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Forage selection and population structure of the Middle Fork elk herd

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FORAGE SELECTION AND POPULATION STRUCTURE OF THE MIDDLE FORK ELK HERD

By

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ABSTRACT

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The third of a series of elk (Cervus elaphus nelsoni) studies was conducted in the Great Bear Wilderness and surrounding lands, Flathead National Forest, Montana. Aspects studied included population structure and dynamics, influence of hunting on the elk population, relationship of accessibility and hunting pressure, seasonal food habits, and diet quality. Estimates of sex ratios were 27 bulls:100 cows in 1978 and 16:100 in 1979. Hunting accounted for 91% of all documented mortality. Mean age at death was 3.4 years among hunter-killed elk and 5.5 years among natural mortalities. Calf:cow ratios in winter trend counts have declined significantly overall since 1936, but no significant trend was detected in counts from 1969 to present. The average calf:cow ratio in these counts since 1969 (22:100) was considered as the lowest likely level of recruitment. Ratios based on intensive winter field work since 1977 averaged 37:100, which was considered the maximum likely recruitment rate for the herd. Considering probable conservative and liberal biases in the 2 estimates, a moderate rate of about 28 calves:100 cows was believed close to the actual value for the herd. At current levels of mortality, declines in the population were predicted by most feasible combinations of recruitment and prior population trend. Hunter days increased but hunter success decreased with increasing levels of accessibility. Hunter success was an insensitive measure of apparent elk density. Combining data from both years, conifers were the most frequently utilized winter forage, forbs predominated in spring and summer diets, and shrubs dominated the diet the rest of the year. Range surveys indicated that shrub production was inadequate for winter maintenance. Digestibility of key browse species was low, and the population suffered malnutrition during most winters.

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Finally I thank my family for supporting and encouraging me throughout my education. Extra special appreciation goes to my grandfather, whose fireside stories and love of the out-of-doors instilled my appreciation for the wildlife resource.

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CHAPTER I

INTRODUCTION

Three studies concerned with the elk of the Middle Fork of the Flathead River were conducted from 1977 through 1979. Smith (1978) reported on movements, seasonal ranges, and habitat selection during the summer and fall of 1977. McDonald (In prep.) described winter habitat selection, herd composition, winter severity, and mortality for winters of 1977 and 1978. Between 1 January 1978 and 1 December 1979, I conducted field work on the Middle Fork in order to:

1) determine age and sex structure;
2) calculate the population dynamics;
3) determine the influence of hunting on the population;
4) determine seasonal food habits; and
5) ascertain the health and nutritional status of the herd.

CHAPTER II

DESCRIPTION OF STUDY AREA

Detailed descriptions of the study area were reported by Smith (1978) and McDonald (In prep.). Briefly, the study area comprises about 200 square miles (518 km^2) of the Great Bear Wilderness and adjacent lands. The area lies southeast of Glacier National Park, west of the Continental Divide, and north and east of the divide between the South and Middle forks of the Flathead River (Fig. 1). Topography is a rugged mountain range dissected by narrow canyons, with elevations ranging from 4200 feet (1280 m) to over 8000 feet (2460 m). Most of the study area is accessible only by hiking.

The Middle Fork typically has cold weather with deep snow during winter, followed by cool, wet springs and warm, dry summers. Autumn is usually cool, moist, and of short duration. Snow usually begins during September in the high country and often starts to accumulate in the valleys by late October.

Three elk herds from the South Fork and Middle Fork intermix slightly during the summer, but segregate onto distinct winter ranges (Simmons 1974, Biggins 1975, Fuller 1976, Smith 1978, McDonald in prep.). Consequently, the summer food habits portion of this thesis are applicable to all elk summering on the Middle Fork. The winter food habits and population analysis, however, apply only to those elk that winter in the Lunch Creek area along the Middle Fork.

CHAPTER III

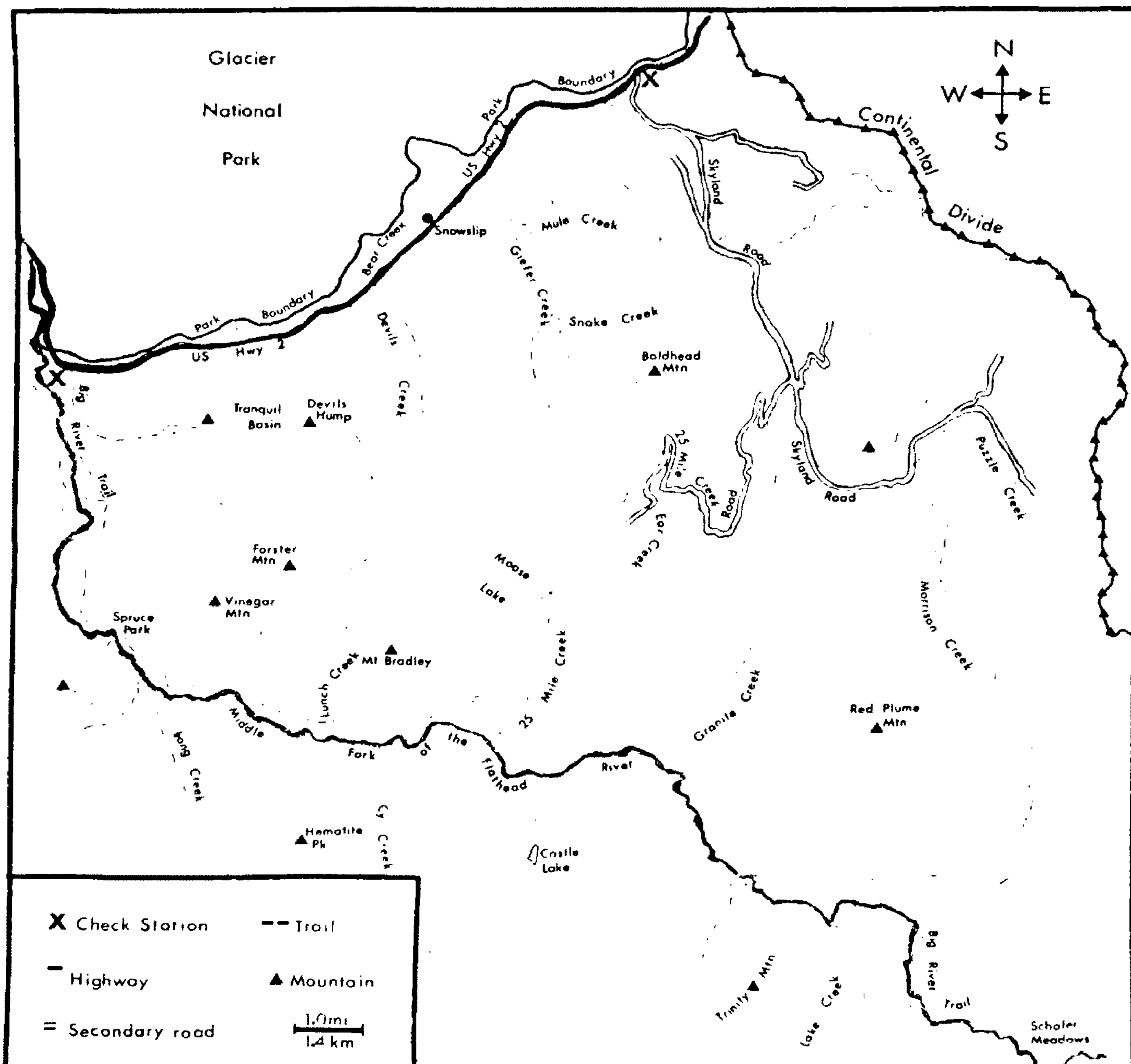
METHODS

Population Description and Dynamics

Whenever elk were encountered in the field, they were assigned to age and sex categories. Ground surveys were conducted periodically throughout the study period, and aerial surveys were flown monthly from January 1978 through May 1979. Data from those surveys were used to calculate calf:cow ratios, as were classifications made during Montana Department of Fish, Wildlife and Parks (FWP) winter aerial trend surveys. I also calculated calf:cow ratios based on sightings reported to me during hunter interviews. The 3 sources of data are independent.

Mortality was documented whenever observed. Instances of natural mortality were recorded during the course of field work, and hunting mortality was monitored at checking stations during the general elk season. One station, located at the junction of State Highway 2 and Skyland Road (Fig. 1), was operated each day for the first 10 days of the season, and Thursday afternoons through Tuesdays thereafter. The location of this station made it possible to intercept hunters traveling the only road into the study area. A second station,

Fig. 1. Road and trail systems of the study area.



located at the head of Big River Trail, was operated only on weekends. Logistic restrictions in 1979 forced the closure of this station. Many local residents cooperated by providing reports of hunting activities or kills. These reports were investigated during evenings or slow periods at the checking stations.

I estimated that 85 to 90% of all elk hunters in the area were contacted in 1978 and 80 to 85% in 1979. Ages of elk killed by hunters and by natural mortality factors were estimated by the eruption-wear technique (Quimby and Gaab 1957). In addition, most age estimates were verified or corrected by sectioning incisor 1 and counting cementum annuli (Keiss 1969, Humason 1972).

Because the age distribution of the hunter-killed sample was discontinuous and irregular in the upper age classes and thus difficult to work with analytically, I smoothed the age structure. The expected number of calves was determined from calf:cow ratios and the number of adults in the sample. Then a log plot of the age classes was constructed and a regression line calculated. The smoothed age distribution was rescaled relative to 1000 calves.

To predict likely future population trends, time-specific life tables were constructed for several possible combinations of survivorship (l_x) and fecundity (m_x). Under the basic assumption that age structure (S_x) was constant and that the finite rate of increase was 0.0 ($\lambda = 1.0$), survivorship (l_x) was initially set equal to S_x (Caughley

1977). A long-term finite rate of change (λ_L) was computed as: $\lambda_L = e^{rt}$, where $t = 1$, and r = instantaneous rate of population change. Estimation of r was by: $\hat{r} = \frac{\ln R_o}{T}$, where R_o = the net replacement rate, and T = mean generation time.

If a population has not been stable prior to the time of sampling (i.e., $\lambda \neq 1.0$), then age structure (S_x) will not equal survivorship (l_x), but must be adjusted to account for the prior rate of population change. The correct l_x for a changing population is provided by the formula: $l_x = S_x \lambda^x$, where x designates individual age classes, and λ = finite rate of population change prior to sampling.

The prior population trend of the Middle Fork herd was unknown, so 4 values of λ (4 possible prior trends) were used to restructure l_x and predict future trends. In addition to the prediction based on the assumptions of $\lambda = 1.0$ and $l_x = S_x$, a life table derivation of λ_L based on these assumptions was used to predict future trend. The bracket values of $\lambda = 0.9$ (10% population decline) and $\lambda = 1.1$ (10% population growth) were selected as the maximum probable prior trends. Each of these values was used to restructure l_x, and predictions of future population trends were made.

In addition to calculating long-term rates of change (λ_L), I calculated short-term finite rates of change over the coming year (λ_S), using the formula:

$$\lambda_s = \frac{N_{t+1}}{N_t} = \frac{\sum_{x=o}^{\infty} (S_{xt} (1 - q_x)) + \sum_{x=o}^{\infty} (S_{xt} (1 - q_x) m_x)}{\sum_{x=o}^{\infty} S_{xt}} ,$$

where S_{xt} = number presently in each age class, $(1 - q_x)$ = survival rate, and m_x = age-specific fecundity. The derivation and function of λ_s is provided in Appendix A.

Hunter Distribution and Elk Response

Data were collected by interviewing hunters at check stations, hunting camps, and local businesses. Hunters were asked to report:

1) area hunted (i. e., drainage, mountain, landmarks, etc.);

2) number of hunters in the party;

3) number of elk killed;

4) number of elk seen but not killed; and

5) location of sightings and kills.

After the data were collected and hunting locations plotted, hunting subunits were subjectively delineated. Each subunit was then assigned an accessibility rating based on the distance to the nearest road, the extent and quality of the trail system, and other factors that influence ease of access (steepness of terrain, density of forest stands and understory, etc.):

Access Rating		Description
1. Backcountry	--	requires overnight camping for effective hunting;
2. Difficult	--	requires > 45-minute walk from a road; trails are poorly maintained or nonexistent;
3. Moderate	--	requires > 15-minute but < 45-minute walk from a road; trails are good or tread is easy; and
4. Easy	--	roads and areas that require < 15-minute walk from a road.

Apparent elk density was defined as number of surviving elk seen per hunter day. Restricting this measure to surviving elk maintained statistical independence for a subsequent comparison between elk density and hunter success. Apparent susceptibility was defined as the ratio of dead to surviving elk among those seen by hunters, or:

$$\frac{\text{no. of elk killed/hunter day}}{\text{no. of elk seen but not killed/hunter day}} = \frac{\text{no. elk killed}}{\text{no. elk seen but not killed}}.$$

Values generated by this scheme are indices that can only be used to compare similarly treated data.

Distance to roads is the classic approach to documenting elk-human interactions; consequently, distances between kills and the nearest trail and open road were recorded for comparison to previous research.

Food Habits and Forage Quality

Fecal analysis provided the only feasible method for gathering food habits data that could be compared between seasons and between years. From each fresh fecal pile encountered in the field, I collected 2 pellets (approximately 2 g). Samples were labeled, preserved, grouped by season, and sent to the Composition Analysis Laboratory (Hansen et al. 1979) for analysis. Each sample was examined on 100 microscope fields, and composition was reported by genera as relative frequency of occurrence (r.f.o.). Seventeen composite samples were analyzed, representing 12 seasons of study.

Nomenclature of seasons, and designation of starting and ending dates of seasons were based on changes in habitat selection reported by Smith (1978). The system includes 6 seasonal periods, with starting and ending times keyed to weather conditions and changes in habitat selection by the elk.

