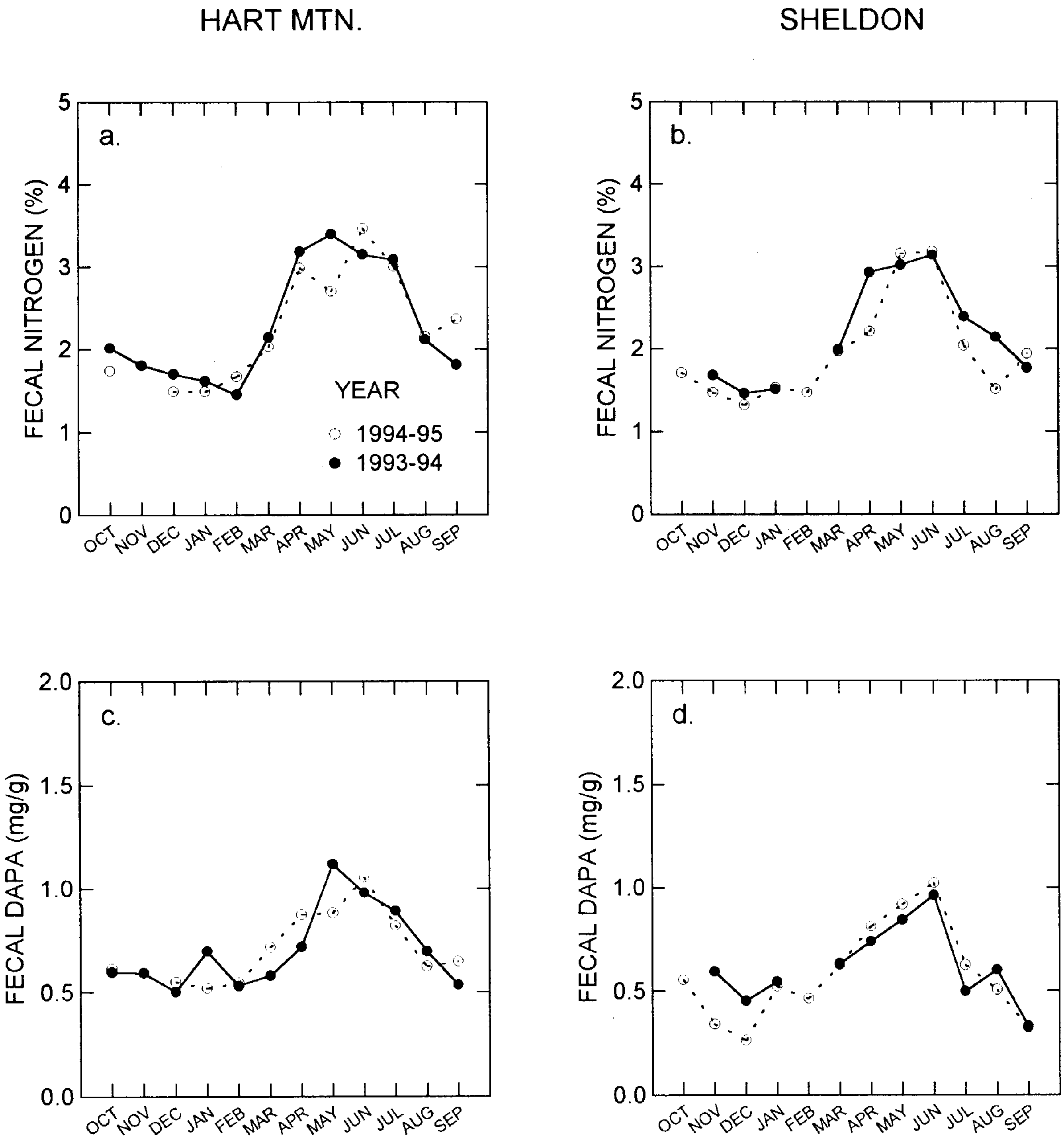


Fig. 5. Fecal nitrogen and fecal DAPA measurements from pronghorn at HMNAR and SNWR from October 1993 to September 1995.

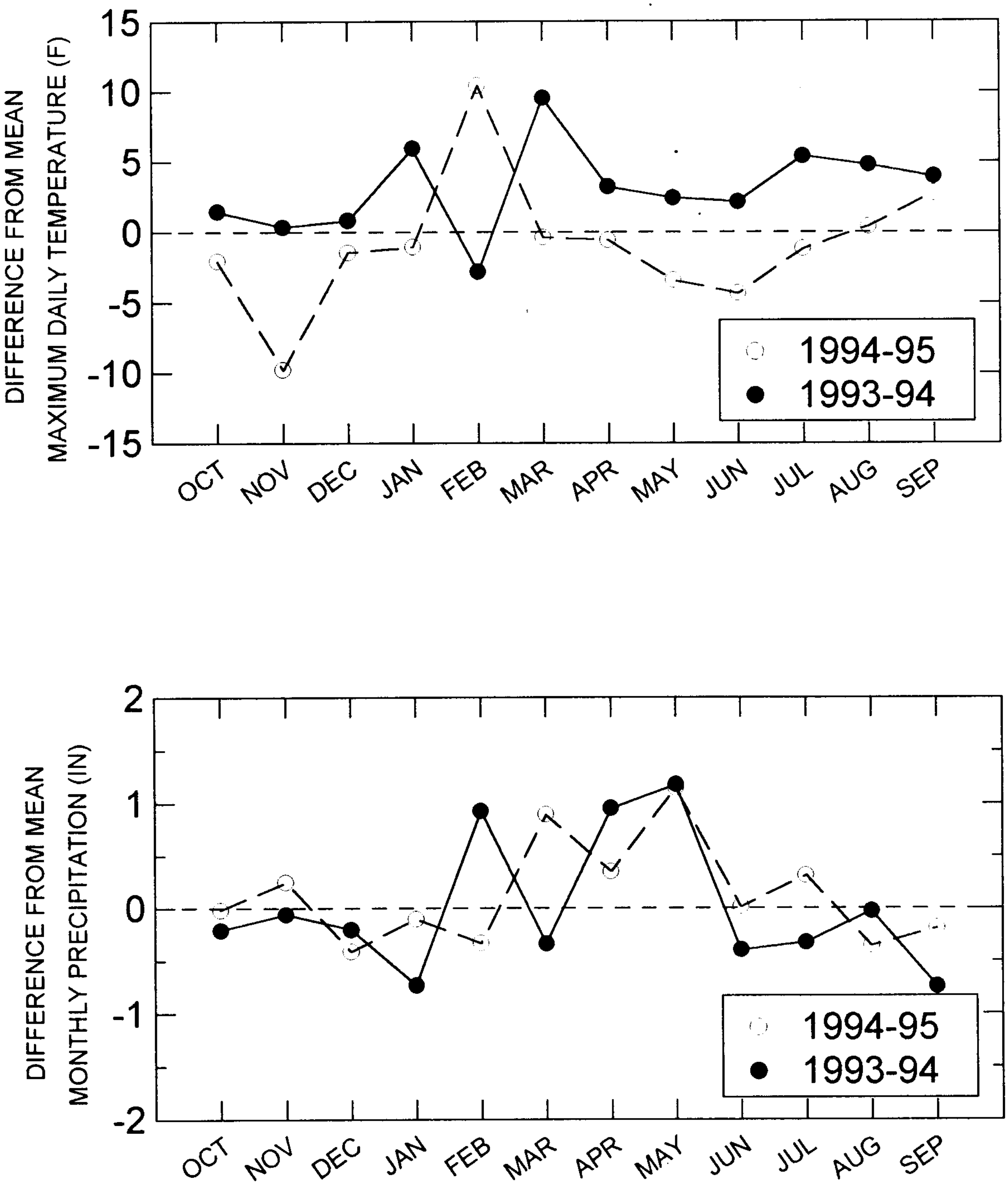


Fig. 6. Difference from mean maximum daily temperature (F) and mean monthly precipitation (in) for each month between October 1993 and September 1995 on the HMNAR.