Back-track browse surveys were conducted during the winter of 1978-79. At 10 locations, the tracks of feeding elk were followed and the relative percent abundance of each plant species along the trail was estimated. All instances of use were recorded and, in addition, intensity of use was classified as: class 1, < 50% of current annual growth (CAG) removed; class 2, 50 to 100% of CAG removed; or class 3, growth 2 or more years old removed. All intensity-of-use estimates were based on available vegetation only (plant material protruding above the snowline but < 6 feet above the ground).

Range trend surveys (Cole 1963) were used to determine the adequacy of shrubby forage production on the winter range. Transects were established at known elk feeding sites (n = 13) and at random sites in what I considered typical elk habitat (n = 6). Forage species examined during these surveys were *Acer glabrum*, *Amelanchier alnifolia*, *Cornus stolonifera*, and *Salix* spp.

Forage quality was assessed by in vitro digestibility trials on 5 browse species that showed frequent utilization during back-track feeding surveys (*Acer glabrum*, *Amelanchier alnifolia*, *Cornus stolonifera*, *Populus* spp., and *Salix* spp.). Samples for digestibility trials were collected from unbrowsed portions of browsed plants when possible, otherwise portions of nearby shrubs were sampled. Both CAG and 2-year-old material was collected. Samples were chilled in the field and frozen in the lab to prevent respiration and preserve chemical constituents, then ground in a Wiley Mill to pass through a 1 mm screen, redried for 24 hours, and stored in desiccators until analyzed.

Inoculum was obtained from a 2-year-old bull elk provided by the National Bison Range, Moiese, Montana. The animal was hand-fed the 5 test species in approximate proportion to their use on the study area for 2 weeks to assure that rumen microbes were adjusted to the diet. Following the feeding period, the animal was killed and rumen fluid was collected by hand-squeezing the rumen contents into a prewarmed 2-liter thermos. The rumen fluid was immediately transported to the laboratory, strained through cheesecloth to remove ingesta, and measured into digestion chambers. Elapsed time from collection to inoculation was 65 minutes, well within the standard set by Schwartz and Nagy (1972).

The digestion method was adapted from Tilley and Terry (1963). Apparent digestibility was calculated by the formula:

$$\text{IVDMD} = 100 \times \frac{\text{original sample wt.} - \text{final sample wt.} - \text{reagent wt.}}{\text{original sample wt.}}$$

Four replications were run for each age class of each browse species. Analysis of variance was used to test for significant differences at the species and age class levels. Paired sample t-tests were employed to measure differences between individual species and age classes.

The physical condition and health of elk can provide the ultimate assessment of quantity, quality, and availability of forage. Though chances to gather this type of information were limited, I utilized all available opportunities to observe live elk and examine dead ones for evidence of malnutrition and/or parasites and diseases.

CHAPTER IV

RESULTS

Population Description and Dynamics

Although the sex ratio of calves was assumed to be 1:1 (Johnson 1951, Kittams 1953, Peek et al. 1967), the older cohorts differed substantially from equality (Table 1). Including yearlings (spikes), the 3-year average winter sex ratio was 23♂:100♀. Branch-antlered bulls averaged 14 per 100 cows over the 3-year period. No spikes and only 8 branch-antlered bulls were seen on the winter range in 1979, substantially fewer than in previous years.

Calf:cow ratios from FWP winter aerial trend counts showed downward trend overall since 1936 (Cox-Stuart test for trend, P = 0.02), but no significant trend (P = 0.23) since 1969 (Fig. 2). Average ratio for the 11-year period of no trend (22 calves:100 cows) was considered as the minimum likely estimate of recruitment and was used to predict population trend. Winter classifications recorded in this study and by McDonald (In prep.), and as reported in hunter interviews, ranged from 27 to 48 calves:100 cows. Total animals classified equalled 954, and the average calf:cow ratio was 37:100 when weighted by sample size. This figure was used as an estimate of maximum likely recruitment.

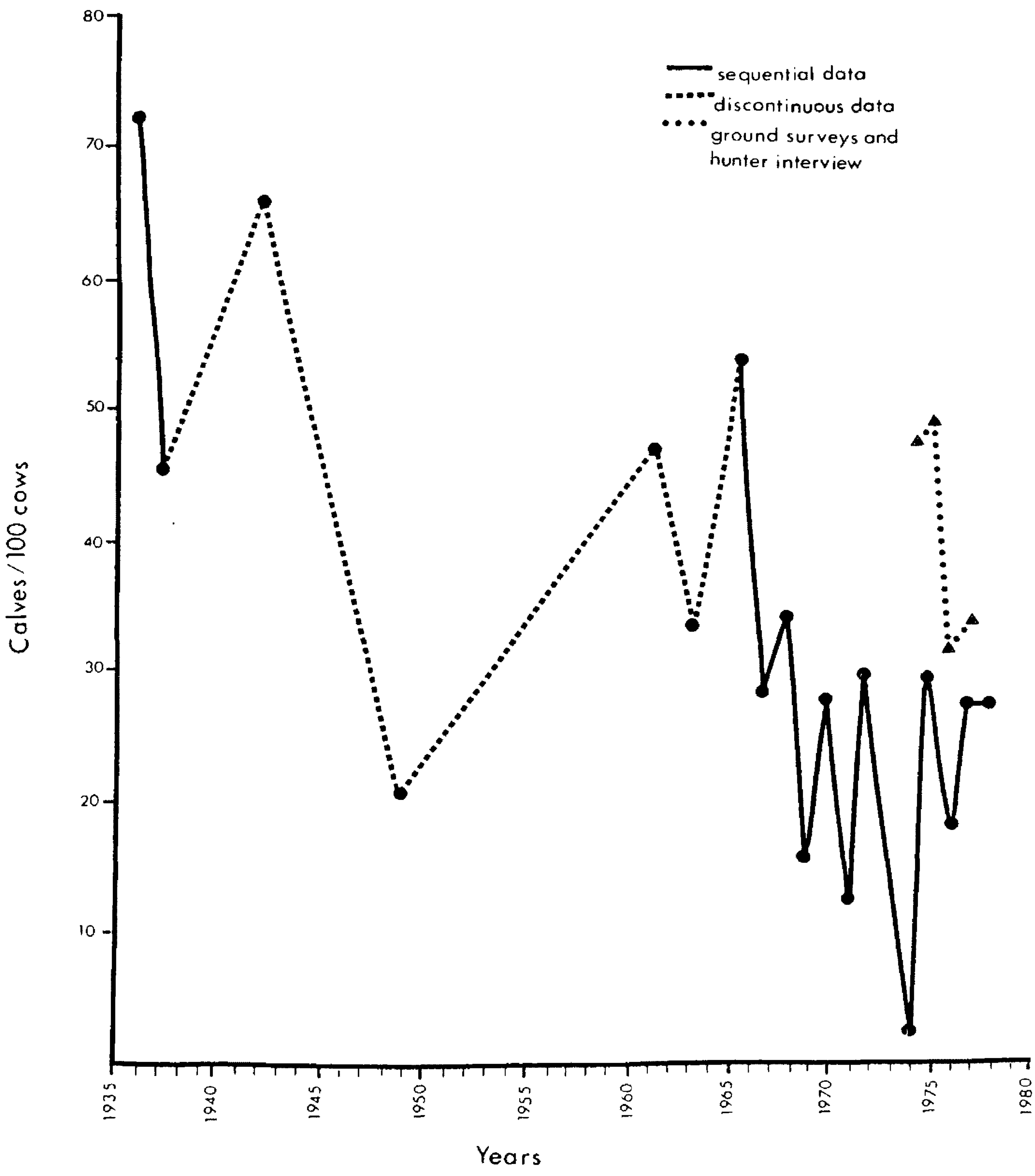
Table 1. Herd structure during the winters of 1977 through 1980, as determined by ground surveys.

Source	Year	Calves	Cows	Spikes	BAB[a]	Total	BAB:100♀	♂:100♀	Ca:100♀
McDonald (In prep.)	1977	35	74	7	23	139	31	41	47
	1978	154	321	47	16	538	5	20	48
This study	1979	48	137	0	8	193	6	6	35
	1980[b]	9	24	3	3	39	13	25	37
Total		246	556	57	50	909	9	19	44

[a]BAB = Branch-antlered Bull.

[b]Only 1 survey was conducted in 1980.

Fig. 2. Long-term survival trend from FWP aerial surveys and the 4-year production trend from winter range ground surveys and hunter interviews. Long-term data from Region 1 Files, Montana FWP Office, Kalispell, Montana.



McDonald (In prep.) reported no natural mortality during the winter of 1977, but 4 cases were observed in 1978 (Table 2). Although no carcasses could be located during the winter of 1979, relatively fresh jaws of 3 calves and 1 13.5-year-old elk were recovered after spring snowmelt and attributed to natural mortality (Tables 2 and 3). In addition, the carcass of a 5.5-year-old cow, radio marked 2 years earlier, was found in an avalanche chute by a packer during the 1979 hunting season.

Table 2. Distribution of mortality by cause and year.

	Cause of death					
	Hunting		Winter kill		Predation	
	1978	1979	1978	1979	1978	1979
Observed	25	39	3	4	1	0
Reported	3	24	0	1	0	0
Total	28	63	3	5	1	0
% of total	28	63	3	5	1	0
	91		8		1	

The mean ages of hunter kills and natural mortalities were 3.4 and 5.5 years. While natural mortality occurred primarily in the extreme age classes, most hunting mortality fell on those age classes least susceptible to natural mortality (Table 3). Hunting accounted for 88% and 93% of the known mortality in 1978 and 1979 (Table 2).

Table 3. Age distribution of the observed mortality.

		Age (in years)														
Year	Cause of death	.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	Average
1978	Hunting	5	6	1	3	3	0	0	1	2	0	0	0	0	0	
	Natural causes	0	0	0	1	0	0	0	1	0	0	0	0	1	0	
1979	Hunting	4	8	4	4	8	1	0	1	1	0	1	0	1	0	
	Natural causes	3	0	0	0	0	1	0	0	0	0	0	0	0	1	
Total	Hunting (N = 54)	9	14	5	7	11	1	0	2	3	0	1	0	1	0	3.35
	Natural causes (N = 8)	3	0	0	1	0	1	0	1	0	0	0	0	1	1	5.50

Age structure of the hunted sample used in the construction of survivorship (l_x) life tables is summarized in Table 4. Probably because of hunter selectivity, calves were clearly underrepresented in the sample. An estimate based on observed calf:cow ratios was believed to be adequate for use in regression smoothing of the age distribution (Fig. 3).

Predicted population trends at several possible levels of recruitment, survivorship, and previous trend are summarized in Table 5. At the maximum estimate of 37 calves:100 cows ($m_x = 0.36$), and assuming a previously stable age structure, the predicted long-term rate of population change was -0.3% per year ($\lambda_L = 0.997$) and the short-term rate was -0.4% per year ($\lambda_S = 0.996$).

Restructuring survivorship (l_x) for a prior decline of 0.3% per year decreased λ_L to 0.993 (-0.7%/year) and λ_S to 0.992 (-0.8%/year). By assuming a previous population dynamic of $\lambda = 0.90$ (-10.0%/year), λ_L became 0.878 (-12.1%/year). Positive population growth was predicted only under the assumption of a prior population trend of +10% per year. However, the rate of increase slowed 1% per year over the long term ($\lambda_L = 1.09$), but remained constant over the next year ($\lambda_S = 1.10$).

At the minimum likely calf:cow ratio of 22:100, predicted trends were about 8% below the assumed prior trend. This means that if the population was assumed to have been stable at the time of

Table 4. Age distribution of hunter kills, natural mortality, and the approximate age structure of the population as determined by regression analysis.

Age	Hunter sample	Age structure from regression	Age structure scaled to 1000 calves	Natural mortality sample	Age structure from hunter and natural mortality samples combined
.5	9	10.950	1000	3	12
1.5	14	9.024	824	0	14
2.5	5	7.437	679	0	5
3.5	7	6.128	560	1	8
4.5	11	5.050	461	0	11
5.5	1	4.162	380	1	2
6.5	0	3.430	313	0	0
7.5	2	2.827	258	1	3
8.5	3	2.330	213	0	3
9.5	0	1.920	175	0	0
10.5	1	1.582	144	0	1
11.5	0	1.303	119	0	0
12.5	1	1.074	98	1	2
13.5	0	0.0	0	1	1
Sample size	54			8	62

Fig. 3. Regression used in smoothing the age distribution of hunter kills to derive the approximate age structure of the population.

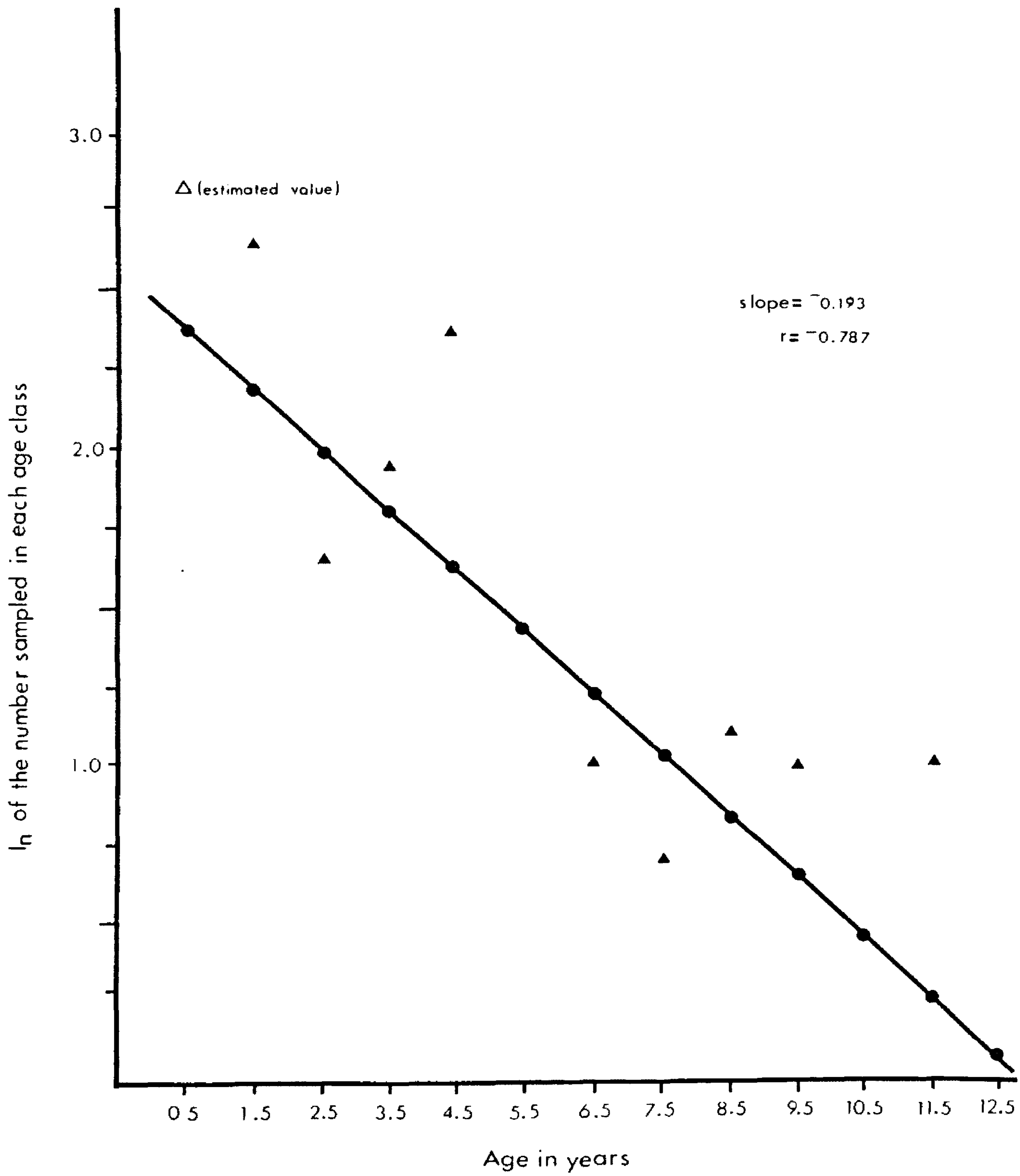


Table 5. Predicted population trends at 4 possible levels of recruitment, with age distribution restructured for 4 levels of assumed λ[a].

Recruitment			Assumed prior trend		Predicted annual trend			
					Long-term		Short-term	
Repro. ♀:♀	Young:♀	m_x	λ	% chg.	λ_L	% chg.	λ_S	% chg.
(Maximum likely)								
52:100	37:100	0.36	1.000	±0.0	0.997	-0.3	0.996	-0.4
			0.997	-0.3	0.993	-0.7	0.992	-0.8
			0.900	-10.0	0.891	-10.9	0.878	-12.1
			1.100	+10.0	1.090	+9.0	1.100	+10.0
(Minimum likely)								
52:100	22:100	0.22	1.000	±0.0	0.918	-8.2	0.923	-7.7
			0.920	-8.0	0.835	-16.5	0.844	-15.6
			0.900	-10.0	0.813	-18.7	0.823	-17.7
			1.100	+10.0	1.020	+2.0	1.010	+1.0
(Moderate)								
52:100	28:100	0.27	1.000	±0.0	0.949	-5.1	0.949	-5.1
			0.950	-5.0	0.898	-10.2	0.897	-10.3
			0.900	-10.0	0.844	-15.6	0.893	-10.7
			1.100	+10.0	1.050	+5.0	1.040	+4.0
(Maximum possible)								
52:100	52:100	0.50	1.000	±0.0	1.050	+5.0	1.070	+7.0

[a]Assumptions inherent in all calculations: mortality rates are constant, calf sex ratio = 1:1, and $l_x = S_x \lambda^x$.

sampling, it may be expected to decline at about 8% per year in the future. Only the unlikely assumption that prior trend was +10% resulted in the prediction of a positive future trend.

At the moderate level of 28 calves:100 cows, a population that was presumed stable at the time of sampling could be expected to decline at about 5% annually in the future. If the population had been increasing at 10% annually, that increase would be expected to slow to about 5%.

An elk population reproducing at its maximum potential (m_x = 0.50), and experiencing mortality comparable to that of the Middle Fork herd, could be expected to increase at 5 to 7% yearly from a stable condition (Table 5).

Hunter Distribution and Elk Response

Throughout this study, the general elk season opened in late October and ran through Thanksgiving weekend. In both 1978 and 1979, snow fell the night before opening day of the general elk season and hunting conditions were excellent. Periodic snows and thaws caused variable hunting conditions throughout the first half of both seasons. Snow began to accumulate during the second half of both seasons, making most of the study area inaccessible during the last week.

Hunting effort was highest on opening day during both 1978 and 1979, and about half as many hunters were in the field the second day of each season (Fig. 4). In 1978, hunting effort fluctuated during the remainder of the opening week, whereas in 1979 it continued to decrease. Hunting effort stabilized at a relatively low level for the remainder of both seasons except for moderate increases on weekends. About 50% of total hunting effort was expended in the first 4 days of the 1978 season and the first 5 days in 1979; 20 and 23 more days were required to reach the 95% level in 1978 and 1979, respectively.

Although hunting effort was similarly distributed in 1978 and 1979, the distribution of kills was markedly different (Figs. 4 and 5). No kills were reported for opening day in 1978, whereas 46% of the total kill occurred on opening day in 1979. The tally of successful hunters increased slowly in 1978 so that the 92% level of total kill was not reached until the 15th day of the season. In 1979, hunter success declined after opening day, but remained high enough that 90% of total kill had been reported within 9 days.

Accessibility had an impact on hunter density that was extreme and quite consistent between years. Hunting pressure increased exponentially as accessibility increased (Fig. 6). As one might expect, apparent elk density was lowest in Easy access areas and increased substantially through Difficult access areas (Fig. 7). Backcountry areas, however, exhibited lower apparent elk densities than any except Easy access areas.

Apparent elk density was higheat at about 1.5 hunter days per

Fig. 4. Distribution of hunting effort in 1978 and 1979.

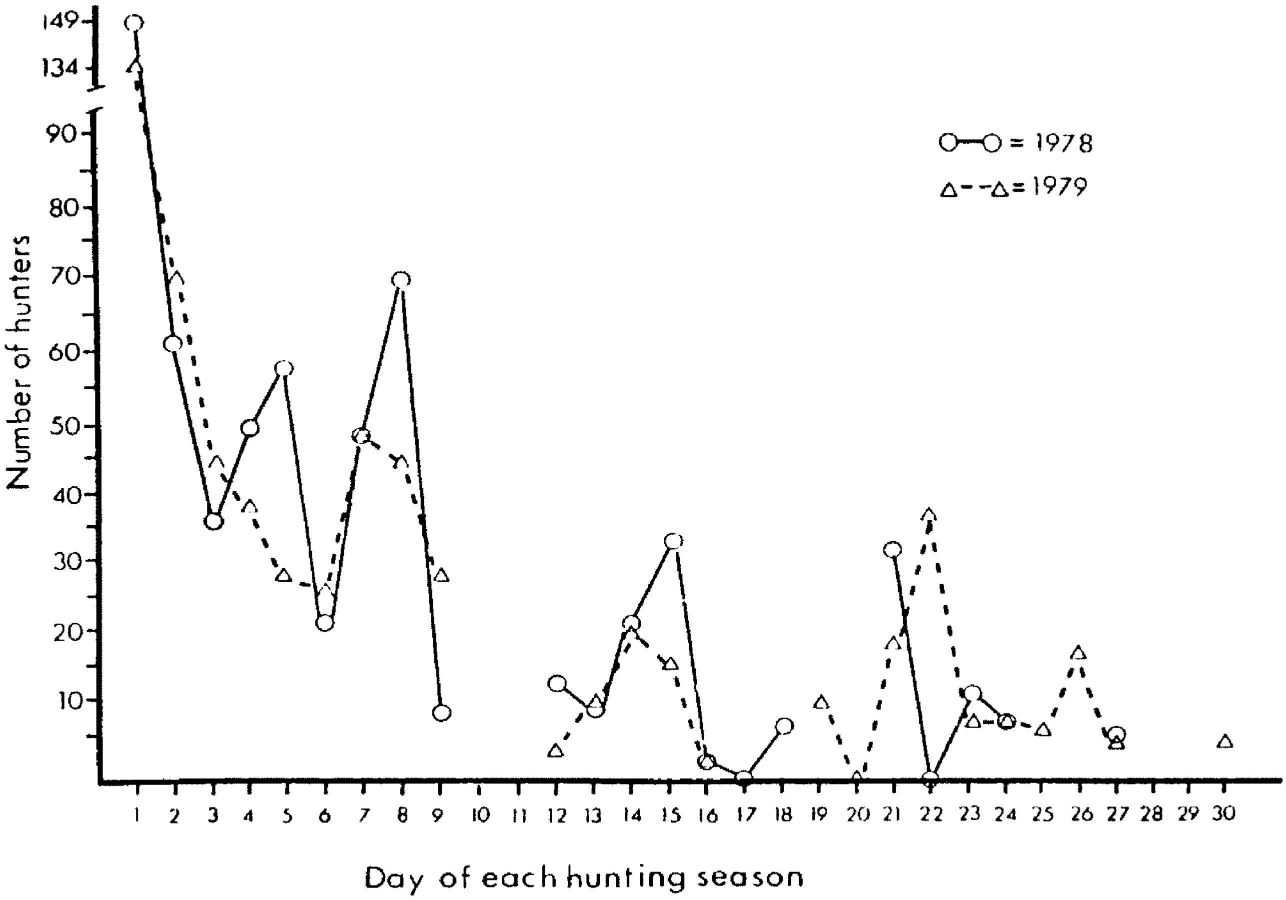


Fig. 5. Distribution of hunter kills in 1978 and 1979.

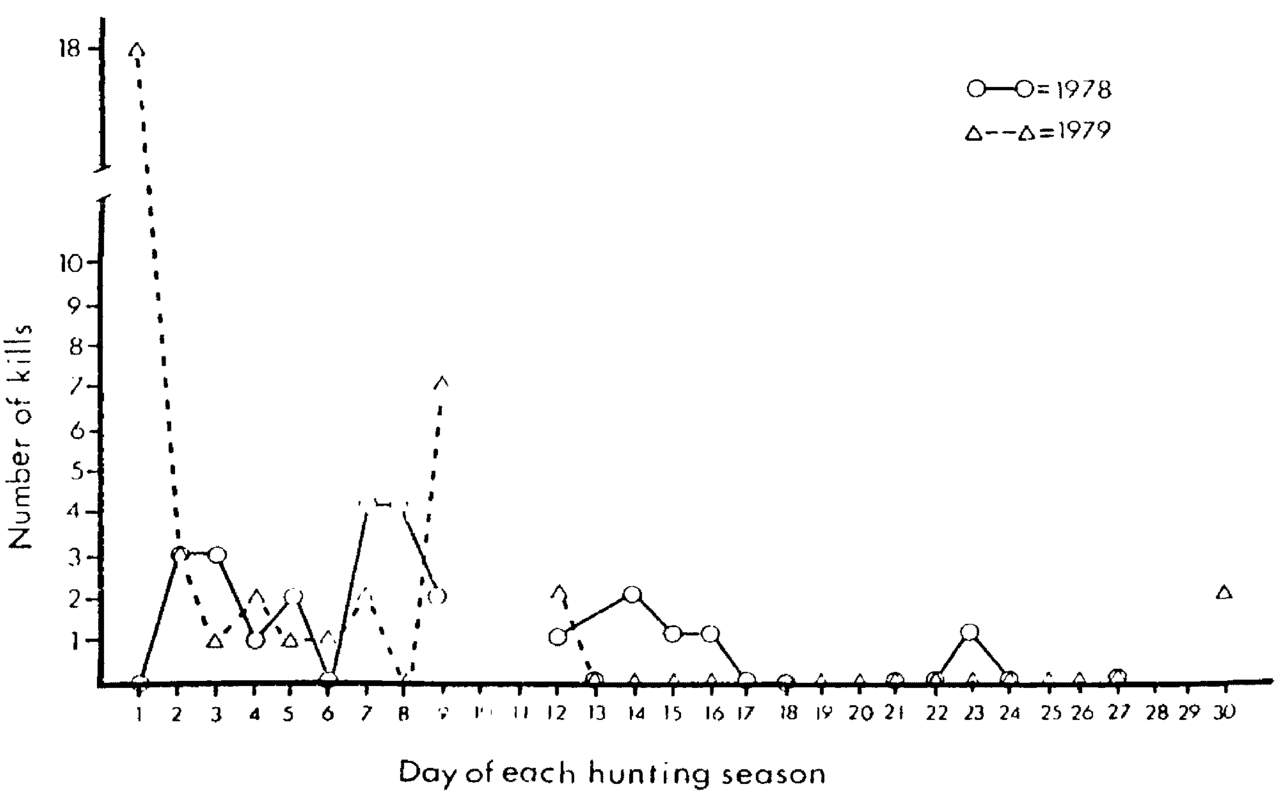


Fig. 6. The relationship between hunter density and accessibility.