Compared to previous studies (Mason 1952, Sneva and Vavra 1978, Hanley and Hanley 1982, Hansen 1982, McInnis 1984), pronghorn consumed a high percentage (71% on HMNAR) of forbs during winter (Table 2). Wildlife and range managers often assume forbs "dry up and blow away" during winter, but pronghorn consume greater quantities of forbs when available during winter than previously believed.

The value of digestibility correction factors has been investigated for mule deer (Holochek and Valdez 1985) and Dall's sheep (Hansen 1996), but were not used for pronghorn prior to this project. These correction values are especially important for ungulates, such as pronghorn, that consume large quantities of forbs. The only pronghorn diet study on HMNAR prior to this project was conducted more than 40 years earlier by Mason (1952) when the technique of digestibility correction factors was not in use for wild ungulate diet studies. While our uncorrected data are similar to Mason's (1952), the digestibility correction process suggests that pronghorn selected considerably more forbs than previously accepted.

The greater use of forbs at HMNAR may have resulted from 1 or more factors. First, rangelands may have been in better vegetative condition than the SNWR as a result of longer rest from cattle grazing. Second, more of the rangeland at HMNAR has been burned by wild and prescribed fires which promotes greater abundance of herbaceous vegetation. And third, HMNAR offers greater elevation relief, allowing pronghorn access to plants in early phenological stages for an extended time by moving with the seasons. Further research could help distinguish which of these factors are most important.

Early publications pertaining to pronghorn food habit studies emphasized the importance (forage composition, nutritional values) of shrubs for pronghorn survival during severe winters with deep snow (Sundstrom et al. 1973). Later studies documented the importance (preference, succulence, nutritional values) of forbs for fetal development and lactation (Ellis 1970, Yoakum 1990). Our study indicates that forbs are highly preferred and nutritious forage. We found that when forbs were available during winter, pronghorn used this forage class for as much as 70% of their diet. Some of these forbs were perennial and maintained higher digestibility and nutritional values than other forage classes (Barnett and Crawford 1994, Vrba and Schaller 2000). Forbs are of greater importance to pronghorn for all seasons of the year because they have high nutritional value. Pronghorn are predominantly forb consumers and our results indicate forbs may be even more important than previously thought; consequently, managers need to consider enhancing forb production and diversity on pronghorn habitat.

Most of the annual variations in diet probably resulted from differences in weather between years. The early, heavy snowpack in 1994-95 prevented pronghorn access to the lower growing forbs, so pronghorn compensated by consuming more shrubs. Conversely, the large increase in forb use in summer

Table 6. Weather factors that influenced (P<0.05) quality indices of monthly pronghorn diets on Hart Mountain National Antelope Refuge, 1993-1995.

Diet Index	N	Factor	Parameter Estimate	SE	t	P
FN	23	Precipitation in prior month	0.370	0.081	4.541	<0.0001
		Mean temperature	0.027	0.005	5.696	<0.0001
		Interaction of mean Temperature and current Precipitation	0.007	0.002	3.825	0.001
DAPA	23	Precipitation in prior month	0.113	0.024	4.706	<0.0001
		Mean temperature	0.006	0.001	3.917	0.001
		Interaction of mean Temperature and current Precipitation	0.002	0.001	3.491	0.002

Uncorrected diets were similar to those reported for pronghorn and other ungulates on the SNWR (Hansen 1982). One of the most apparent differences was the relatively slow changes in use among forage classes reported by Hansen (1982) compared with rapid shifts among forage classes in our study that were probably related to rapid changes in weather. Further, Hansen (1982) tracked diets for 1 year and was not able to address the annual variation reported in this project. Finally, consumption rates reported for forbs and grasses during our study often were larger than reported by Hansen (1982) as a result of the digestibility correction employed. Use of forbs and grasses in this study also was higher than reported for studies of pronghorn in other Great Basin environments (Vavra and Sneva 1978, Hanley and Hanley 1982, McInnis 1984, Yoakum 1990).