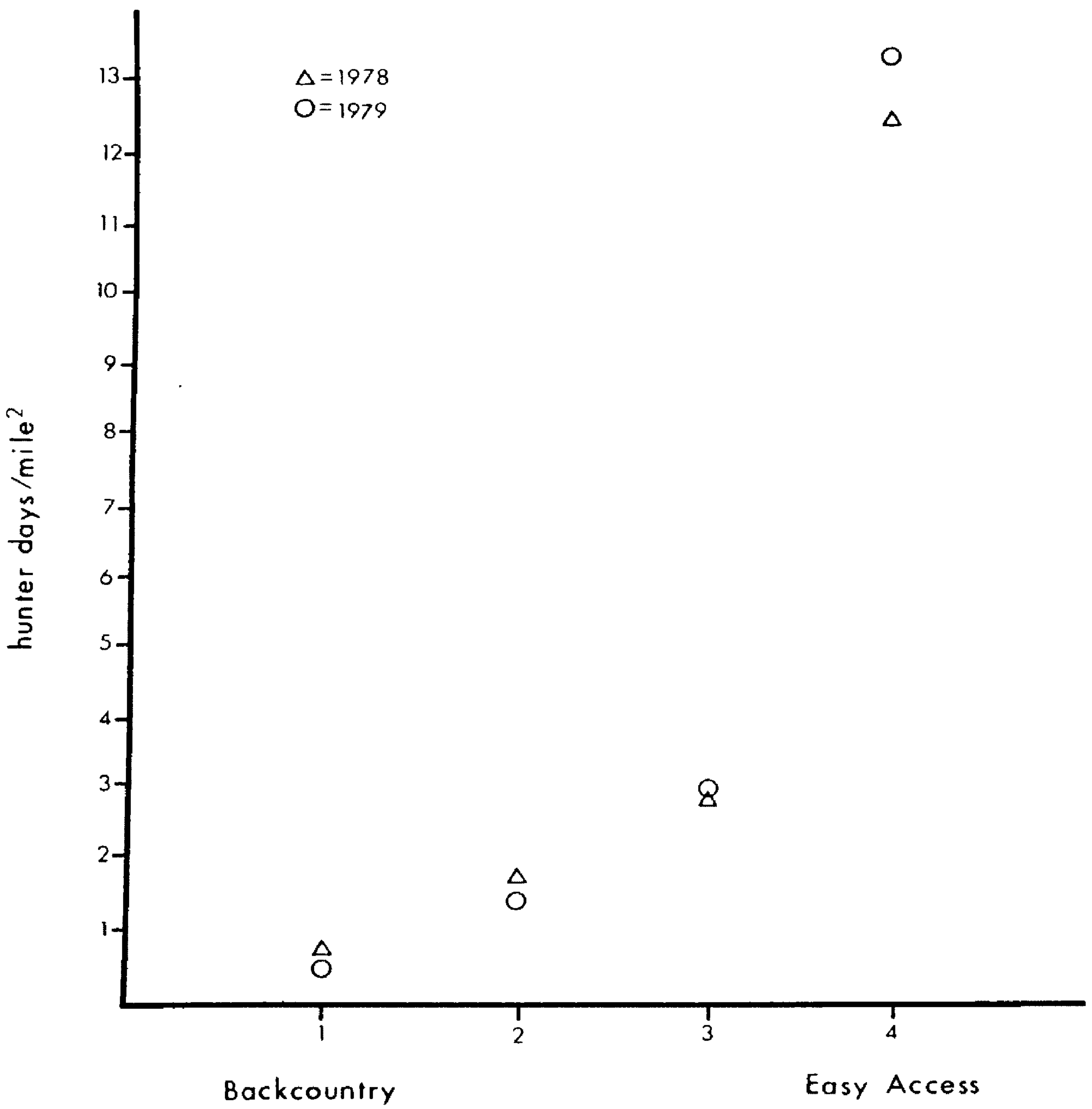
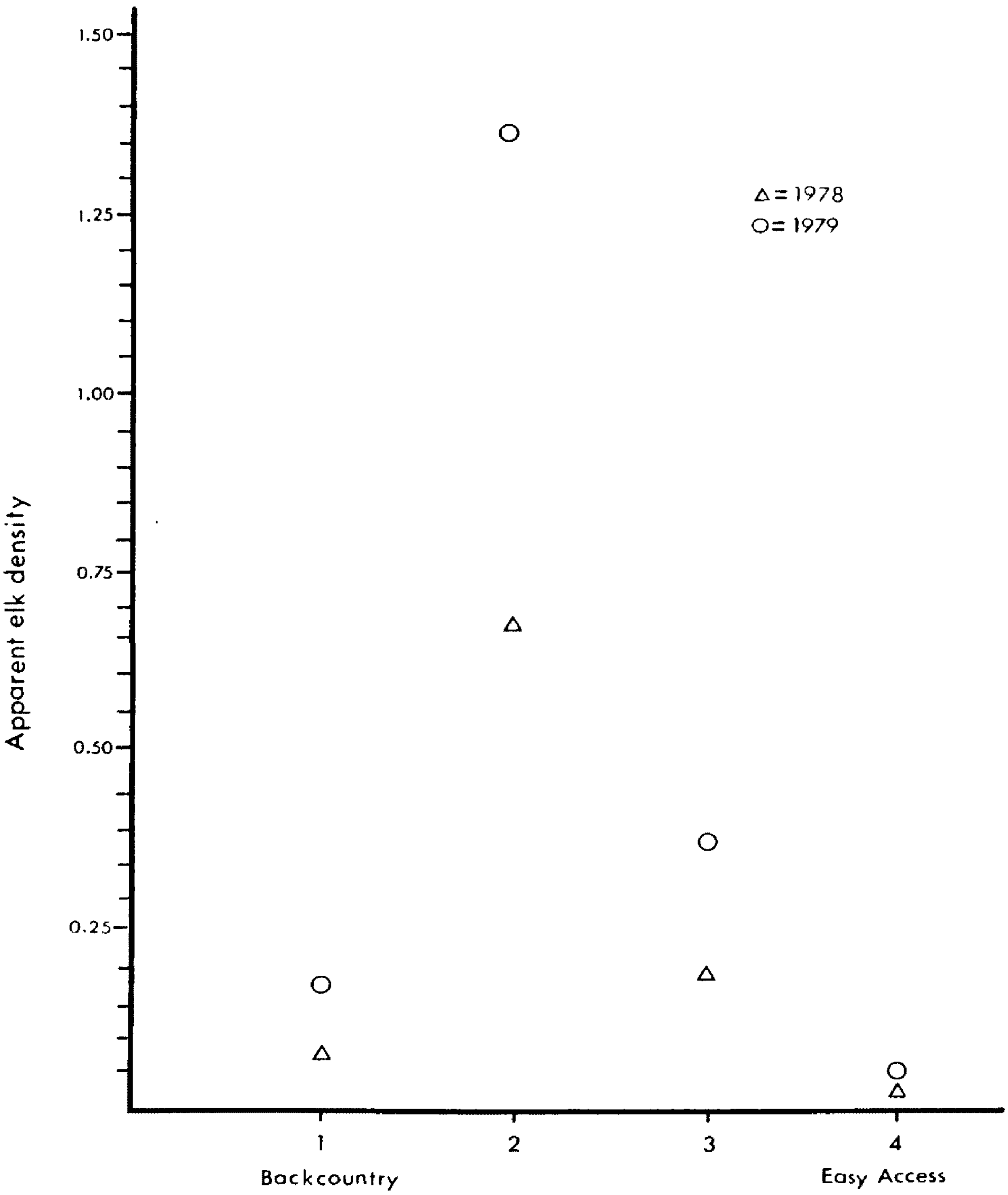


Fig. 7. The relationship between apparent elk density and accessibility.



square mile and declined sharply as hunter density increased (Fig. 8). Although hunter density was low in Backcountry, apparent elk density was also quite low.

The relationship between apparent elk density and hunter success appeared to be direct and linear, although at least in 1978, Backcountry hunters were somewhat more successful than other hunters at similar elk densities (Fig. 9). The slope of the regression line, however, was exceedingly low (b = 0.036).

Elk were consistently more susceptible to hunting in Easy access areas than in any other (Fig. 10). In 1978, Backcountry areas had the second highest level of susceptibility, but those areas were third in 1979. Differences in variability resulted in Backcountry areas having the highest overall susceptibility when the weighted average from both years' data was determined. Difficult access areas consistently showed the lowest susceptibility.

The median distance of kills from open roads was 1.4 miles (2.2 km) and 1.2 miles (1.9 km) in 1978 and 1979, respectively (Table 6). In 1978, approximately 40% of all kills were less than a mile (1.6 km) from any road, and in 1979 44% were within this range. In 1979, 94% were less than 2.5 miles (4.0 km) from a road, whereas 11 miles (17.6 km) were required to account for 87% of all kills in 1978.

Fig. 8. The relationship between apparent elk density and hunter density.

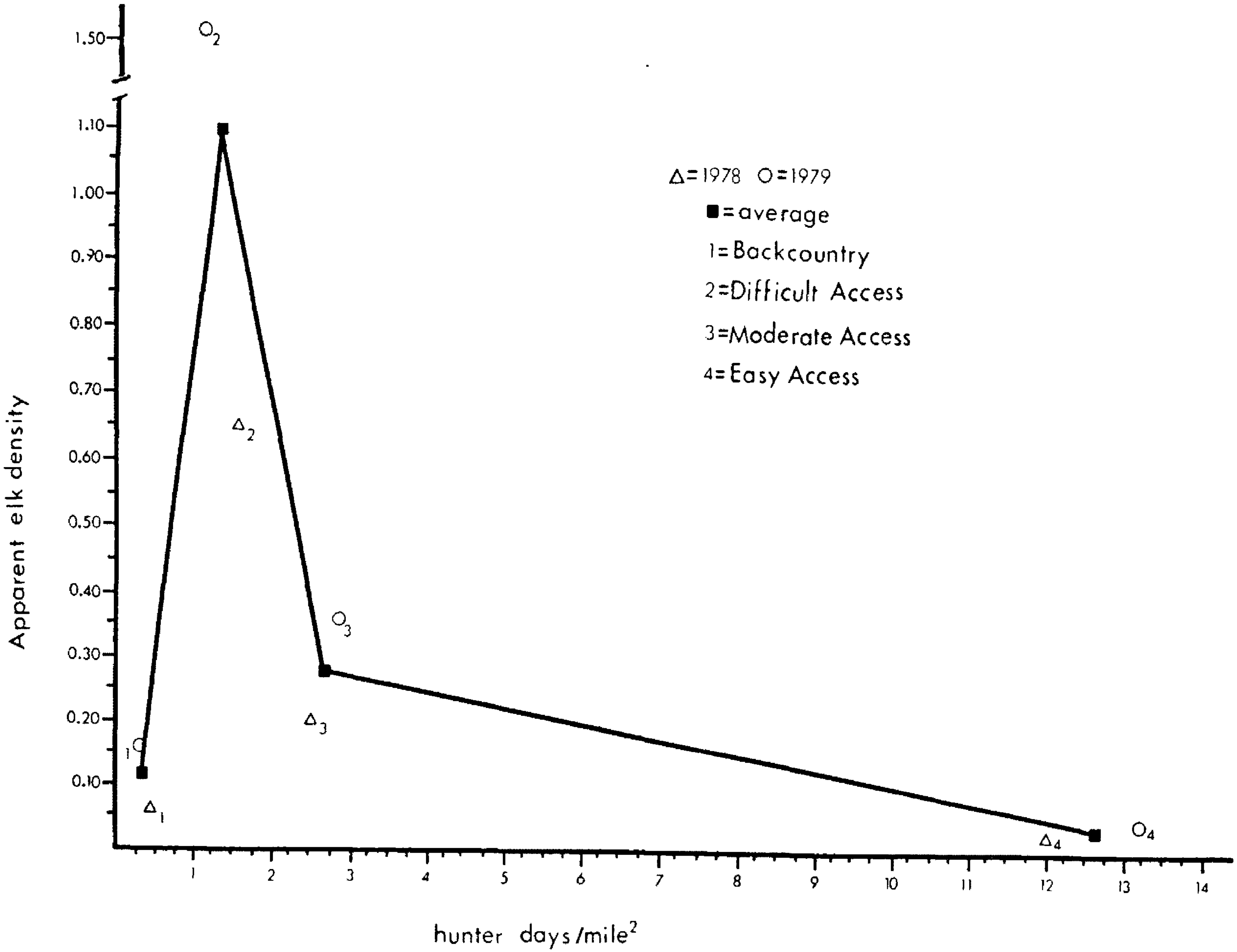


Fig. 9. The relationship between hunter success and apparent elk density.

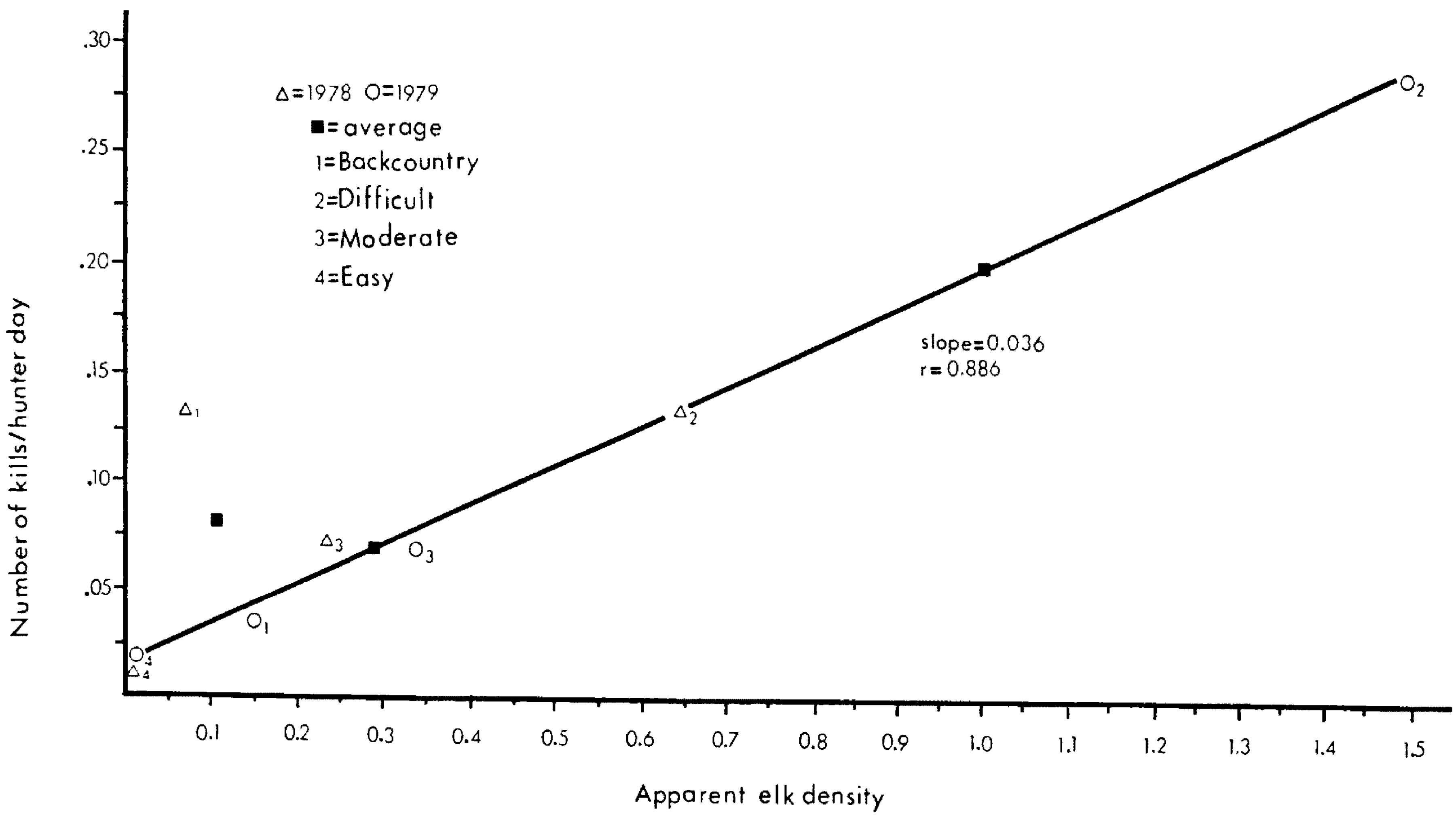


Fig. 10. Susceptibility of elk to hunting at each level of accessibility.