1995 over summer 1994 for pronghorn at HMNAR was due to increased availability of forbs during the winter season.

At times diet overlap can appear minimal when data are summed over the four seasons and several years. This may have been the case for pronghorn and feral horses on HMNAR for winter. Feral horses consumed 13% forbs during winter--a season when pronghorn were likewise seeking and consuming large quantities (71%) of many of the same forbs. Forbs are not abundant on certain Great Basin pronghorn habitats, especially during winter (Ellis 1970). A horse can consume 6 times as much forage daily as a pronghorn (Heady and Child 1994). Consequently, large numbers of horses on winter habitats with low biomass of forbs, could compete with pronghorn.

Pronghorn consume large amounts of shrubs known to contain nitrogen binding compounds, rendering FN less useful. DAPA is a relatively new index and little information is available to relate it with nitrogen requirements of pronghorn. Therefore, FN and DAPA are not especially useful for determining whether diets are deficient in protein. They are useful for within season comparisons among years, or increases of similar diet composition among areas (Leslie and Starkey 1987).

Seasonal trends in DAPA followed FN closely, but DAPA measurements exhibited more variation within each month so that it was more difficult to determine whether differences were significant. It may be that DAPA was the most accurate diet quality measure and that FN was elevated in summer by nitrogen binding compounds (Leslie and Starkey 1987, Robbins et al. 1987).

Goldsmith (1988) working with pronghorn in a Great Basin shrubsteppe in Adobe Valley, California, also found DAPA and FN varied seasonally with plant phenology, and had the lowest levels during winter and early spring.

Weather Factors.-- Diet quality for pronghorn is largely a function of plant species composition, nutritional values and phenology. Therefore, seasonal and annual weather variation, elevation and other topographic influences, as well as vegetation status and forage competition can affect diet quality. Region-wide weather phenomena, such as heavy snow and low precipitation, affect diet quality in ways that are difficult for pronghorn to compensate. Diet quality was related to weather, especially temperature and precipitation. Lower pronghorn diet quality in the winter of 1994-95 compared to 1993-94 was likely a result of colder 1994-95 temperatures. The greatest differences in diet quality between the 2 study years occurred from September to November and again in May, which coincide with 2 critical times of year for pronghorn reproduction--conception and parturition. Reductions in maternal diet quality can reduce maternal weight, birth weight of fetuses, and milk production in pronghorn and other ungulates (Ellis 1970, Oftedal 1985). Neonatal survival is reduced by low maternal diet quality, and reductions in diet quality for longer durations closer to parturition and early lactation have the greatest effect (Price and White 1985). Consequently, our diet quality data suggest that pronghorn recruitment in 1995 should have been lower than in 1994, which was confirmed (U.S. Fish and Wildlife Service 1996). More years of data are needed to refine the relationships between weather, diet quality and pronghorn recruitment.

We obtained limited snowfall timing or snow depth records for HMNAR. Snowfall and snow depth are functions of temperature and precipitation, and during the winter may be more closely related to diet quality than either temperature or precipitation. Such information could improve the predictive ability of our regression equations.

Management and Research Implications.-- This project was designed to provide basic information on the diets of pronghorn, bighorn sheep, mule deer, feral horses and burros to measure future change in refuge management practices. We sampled from 2 separate years with different weather patterns and found variable diet composition and quality between the years. While this variation gives managers a good indication of the range of diet composition and quality possible, it may make it difficult to discern small changes that result from applying varying management programs.

Our analysis disclosed that diet quality was related to temperature and precipitation for these 2 years. We recommend the relationship between annual changes in weather, corresponding vegetation production, and ungulate production be studied further.

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