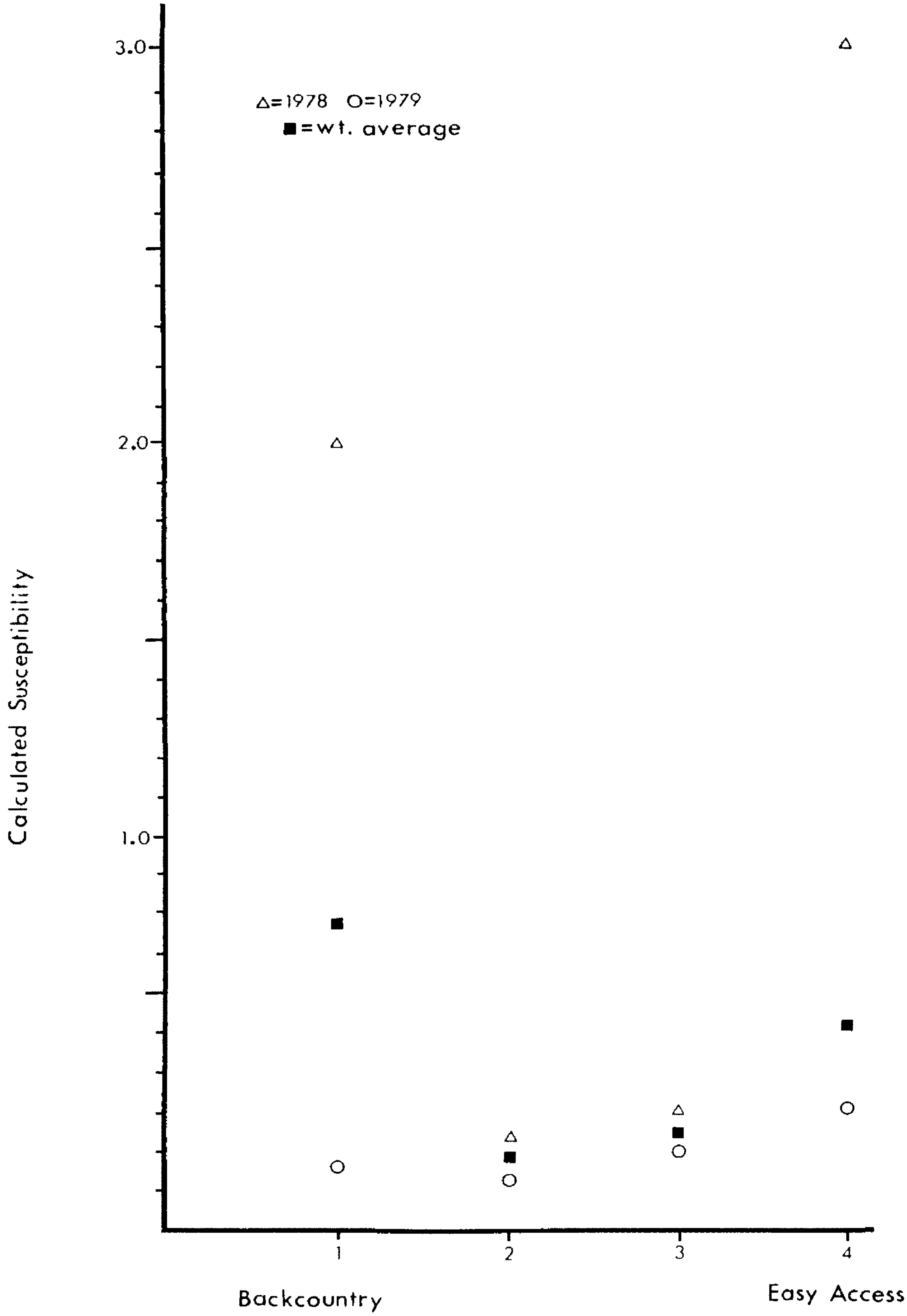


Table 6. Distribution of elk kills relative to distance from trails and open roads.

Distance (miles)	Trails			Roads		
	1978	1979	Total	1978	1979	Total
<0.25	8	4	12	7	4	11
0.26-0.50	9	1	10	2	4	6
0.51-0.75	4	4	8	0	3	3
0.76-1.00	3	9	12	3	0	3
1.01-1.25	3	3	6	0	4	4
1.26-1.50	4	0	4	3	2	5
1.51-2.00				0	6	6
2.01-3.00				2	7	9
3.01-4.00				5	1	6
4.01-5.00				4	1	5
5.01-6.00				1	0	1
>6.00				5	0	5

Food Habits and Diet Quality

Winter

Although the winter was more moderate in 1978 than in 1979, there was little difference in forage selection. Conifers (primarily *Abies* and *Pseudotsuga*) were the predominant forage class both years, comprising 66.0% and 60.0% r.f.o. in 1978 and 1979, respectively (Table 7). Shrub utilization increased from 26.0% in 1978 to 32.0% in 1979. Important shrubs identified by fecal analysis include *Berberis*, *Salix*, and *Physocarpus* which ranked 3, 4, and 7, respectively (Table 8). Although not reported by fecal analysis, several other shrub species were heavily utilized. *Acer glabrum*, *Amelanchier alnifolia*, and *Cornus stolonifera* were present and heavily browsed on 5 or more of the 10 back-track surveys (Fig. 11). *Populus tremuloides*, *Betula* spp., *Shepherdia canadensis*, *Rubus parviflorum* and an unidentified forb were all utilized relatively heavily, but occurrence was quite low. A total of 6 taxa, including some common and heavily used species, were identified in back-track surveys but not in winter fecal samples. None of the species showed more than 5% of the plants in the <50%-CAG-used category, and most had over 70% of the plants showing consumption of 2-year-old and older growth (Table 9).

When these same species were examined after snowmelt, very heavy and persistent use was evident. The 13 range trend survey

Table 7. Elk forages identified by fecal analysis, percent relative frequency of occurrence, and season of use.

Forage class	Food item	Season[a]	% Relative frequency of occurrence 1978	1979	Two-year average	Change between years
Graminoids	Agropyron (wheatgrass)	winter	3.8	0.5	2.1	-3.3
		spring	10.3	6.5	7.4	-3.8
		early summer	19.5	0.0	9.7	-19.5
		late summer	3.2	0.0	1.6	-3.2
		early autumn	1.3	0.0	0.6	-1.3
	Bromus (brome)	early autumn	0.0	0.3	0.1	+0.3
	Calamagrostis	winter	0.0	0.9	0.5	+0.9
		late autumn	0.2	0.0	0.1	-0.2
	Carex (sedge)	winter	2.8	4.9	3.8	+2.1
		spring	11.0	6.5	8.8	-4.5
		early summer	8.2	10.5	9.4	+2.3
		late summer	17.4	0.9	9.2	-16.5
		early autumn	0.6	2.8	1.7	+2.2
		late autumn	8.4	47.5	27.9	+39.1
	Festuca (fescue)	spring	0.4	0.6	0.5	+0.2
		early summer	0.0	2.0	1.0	+2.0
		early autumn	0.0	0.7	0.4	+0.7
		late autumn	0.0	0.6	0.3	+0.6
	Koeleria (Junegrass)	spring	0.6	0.6	0.6	-0.0
	Poa (bluegrass)	winter	1.0	0.7	0.9	-0.3
		spring	15.7	2.5	9.1	-13.2
		early summer	3.1	6.4	4.8	+3.3
		late summer	3.2	0.0	1.6	-3.2
		early autumn	0.6	0.4	0.5	-0.2
		late autumn	1.6	1.2	1.4	-0.4
Forbs	Antennaria or Cirsium (pussytoes or thistle)	spring	3.8	0.6	2.2	-3.2
		early autumn	0.0	18.2	9.1	+18.2
	Astragalus (locoweed)	spring	0.0	7.9	4.0	+7.9
	Composite (daisy, sunflower, etc.)	winter	0.2	0.0	0.1	-0.2
		spring	0.5	0.0	0.3	-0.5
		early summer	0.5	5.4	3.0	+4.9
		late summer	5.2	4.3	4.7	-0.9
		early autumn	2.6	5.8	4.0	+3.2
		late autumn	0.4	1.2	0.8	+0.8
	Cryptantha (forget-me-not)	spring	0.5	0.0	0.3	-0.5
		early summer	0.5	0.0	0.3	-0.5
	Descurainia (tansy mustard)	spring	0.2	0.0	0.1	-0.2
	Epilobium (fireweed)	early autumn	0.6	0.4	0.5	-0.2

Table 7. (continued)

Forage class	Food item	Season[a]	% Relative frequency of occurrence 1978	1979	Two-year average	Change between years
Forbs (cont.)	*Equisetum* (horsetails)	spring	0.2	0.0	0.1	-0.2
		early summer	0.5	0.0	0.3	-0.5
	fern	early summer	0.0	0.7	0.3	+0.7
	Geranium (geranium)	early summer	0.0	2.0	1.0	+2.0
	Gutierrezia (snakeweed)	spring	0.2	0.0	0.1	-0.2
	Lupinus (lupine)	spring	25.6	20.4	23.0	-5.2
		early summer	28.4	15.3	21.8	-13.1
		late summer	0.6	6.1	3.4	+5.5
		early autumn	0.0	30.6	15.3	+30.6
		late autumn	2.1	4.2	3.1	+2.1
	Melilotus or *Medicago* (sweetclover or alfalfa)	spring	0.7	0.0	0.3	-0.7
		early summer	0.5	4.7	2.6	+4.2
	Potentilla (cinquefoil)	winter	0.0	0.5	0.2	+0.5
		spring	3.2	13.1	8.1	+9.9
		early summer	6.5	11.3	8.9	+4.8
		late summer	0.0	0.4	0.2	+0.4
		early autumn	0.0	2.3	1.1	+2.3
		late autumn	1.4	0.0	0.7	-1.4
	Taraxacum (dandelion)	spring	12.4	14.6	13.5	+2.2
	Unknown forb	spring	0.6	0.6	0.6	+0.0
		early summer	0.5	0.7	0.6	+0.2
		late autumn	0.6	0.0	0.3	-0.6
Shrubs & half-shrubs	*Acer* (mountain maple)	spring	0.0	7.2	3.6	+7.2
		early summer	0.0	9.0	4.5	+9.0
		late summer	0.0	0.4	0.2	+0.4
		early autumn	0.0	0.3	0.1	+0.3
	Amelanchier (serviceberry)	spring	0.0	1.9	1.0	+1.9
		early summer	0.0	6.4	3.2	+6.4
	Atriplex (saltbush)	winter	0.3	0.0	0.1	-0.3
	Berberis (Oregon grape)	winter	9.1	20.8	15.0	+11.7
		spring	7.3	1.3	4.3	-6.0
		early summer	1.0	0.0	0.5	-1.0
		late summer	1.9	0.4	1.2	-1.5
		early autumn	2.6	2.1	2.3	-0.5
		late autumn	31.3	19.0	25.2	-12.3
	Ceanothus (buck brush)	winter	4.1	1.9	3.0	-2.2
		spring	0.4	0.0	0.2	-0.4
		early summer	0.0	1.3	0.7	+1.3
		early autumn	0.0	0.3	0.1	+0.3

Table 7. (continued)

Forage class	Food item	Season[a]	% Relative frequency of occurrence 1978	1979	Two-year average	Change between years
Shrubs & half-shrubs (cont.)	Cornus (dogwood)	spring	0.0	0.6	0.3	+0.6
		early summer	0.0	2.6	1.3	+2.6
		early autumn	0.0	0.9	0.4	+0.9
		late autumn	0.0	1.8	0.9	+1.8
	Crataegus (hawthorne)	winter	0.0	2.4	1.2	+2.4
		spring	0.0	6.1	3.1	+6.1
		late autumn	0.2	0.0	0.1	-0.2
	Juniperus (juniper)	winter	1.5	0.5	1.0	-1.0
		early autumn	19.9	0.0	10.0	-19.9
	Physocarpos (ninebark)	winter	1.7	0.2	1.0	-1.5
		spring	1.7	0.0	1.0	-1.7
		early summer	6.5	4.0	5.2	-2.5
		late summer	3.2	26.9	15.0	+23.7
		early autumn	6.3	12.5	9.4	+6.2
		late autumn	0.0	2.4	1.2	+2.4
	Ribes (currants)	early summer	0.0	0.7	0.3	+0.7
		early autumn	1.3	0.0	0.6	-1.3
		late autumn	1.2	0.0	0.6	-1.2
	Salix (willow)	winter	6.4	3.6	5.0	-2.8
		spring	1.5	0.6	1.0	-0.9
		early summer	2.1	10.5	6.3	+8.4
		late summer	58.3	37.8	48.1	-20.5
		early autumn	35.6	12.7	24.2	-22.9
		late autumn	43.3	18.2	30.8	-25.1
	Shepherdia (buffalo-berry)	winter	3.2	2.1	2.6	-1.1
		spring	0.7	0.6	0.7	-0.1
		early summer	18.0	2.6	10.4	-15.4
		late summer	5.2	13.7	9.4	+8.5
		early autumn	12.6	5.3	8.9	-7.3
	Symphoricarpos (snowberry)	winter	0.0	0.5	0.2	+0.5
		spring	0.0	2.5	1.3	+2.5
		late summer	0.6	0.0	0.3	-0.6
		early autumn	0.6	0.3	0.5	-0.3
Trees	Abies (fir)	winter	33.6	37.0	35.3	+3.4
		spring	2.3	0.0	1.1	-2.3
		early summer	3.7	4.0	3.8	+0.3
		late summer	1.3	1.8	1.5	+0.5
		early autumn	3.9	1.7	2.8	-2.2
		late autumn	0.6	2.4	1.5	+1.8
	Picea (spruce)	winter	0.0	0.2	0.1	+0.2
		spring	0.0	3.2	1.6	+3.2
		late summer	0.0	0.4	0.2	+0.4
	Pinus (pine)	winter	2.5	0.0	1.2	-2.5
		spring	0.0	2.5	1.3	+2.5
		early autumn	0.6	0.0	0.3	-0.6
		late autumn	0.8	1.2	1.0	+0.4
	Populus (aspen or cottonwood)	late summer	0.0	3.6	1.8	+3.6
		early autumn	1.3	2.1	1.7	+0.8
		late autumn	0.6	0.6	0.6	-0.0

Table 7. (continued)

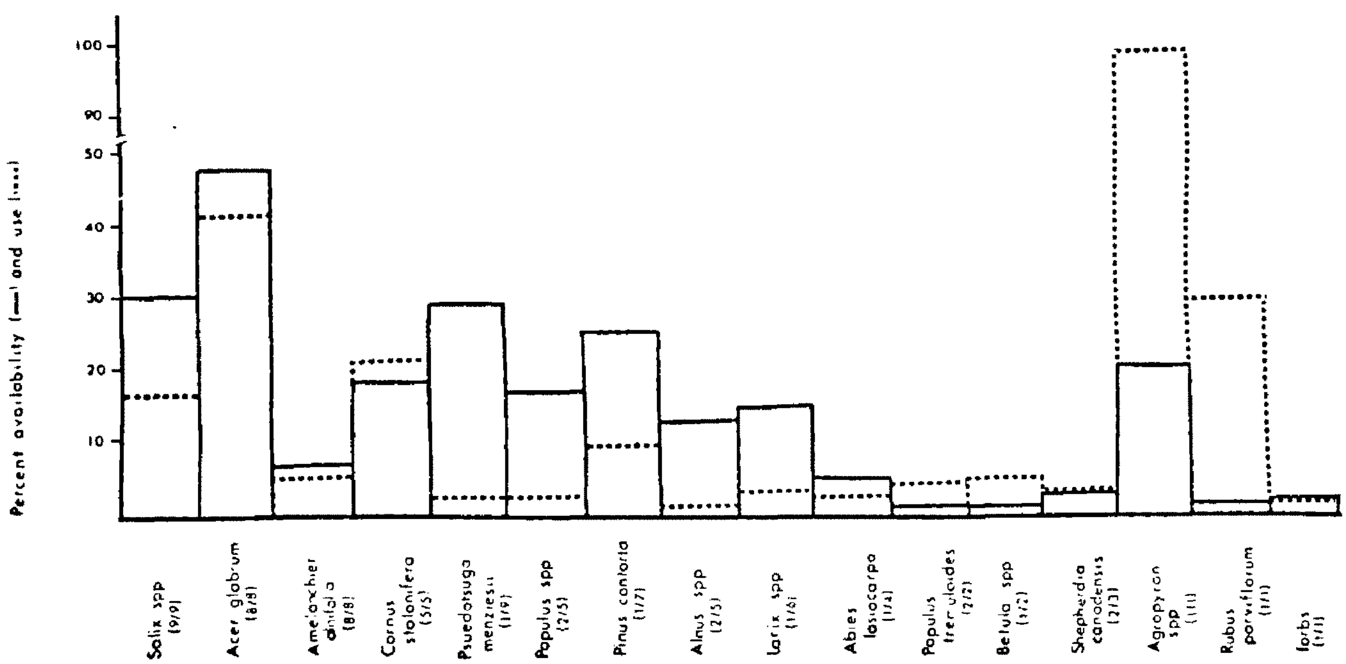
Forage class	Food item	Season[a]	% Relative frequency of occurrence 1978	1979	Two-year average	Change between years
Trees (cont.)	Pseudotsuga (Douglas-fir)	winter	29.6	22.7	26.2	-6.9
		spring	0.0	0.6	0.3	+0.6
	Taxus (yew)	winter	0.0	0.2	0.1	+0.2
	Thuja (cedar)	winter	0.3	0.2	0.2	-0.1
Other	moss	early summer	0.5	0.0	0.3	-0.5
		late autumn	4.0	0.0	2.0	-4.0
	seed	late summer	0.0	3.2	1.6	+3.2
		early autumn	10.0	0.6	5.1	-9.4
		late autumn	1.2	0.0	0.6	-1.2
Graminoids	all	winter	7.6	7.0	7.3	-0.6
		spring	37.9	14.8	26.4	-23.1
		early summer	30.8	18.9	24.9	-11.9
		late summer	23.8	0.9	12.3	-22.9
		early autumn	2.6	4.2	3.4	+1.6
		late autumn	10.0	49.2	29.6	+39.2
Forbs	all	winter	0.2	0.5	0.3	+0.3
		spring	48.0	57.3	52.7	+9.3
		early summer	37.4	39.9	38.7	+2.5
		late summer	5.8	10.8	8.3	+5.0
		early autumn	3.2	56.8	30.0	+53.6
		late autumn	4.5	5.4	4.9	+0.9
Shrubs & half-shrubs	all	winter	26.2	32.1	29.2	+5.9
		spring	11.5	20.9	16.2	+9.4
		early summer	27.6	34.5	31.1	+6.9
		late summer	69.2	79.3	74.2	+10.1
		early autumn	78.8	34.4	56.6	-44.4
		late autumn	76.1	41.3	58.7	-34.8
Trees	all	winter	66.0	60.4	63.2	-5.6
		spring	2.3	6.3	4.3	+4.0
		early summer	3.7	4.0	3.8	+0.3
		late summer	1.3	5.9	3.6	+4.6
		early autumn	5.8	3.8	4.8	-2.0
		late autumn	2.0	4.1	3.1	+2.1
Other	all	early summer	0.5	0.0	0.3	-0.5
		late summer	0.0	3.2	1.6	+3.2
		early autumn	10.0	0.7	5.1	-9.3
		late autumn	5.2	0.0	2.6	-5.2

[a]Winter = 1 December to 1 May.
Spring = 1 May to 1 July in 1978 and to 16 June in 1979.
Early summer = 1 July to 1 August in 1978 and 16 June to 1 August in 1979.
Late summer = August.
Early autumn = September in 1978 and 1 September to 25 October in 1979.
Late autumn = 1 October to 1 December in 1978 and 25 October to 1 December in 1979.

Table 8. List of elk forage plants identified by fecal analysis, 1978 and 1979, in decreasing order of average relative frequency of occurrence, the number of total samples each occurred in 17 samples, and the seasonal rank. The year of occurrence is noted when the genus appeared in only 1 year.

Taxa in order of predominance	No. of samples out of 17 each occurred	Rank by season						No. of seasons reported
		Winter	Spring	Early summer	Late summer	Early autumn	Late autumn	
1. Salix	17	4	15	6	1	1	1	6
2. Lupinus	10	--	1	1	6	2	4	5
3. Abies	15	1	13	10	10	10	6	6
4. Berberis	14	3	7	18	11	11	3	6
5. Carex	16	5	4	4	4	12	2	6
6. Pseudotsuga	5	2	22	--	--	--	--	2
7. Physocarpus	12	11	16	7	2	4	8	6
8. Shepherdia	12	7	17	2	3	6	--	5
9. Agropyron	9	8	6	3	9	15	--	5
10. Poa	13	12	3	8	9	16	7	6
11. Potentilla	9	14	5	5	13	14	12	6
12. Antennaria-Cirsium	4	--	11	--	--	5	--	2
13. Taraxacum	3	--	2	--	--	--	--	1
14. Composite	11	16	23	12	5	9	11	6
15. Juniperus	3	11	--	--	--	--	--	1
16. Acer	4	--	9	9	13	21	--	4
17. Seed	5	--	--	--	7	7	13	3
18. Crataegus	3	10	10	--	--	--	17	3
19a. Pinus	5	9	14	--	--	20	9	4
19b. Populus	6	--	--	--	8	13	14	3
20. Moss (1978)	3	--	--	20	--	--	5	2
21. Ceanothus	6	6	25	16	--	21	--	4
22. Amelanchier (1979)	2	--	15	11	--	--	--	2
23. Astragalus (1979)	1	--	8	--	--	--	--	1
24. Cornus (1979)	4	--	22	14	--	18	10	4
25. Melilotus-Medicago	3	--	21	13	--	--	--	2
26. Festuca	7	--	20	15	--	19	16	4
27. Symphoricarpos	5	14	14	--	12	17	--	4
28. Unknown forb	7	--	18	17	--	--	15	3
29. Ribes	3	--	--	19	--	15	13	3
30. Picea	3	15	12	--	13	--	--	3
31. Geranium (1979)	1	--	--	15	--	--	--	1
32. Calamagrostis	2	13	--	--	--	--	17	2
33. Koeleria	3	--	19	--	--	--	--	1
34a. Epilobium	2	--	--	--	--	16	--	1
34b. Cryptantha (1978)	2	--	24	20	--	--	--	2
35a. Equisetum (1978)	2	--	26	20	--	--	--	2
35b. Thuja	2	14	--	--	--	--	--	1
36. Fern (1979)	1	--	--	19	--	--	--	1
37a. Bromus (1979)	1	--	--	--	--	21	--	1
37b. Descurainia (1978)	1	--	26	--	--	--	--	1
37c. Gutierrezia (1978)	1	--	26	--	--	--	--	1
37d. Atriplex (1978)	1	15	--	--	--	--	--	1
37e. Taxus (1979)	1	15	--	--	--	--	--	1
Total 46		21	31	24	16	23	19	

Fig. 11. Site specific availability versus use of forage items as determined by back-track surveys. Availability equals average relative abundance of a species at all sites where that species occurred. Use equals average percent of total utilization (at sites where the species occurred) that was made up by that species. Numbers in parentheses equal (number of sites where a species occurred/number of sites where any use of that species was observed).



routes that intersected known elk feeding sites indicated that most of the plants were heavily hedged (classes 3 and 6), decadent-dead (class 8), or unavailable (class 7). These classes accounted for 98% of all Acer glabrum sampled, 91% of Amelanchier alnifolia, 85% of Cornus stolonifera, and 100% of Salix spp. Comparable values from the 6 survey routes that did not intersect known feeding sites were Acer glabrum, 82%; Amelanchier alnifolia, 92%; Cornus stolonifera, 75%; and Salix spp., 14%. Most instances of use observed during all surveys involved consumption of more than the current year's production. In vitro digestibilities for the 5 species most frequently encountered during back-track surveys were low.

Table 9. Intensity of browsing for the 5 most thoroughly consumed species as determined by back-track browse surveys.

Species	Class 3 2+-year-old growth consumed	Class 2 50-100% CAG consumed	Class 1 < 50% CAG consumed
Acer glabrum	81.2%	14.4%	4.5%
Cornus stolonifera	80.4%	16.5%	3.2%
Salix spp.	71.8%	23.9%	4.3%
Amelanchier alnifolia	70.6%	29.4%	0.0%
Populus spp.	67.5%	27.5%	5.0%

Populus trichocarpa averaged 36.6% dry matter loss (DML), significantly higher than any other species (Table 10). Amelanchier alnifolia and Acer glabrum (25.8% and 24.4% DML) did not differ significantly, but were significantly higher in DML than Salix spp. (19.5%) and Cornus stolonifera (15.9%). CAG was consistently, though not significantly, higher in digestibility than 2-year-old growth.

Most elk appeared to be malnourished by 1 March during both winters of study. Signs of malnutrition were lethargy, protruding ribs and pelvic girdles, and rough pelage. Three carcasses were located in winter 1978 and 1 cow that appeared near death was seen in 1979. A few additional winter mortalities undoubtedly went undetected each year.

Spring

In 1978, the spring season was wet and extended to 30 June. The 1979 spring was also wet, but the duration was several weeks shorter.

Forbs were the predominant forage class both years. Important genera included Lupinus, Taraxacum, Potentilla, and Antennaria or Cirsium (Table 7). These species ranked 1, 2, 5, and 11, respectively (Table 8).

Graminoids were the second most important forage class in 1978 with 38% r.f.o., but shrubs were more important than graminoids

Table 10. *In vitro* digestibility of current annual growth and 2-year-old growth in 5 browse species.

Species	% Dry Matter Loss (S.D.)			% Moisture	
	CAG	2-year growth	x[a]	CAG	2-year growth
Populus trichocarpa (cottonwood)	40.1 (1.2)	33.0 (6.2)	36.6	42.3	40.7
Amelanchier alnifolia (serviceberry)	26.1 (2.2)	25.5 (14.6)	25.8 ┐	42.0	--
Acer glabrum (mountain maple)	26.1 (6.5)	22.6 (8.2)	24.4 ┘	59.0	18.6
Salix spp. (willows)	20.1 (7.1)	18.9 (5.4)	19.5 ┐	43.4	28.6
Cornus stolonifera (dogwood)	17.7 (1.7)	14.1 (8.8)	15.9 ┘	43.1	38.7

[a]Bracketed means are not significantly different.

in 1979 with only 21% r.f.o. Predominant graminoids both years were Poa, Carex, and Agropyron (Table 8). Berberis was the predominant shrub both years (Table 7). Salix and Shepherdia occurred in small amounts both years and all other species occurred in only 1 of the yearly samples.

Use of trees declined dramatically from winter to spring, with only 4% average r.f.o. recorded. This class remained below 5% average r.f.o. during all subsequent seasons.

Summer

Summer conditions began earlier in 1979 than in 1978, lasted longer into the autumn months, and were hotter and drier.

As the forest dried, forbs and graminoids decreased in occurrence and shrubs increased. However, Lupinus was the predominant early summer forage (22% r.f.o.), giving way to Salix during late summer (38% r.f.o.; Tables 7 and 8). Shepherdia was the second most frequently utilized shrub (Table 8) showing approximately 10% average r.f.o.

Carex was a consistently important graminoid, ranking 4th throughout the summer (Table 8). Although Agropyron outranked Carex during early summer, it dropped from 3rd place to 9th as the season progressed (Table 8).

Early Autumn

In 1978, early autumn weather changed gradually from warm and dry to cool and moist as the season progressed. In 1979, the entire season was relatively hot and dry.

Shrubs were the predominant early autumn forage class in 1978, but forbs ranked highest in 1979. The predominant shrub both years was Salix. However, use declined between years from 36% in 1978 to 13% in 1979 (Table 8). Juniperus showed 20% r.f.o. in 1978 but was not reported for 1979. Physocarpus was the only shrub with a substantial increase between years.

Shade tolerant Lupinus was the predominant forb in 1979 and also showed the greatest increase between years (Table 7). Other important forbs included Antennaria or Cirsium and composite (Table 8).

Graminoids were lightly utilized and, except for Carex, showed either a decline or trivial increase between years (Table 7). Carex showed an increase from trace in 1978 to 3% in 1979.

Seeds were a frequently encountered item in 1978 but only a trace occurred in 1979.

Late Autumn

With the sudden reprieve from drought in 1979, graminoids jumped to the most frequently utilized forage class and forbs declined precipitously. A slight increase in graminoid use was also noted in 1978 although the change was much less than in 1979. Almost all of the increased graminoid use was attributed to *Carex* and to a lesser extent *Poa* (Table 7).

Shrubs were the predominant late autumn forage class in 1978, maintaining that status since the previous summer. *Salix*, *Berberis*, and *Shepherdia* were frequently encountered genera both years (Table 7).

All elk observed appeared healthy from spring through fall. Physical condition (body, kidney, and visceral fat levels) appeared good on all hunter-killed elk examined except for a 6-point bull presumably depleted during the rut.

Anderson and Medin (1969) linked antler size to summer nutrition in mule deer. While antlers of Middle Fork elk were not impressive in size, development was about normal. The youngest observed ages for 4-, 5-, and 6-point racks were 2.5, 3.5, and 4.5 years. All bulls 4.5 years and older had at least 5 points on 1 side.

CHAPTER V

DISCUSSION AND CONCLUSIONS

Population Dynamics and Description

The predictions of population trend contained in this paper are of concern and potential use only if the assumptions and biological data inputs are reasonably accurate. It is therefore important to assess the potential weaknesses of the analyses.

Although sample sizes were small, they represented substantial portions of the population. Because precision is based upon the proportion of the population that is sampled, not upon raw sample size, I conclude that the sample represents an excellent estimate of age structure. The same arguments apply to the production estimates. The estimates of recruitment based on intensive surveys were possibly biased upward because of poor access and the clumped distribution of cow-calf groups on the winter range (Peek and Lovaas 1968). Ratios derived from FWP aerial trend counts were considered as minimum figures because of a probable downward bias. Such surveys are quite extensive, conducted only once at the end of the winter, and are restricted to individuals that can be seen from aircraft (Lovaas et al. 1966). For these reasons, the moderate estimate

(28 calves:100 cows) seems to be the best estimate for use in decision making. There are several indications that recruitment in the Middle Fork herd is relatively low; it has declined significantly from earlier levels and is below current levels of most other Montana herds. Thus, recruitment is well below maximum biological potentials, approximating levels that will result in population decline at current mortality rates.

A less obvious but potentially important concern is that sexes were combined for estimates of age structure. Male elk usually have higher natural mortality rates than females, and bulls-only hunting would obviously accentuate the trend. Since over half of the hunting kill occurs during the first week of the season when antlerless elk may be taken, the potential effect of hunting kill on sex ratios is moderated somewhat. The major line of evidence that higher mortality rates in males did not seriously bias my estimates of overall mortality rates (and hence predictions of trend) is that the 2 oldest animals in the hunter-killed sample were both bulls. This fact extended estimated cohort longevity considerably and would at least partially offset any conservative bias attributable to combining the sexes for description of age structure.

Many life tables have been constructed on the assumption that λ = 1.0, requiring a constant age structure. This assumption is synonymous with the concept that each cohort started at the same size and followed identical mortality schedules. The population size and subsequently the mortality schedules producing the older cohorts is rarely known, and if it is, the time specific life table is the improper approach. However, by estimating the previous rate of change, the variation in mortality (and survivorship) can be corrected, as was done in this text. When the previous rate of change can not be estimated from the data, the logical recourse is to bracket the range of possibilities. The results obtained provide a series of probable population trends for management decisions.

Caughley (1974) demonstrated the effects of violating the assumption that $\lambda = 1.0$, concluding that age data were inadequate for calculating population dynamics. He noted that age structure will not represent survivorship (l_x) in a changing population because each cohort would have a different dynamic. I corrected for this situation by restructuring l_x for various rates of population change.

Tait and Bunnell (1980) published a method of restructuring l_x for various values of r that is essentially the same technique I used with λ. In the final analysis, they also shed doubt on the feasibility of calculating the population dynamic from age data.

I propose that by restructuring l_x for a previous λ or r, a workable estimate of population trend can be derived. Although the precise dynamic can not be determined (unless the precise previous dynamic is known), the magnitude and direction of population change was extremely consistent and indicative of the population's status.

Overall, I conclude that sample sizes, assumptions, and methodology are adequate enough that managers should be alert for signs of population decline in the Middle Fork herd.

The fact that production is suboptimal suggests that either conception is inadequate or some habitat component is lacking, or both. The ratio of bulls to cows appears to be more than adequate to ensure that all receptive females are bred. However, nutritional deficiency or disrupted breeding behavior could produce unbred or late-bred cows. During the first 3 days of the 1979 general season, numerous hunters reported hearing elk bugle. Also, a 2.5-year-old estrous cow was shot. This evidence suggests that some elk were still in rut when the hunting season opened. Such stress could result in cows producing late calves. Two sizes of calves were occasionally seen on the winter range each winter, reinforcing the possibility of disrupted breeding. The unique weather conditions of 1979 which resulted in late use of open, high country, and possibly in delayed rutting activities by some animals would be unlikely to reoccur often enough to be of much management concern. Although further investigation of possible rut disruption seems warranted, habitat conditions comprise the most likely explanation of consistently poor recruitment.

Hunter Distribution and Elk Response

Some factor(s) other than hunter days account(s) for levels of hunter success and the distribution of the kill. Success was higher in 1979, although hunter effort was higher in 1978. Most of the elk observed early in the 1979 season were in sparsely timbered alpine areas and therefore may have been more vulnerable to hunters. Hunters killing elk in 1979 often reported selecting 1 animal from a herd. In 1978, kills more frequently involved lone animals or were in dense vegetation that prevented accurate counts of additional animals. I believe the unexpected use of high altitude openings resulted from the sudden end to drought and the subsequently increased forage succulence in those areas. If the elk were rutting, as previously suggested, their increased activity would also have made them more vulnerable.

Differences in elk and hunter distributions indicate that elk are fairly efficient at avoiding hunters. Previous researchers (Bohne 1974, Zahn 1974, Lemke 1975, Marcum 1975, Lyon 1979, Marcum et al. 1979) did not document the distribution of people or other disturbances across the study areas. Instead, those workers relied on the distribution of elk relative to open roads. Marcum et al. (1979) reported that elk use increased in areas more than 1350 yards (1230 m) from open roads during hunting season. Roads on their study area were closed on 1 September, and elk showed no avoidance of accessible areas during the subsequent rutting season. However, when hunters started walking the roads a few weeks later, use within 150 yards (140 m) of closed roads was significantly less than availability. Bohne (1974), Lemke (1975), and Grkovic (1976) reported elk movements away from open roads and into heavy cover during hunting season. However, Grkovic (1976) found that elk used roads prior to hunting season, and Marcum (1975) reported that elk selected for closed roads. Apparently roads do not deter elk from using accessible habitats, but hunter activities do. Marcum (1975) concluded, "With respect to open roads, and resulting increased human activity through easier access to an area, elk within the study area avoided the human activity, not the roads." Concurring results were obtained during this study.

Distance from open roads (measured in walking time) was only 1 component used in determining accessibility. When terrain, cover, snow depth, and other factors were considered, several Difficult access areas were found between 0.25 and 0.5 miles (0.4 and 0.8 km) of open roads, indicating that distance is only 1 factor in elk security.

Although elk left accessible areas in response to hunters, apparent elk density remained low in Backcountry. Similar results were reported by Morgantini and Hudson (1979). Ward et al. (1973) found that elk tended to keep a relatively constant distance of 0.5 miles

(0.8 km) between themselves and people, but would stay closer if heavy cover was present. Lyon (1979) also predicted that disturbing influences would be minimized by heavy cover. Similar results by Zahn (1974), Lemke (1975), and Smith (1978) indicate that elk usually move no further than necessary to avoid people. As hunter densities increased in the more accessible areas of my study area, elk shifted toward the inaccessible areas. At some threshold of hunter density (between 1.5 and 3.0 hunter days per square mile in this case), further movement was unnecessary. Thus, a concentration of elk was found in Difficult access areas. As apparent elk densities increased due to this wave-like phenomenon, hunter success also increased.

Almost twice as many elk were killed within 0.25 miles of open roads as in any subsequent 0.25-mile interval. Evidently elk were quite susceptible in the small but highly accessible corridors along roads. These areas had the highest hunter densities, and the lowest apparent elk densities. Although few elk were found in these areas, the density of hunters produced a high probability that those elk present would be found and shot. Backcountry areas were the largest geographically and also received the fewest hunter days. Such a vast searching area and comparatively low elk density could lower hunter success. However, hunter success relative to apparent elk density was highest in these areas. The data indicate that, although hunters in Backcountry areas saw fewer elk, fewer of those seen escaped.

The low susceptibility calculated for Difficult access areas probably results from a disproportionate number of elk per hunter. Hunters were allowed only 1 elk, and each of the few hunters that used Difficult access areas should have seen substantially more elk than they killed if elk did in fact congregate in these areas. Thus, high elk densities and low hunter densities may have resulted in a lower probability of death for any particular elk.

The relationship between hunter success and apparent elk density provides some interesting insight into elk management. With the exception of Backcountry for 1978, a very tight relationship exists between hunter success and apparent elk densities. However, the slope of the line and the location of the data points indicate that most of the variation lies in apparent elk densities. A very slight change in hunter success would therefore indicate a relatively drastic change in the estimated elk population. This relationship suggests that hunter success is an insensitive measure of population size and, probably, a better measure of hunter density.

Food Habits and Diet Quality

During 2 previous studies and this one, deviation from normal weather patterns was noted. Winter conditions ranged from a record mild in 1977 (Smith 1978) through normal temperatures and snowfall in 1978 to severe conditions in 1979. Deep snow and fluctuating temperature extremes in 1979 led to increased avalanche activity and snow conditions that restricted forage availability and elk movements. In 1977, summer precipitation occurred later than normal and was of short duration with drought conditions extending into the autumn (Smith 1978). Spring-Fall 1978 was normal but low precipitation was again noted in 1979 although the precipitation pattern was about normal.

Except during the winter, forage selection reflected weather differences between years. The predominance of conifers in elk diets during both the "normal" winter of 1977-78 and the severe winter of 1978-79 suggests that reliance upon conifers was not strictly a result of exceptionally severe winter weather. Greer et al. (1970) examined 256 winter elk rumen samples from Yellowstone National Park over a 6-year period and found maximum conifer usage of only 15% in comparison to over 60% documented in this study. Because of differences in analysis techniques, my results are not strictly comparable to the Yellowstone study, but would seem adequate to document heavy winter reliance on conifers by the Middle Fork herd. High consumption of conifers is usually considered as indicative of poor range conditions and is often accompanied by drastic weight losses (Geis 1954, Helwig 1955, Boll 1958). Greer et al. (1970) found extensive winter mortality associated with conifer usage of 15% during the winter of 1961-62 in Yellowstone.

Presumably, reliance on coniferous forage resulted from inadequate availability of more valuable forage species. Although little overwinter mortality was observed during this study, apparently the Middle Fork elk were barely subsisting on their present diet. Further evidence of diet inadequacy was provided by range surveys and in vitro trials.

Figures on digestibility of elk forage are relatively rare in the literature, and most are based on the lignin ratio method of analysis. The lignin ratio method tends to inflate digestibility figures slightly (Smith et al. 1956), because mule deer, and presumably elk, are able to digest small amounts of lignin. In spite of this bias, digestibility of important browse species from the study area are apparently inadequate to prevent major weight loss (Table 11). Diet-related low reproductive rates are also possible (Cheatum and Severinghaus 1950, Cowen 1950, Wegge 1975).

Relatively low digestibility of 2-year-old browse material has been documented in mule deer forage by Oelberg (1956), Crampton (1957), Johnston et al. (1968), Hanson and Smith (1970), Merrill (1972), and Short et al. (1972).

Recent controversy has shed some doubt on the adequacy of the Cole (1963) method for determining trend and/or condition (Eddleman 1974, Mackie 1975). I used the method only as an indicator

Table 11. Forage quality and weight response in elk.

Forage type	% Apparent digestibility	Change in body weight	Source--Method
Mixed browse in 1953	15.0	-10.9%/27 days	Geis 1954--LR
Mixed browse in 1954	25.6	-1.9%/27 days	Geis 1954--LR
Bunchgrass & browse (62:38) in 1953	49.8	-0.4%/27 days	Geis 1954--LR
Bunchgrass & browse (66:33) in 1954	44.8	-5.4%/27 days	Geis 1954--LR
Deciduous browse	31.0	-56 lbs/elk	Helwig 1955--LR
Bunchgrass & browse	33.6	-5.2%/27 days	Boll 1958--LR
Cornus stolonifera	37.3	unknown	Ward 1971--IV
Amelanchier alnifolia	34.6	unknown	Ward 1971--IV
Populus trichocarpa	36.6	unknown	This study--IV
Amelanchier alnifolia	25.8	unknown	This study--IV
Acer glabrum	24.4	unknown	This study--IV
Salix spp.	19.5	unknown	This study--IV
Cornus stolonifera	15.9	unknown	This study--IV

of the adequacy of shrubby forage production. Using the standards set by Cole (1963) for allowable use, I established "adequate production" at that level where 40% of CAG remained after winter use. Browsing at this level for 2 years would approximate the moderately hedged form class. Forage production was also considered inadequate if CAG did not extend into the available zone.

Browse species typically important to elk were producing less forage than the elk would voluntarily consume. Also, alternate foods were either insufficient or not attractive enough to reduce the pressure on the "key" browse species. Increased shrub productivity would increase quality as well as quantity. Gill (1972) found increased digestibility of conifers when mixed with deciduous browse. Geis (1954) had similar results with bunchgrass/browse mixtures. Increasing the browse and bunchgrass production may be expected to improve the palatability, availability, and digestibility of the winter diet.

Of major concern in interpreting the results of this study is the fact that several species found important in the winter back-track surveys (especially Acer, Amelanchier, and Cornus) were not identified in winter fecal samples. I believe that the discrepancy resulted from the fact that these shrubs were deciduous. Fitzgerald and Waddington (1979) stated that leaf fragments are much more easily identified in feces than are most other plant fragments. Vavra et al. (1978) found forbs underrepresented in steer feces after the animal was fed known proportions of grass and browse; he thought the discrepancy was due to higher digestibility of forbs.

Winter malnutriton is probably the rule on the Middle Fork range. Poor nutrition is apparently not a problem during the warmer seasons. Although every female killed by hunters was fat, how adequately the summer diet contributed to winter fat reserves could not be measured. Ungulates must begin even mild winters with substantial amounts of fat to subsist. Antler development suggests that the summer forage quality is adequate. Although nutritional deficits during the summer are not a problem, increasing the distribution and quantity of the most palatable forage species would probably increase fat reserves, and decrease the impact of inadequate winter forage.

Succulence apparently replaces availability as the dominant factor in forage selection during the warmer months. Forbs and grasses not only became available in the spring but were also the most succulent species. As these forages dessicated in the summer heat, the elk shifted to understory shrubs and shade-tolerant forbs. With the advent of autumn showers, many forbs and a few grasses became more succulent and the elk shifted their diet correspondingly.

Whether dry or succulent, grasses are an important energy source, becoming most valuable in autumn and winter when elk must conserve fat reserves.

Smith (1978) showed that these elk selected habitats that minimized temperature and moisture stress. Food habits reported by this study correspond to those changes in habitat selection. Whether the elk selected habitats and then consumed immediately available forages or vice versa is uncertain.

Differences in forage selection between years was attributed to different weather patterns. As summer 1979 became hot and dry early, the elk moved into heavy timber and stayed there until precipitation began later than normal. The sudden shift to open site forages following late fall precipitation may have been a response to cravings for forages not available during the extensive stay in timbered areas.

CHAPTER VI

MANAGEMENT RECOMMENDATIONS

The Middle Fork winter range lies within the Great Bear Wilderness, and although animal populations can be manipulated, legal restrictions may limit habitat management opportunities. Because of these complications, summer range (much of which lies outside the wilderness) improvement is stressed.

1) Recommendation: Plan logging sales to protect damp sites.

Rationale: Cool and moist habitats are important components of the Middle Fork summer elk range (Smith 1978). These sites provide a comfortable environment and succulent forage, conditions elk apparently seek. Leaving cool and damp sites intact, and contiguous with unbroken forest, would minimize the impact of logging operations on the summer range. Protection of these sites was also recommended by Bumstead et al. (1978) and Lyon et al. (1979).

2) Recommendation: Make clearcuts long and narrow, and orient them to maximize the shading effect of the remaining timber stand. Long narrow cuts oriented east and west on a north-facing aspect would decrease the soil surface exposed to direct sunlight.

Residual trees in select and seed tree cuts should be left in the sunniest areas of a sale.

Keep cuts small (<80 ha; 200 acres) and remove slash as completely as possible.

Rationale: This procedure should help maintain succulence of open-site forages during the summer. Plants that grow in openings provide more nutritious forage than shaded plants (Oelberg 1956, Short et al. 1972). However, direct exposure to the sun reduces palatability through desiccation. Hoskinson and Tester (1980) and this study found that succulence is an important criterion in summer forage selection by ungulates. Increased succulence of open-site forages may induce these elk to consume better forage, and increase prewinter fat accumulation.

Removing most of the slash and keeping cuts as small as possible should increase elk use (Lyon and Jensen 1980).

The ratio of shade to sunlight that would optimize succulence and forage quality is unknown. Cuts of several shapes and sizes would provide several degrees of forage succulence and increase the probability of achieving the proper balance.

3) Recommendation: Maintain maximum habitat security around feeding sites on autumn ranges.

Rationale: Elk increased their use of graminoids, which provide a high energy diet and aid the animals in accumulating fat reserves, during the autumn months. Many of the selected forages were open-site plants, and their use during autumn increased exposure to hunters. Maintaining cover around open feeding sites would increase the animals' opportunity to maximize fat reserves for the winter.

4) Recommendation: Thin trees and unpalatable shrubs from areas of dense timber on east, north, and west aspects of middle or upper slopes. Maintain at least 70% canopy on 30 to 50 contiguous acres (12 to 21 ha) within or adjacent to thinned sites.

Rationale: Smith (1978) reported that these elk selected upper slopes during early summer and middle slopes during late summer and autumn. Nearly every aspect, except south, was used to some extent. This study documented increased utilization of shade-tolerant forage species during dry months. Thinning the canopy and removing low palatability shrubs from timbered sites would stimulate growth and improve the quality of understory forages (Oelberg 1956, Laycock and Price 1970, Merrill 1972). Thinning should be controlled so that forage succulence and cover are maintained.

Bumstead et al. (1978) recommend a minimum of 30 to 50 acres (12 to 21 ha) for security and thermal cover. By maintaining 30 to 50 acres (12 to 21 ha) of 70% canopy in or adjacent to thinned sites, cover and forage could be provided in good balance.

5) Recommendation: Close the Twenty-five Mile Creek Road a mile or more below the Granite Creek/Ear Creek divide at least 2 weeks before the general elk season each year.

Rationale: Several grassy ridges are located beyond this proposed closure. Decreasing access to these areas would provide the benefits sought by Recommendation 3. However, this closure may also be expected to reduce hunting mortality.

This closure would change approximately 6 sections from Moderate and Easy access into Difficult access. Easy access areas adjacent to this road would become Moderate access areas. Reduced accessibility would increase the amount of area where elk are least susceptible to hunting. Closing all spur roads would add 4 more sections to Difficult access.

These closures would increase hunting quality for those hunters who prefer to walk in, but hunting opportunities for those restricted to roads would be decreased. Unless closures become imperative, public concensus should be sought.

6) Recommendation: Continue operation of the hunter checking station at the junction of Skyland Road and Highway 2. Collect age data and conduct hunter interviews as reported in this work.

Rationale: This checking station provided biological data and reduced the tendency for a few unsportsmen-like hunters to "cheat." Many local residents extended appreciation for this secondary benefit and requested the continuation of the station.

The biological data provided by this station should be analyzed to determine the population response to any management effort. Population trends determined from the data would check demographic management efforts, and the susceptibility determinations would reflect habitat, hunter, and population changes.

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APPENDIX A

THE FUNCTION AND DERIVATION OF λ_s

Long-term lambda (λ_L) used in this text is the finite rate of population change derived by the standard life table approach (Caughley 1977). Short-term lambda (λ_S) is also the finite rate of population change, and each term measures population change per year because the life table data is in annual increments. The functional difference between λ_L and λ_S lies in the conditions under which each is derived.

The standard life table calculation (λ_L) is the projected population trend that will be expressed only if mortality and natality schedules are constant and the population has reached a stable age distribution, and if fecundity remains constant. The time span required to reach a stable age distribution will depend on how much the present age distribution is displaced from stability, generation time, and other factors. In reality, fecundity and age structure frequently change during relatively short intervals. Thus a population may never reach a stable age distribution.

Short-term lambda (λ_S) provides a means of predicting a population trend within more reasonable biological constraints. Calculation of λ_S requires only that fecundity and mortality rates apply to 1 year. By reducing the duration of the constraint, the probability of error is reduced. This reduction in error will result because:

1) the age structure of the population is less likely to change in 1 year than across several years;

2) any error in the calculation resulting from changes in age structure will not be compounded by previous changes;

3) reproductive rates (especially density dependent reproductive rates) are less likely to change in the shorter time span; and

4) λ_S provides an immediate prediction that can be corrected subjectively for environmental conditions.

When the population age structure stabilizes, λ_S will equal λ_L. In all other cases, λ_S will deviate from λ_L relative to the difference between the present age structure and the stable age distribution. From this displacement, λ_S will converge towards λ_L as long as natality and mortality rates remain constant. The path the population will take towards stability can be determined by calculating λ_S for several years. This is the basic process of population simulation.

Short-term lambda is derived from life table data by the following logic.

λ_s = the change in population size across the next reproductive cycle.

$$= \frac{N_{t+1}}{N_t} , \qquad (1)$$

where N is population size at time t.

N_{t+1} = the number of individuals presently in the population (N_t) that will survive to the next time period, plus the number of offspring they produce.

This statement can be written mathematically using life table notation as:

$$N_{t+1} = \sum S_{x_{(t+1)}} = \sum_{x=o}^{\infty} (S_{xt}(1 - q_x)) + S_{o(t+1)} , \qquad (2)$$

where S_{xt} is the number of individuals in age class x at time t, $1 - q_x$ is the probability of surviving any particular interval x, and $S_{o(t+1)}$ is the number of fall young surviving to $t+1$.

The number of offspring produced is calculated by multiplying the number of survivors in each age class,

$$S_{xt}(1 - q_x) ,$$

by the number of fall offspring each adult female of age x can be expected to produce,

$$m_x ,$$

and summing all age classes. Combining terms this is expressed by,

$$\sum_{x=o}^{\infty} (S_{xt}(1 - q_x)m_x) . \qquad (3)$$

Combining equations 2 and 3 produces,

$$N_{t+1} = \sum_{x=o}^{\infty}(S_{xt}(1-q_x)) + \sum_{x=o}^{\infty}(S_{xt}(1-q_x)m_x) .$$

The number at time t (N_t) is the sum of individuals presently in each age class,

$$\sum_{x=o}^{\infty} S_{xt} .$$

Returning to equation 1, λ_s is:

$$\lambda_s = \frac{N_{t+1}}{N_t} = \frac{\sum_{x=o}^{\infty}(S_{xt}(1-q_x)) + \sum_{x=o}^{\infty}(S_{xt}(1-q_x)m_x)}{\sum_{x=o}^{\infty} S_{xt}} .$$

APPENDIX B

TAGGING RECORDS

Date marked	Age	Collar type	Ear tags	Date returned	Collection site	Cause of death	Date and location last seen
2/01/77	5.7	rope (GGG-54)	A 2749 A 2750				
3/20/77	3.8	radio #238	A 2751 A 2752				8/07/78 Lynx Creek
3/20/77	0.8	rope (RWW-22)	A 2755 A 2756				
3/20/77	0.8	rope (RRR-36)	A 2757 A 2758				
3/20/77	5.8	radio #239	A 2759 A 2760	10/22/79	Giefer Creek	hunter	10/21/79 Lynx Creek
3/20/77	0.8	rope (RGG-51)	A 2761 A 2762	10/23/78	Patrol Ridge	hunter	
4/05/77	3.8	radio #234	A 2765 A 2766	11/ /79	Cabin Creek	avalanche	8/06/78 Cabin Creek
4/20/77	6.8	radio #237	A 2769 A 2770				8/27/78 Long Creek

Appendix B. Tagging Records (continued).

Date marked	Age	Collar type	Ear tags	Date returned	Collection site	Cause of death	Date and location last seen
4/20/77	7.8	radio ch 1	A 2768 A 2764				8/06/78 Red Plume Mtn.
Winter '78	0.8	rope (WGG-43)	A 2712 A 2711	11/06/78	Lynx Creek	hunter	
Winter '78	0.8	rope (BGG)	A 2718 A 2720				
Winter '78	0.8	rope (RWG-48)	A 2733 A 2732				
Winter '78	1.8	rope (GWG)	A 2704				
Winter '78	5.8	radio ch 4	A 2791 A 2792				10/07/78 Tent Mtn.
Winter '78	3.8	radio #235	A 2796 A 2734				3/ /78 Lunch Creek
Winter '78	2.5	radio #241	A 2743 A 2742				10/27/78 Red Plume Mtn.