WINTER HABITAT SELECTION AND GROUP SIZE OF MOUNTAIN GOATS, SHEEP MOUNTAIN-GLADSTONE RIDGE, COLORADO

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Abstract: Rocky Mountain goats (*Oreamnos americanus*) on Sheep Mountain and Gladstone Ridge in the Sawatch Range of central Colorado were observed for 3 winters, 1978-1980. Goats preferred areas without persistent or melt-crusted snow where cliffs were interspersed with tundra above treeline or with mountain shrub or sparse conifer habitats below treeline. On winter ranges above treeline, group sizes were larger and fewer goats were solitary, compared to ranges below treeline. Further study of group size and of other goat behavior patterns as potential mechanisms of population regulation is suggested.

Mountain goats were introduced in the Sawatch Range of central Colorado in the late 1940's and early 1950's. The original transplant of 9 goats was released on Mount Shavano on 24 May 1948. An additional release of 6 goats was made on Sheep Mountain, 25 km north of Mount Shavano, on 30 June 1950 (Rutherford 1972). The population of mountain goats resulting from these 2 transplants now exceeds 350 animals and is the highest and the southernmost on the continent.

This study was initiated in 1978. Objectives included: 1) determine winter distribution of mountain goats on Sheep Mountain-Gladstone Ridge, 2) measure preference for habitat types found on the study area, and 3) measure sociality of mountain goats in relation to habitat. The project was funded by the National Wildlife Federation, International Order of Rocky Mountain Goats, Colorado State University, and Colorado Division of Wildlife. Use of the cabin of Mrs. N. G. Maben as a field headquarters is gratefully acknowledged.

STUDY AREA

The study area (38°48'N, 106°20'W) was located 11 km west of Buena Vista, Colorado. Boundaries of the study area were the Continental Divide, Middle Cottonwood Creek, and South Cottonwood Creek. Major geographic features of the study area included Sheep Mountain (3640 m), Gladstone Ridge (4027 m), Jones Mountain (4031 m), and Mount Kreutzer (4000 m). Elevation ranged from 2775 m at the confluence of South and Middle Cottonwood Creeks to 4031 m at the summit of Jones Mountain (Fig. 1).

Treeline occurs at about 3600 m depending on topography. Tundra vegetation consists mainly of grasses, sedges, and forbs with patches of Englemann spruce (Picea englemanni), bristlecone pine (Pinus aristata) and willow (Salix spp.). Common plants include Carex spp., Agropyron scribneri, Oreoxis alpina, Trifolium nanum, and Geum rossii. Below treeline is a forested zone dominated by Englemann spruce, Douglas-fir (Pseudotsuga menziesii), limber pine (Pinus flexilis), and bristlecone pine. Other major plants below treeline include Muhlenbergia montana, Festuca arizonica, Artemisia frigida, and Hallodiscus dumosus. Previous research on this study area has been reported by Bailey and Johnson (1977) and by Johnson et al. (1978).

METHODS

Data were collected during 3 winter field seasons. Field work was conducted from 6 January to 3 April 1978, 15 January to 10 April 1979, and 14 January to 14 March 1980. Helicopter surveys were made on 23 February 1979 and 22 January 1980.

When mountain goats were observed, the date, time, weather conditions, location, group composition, group activity, and habitat characteristics, such as slope, aspect, vegetation types, elevation, and snow depth, were recorded. Locations were taken from a 15-minute U.S.G.S. topographic map gridded in 16-ha squares. Locations were recorded to the nearest ha.

To determine winter habitat preference, the relative abundance of each vegetation type available to mountain goats in winter was determined (Fig. 2). On the alpine tundra, the area within the boundaries of summer mountain goat distribution and west of where timberline bisects Gladstone

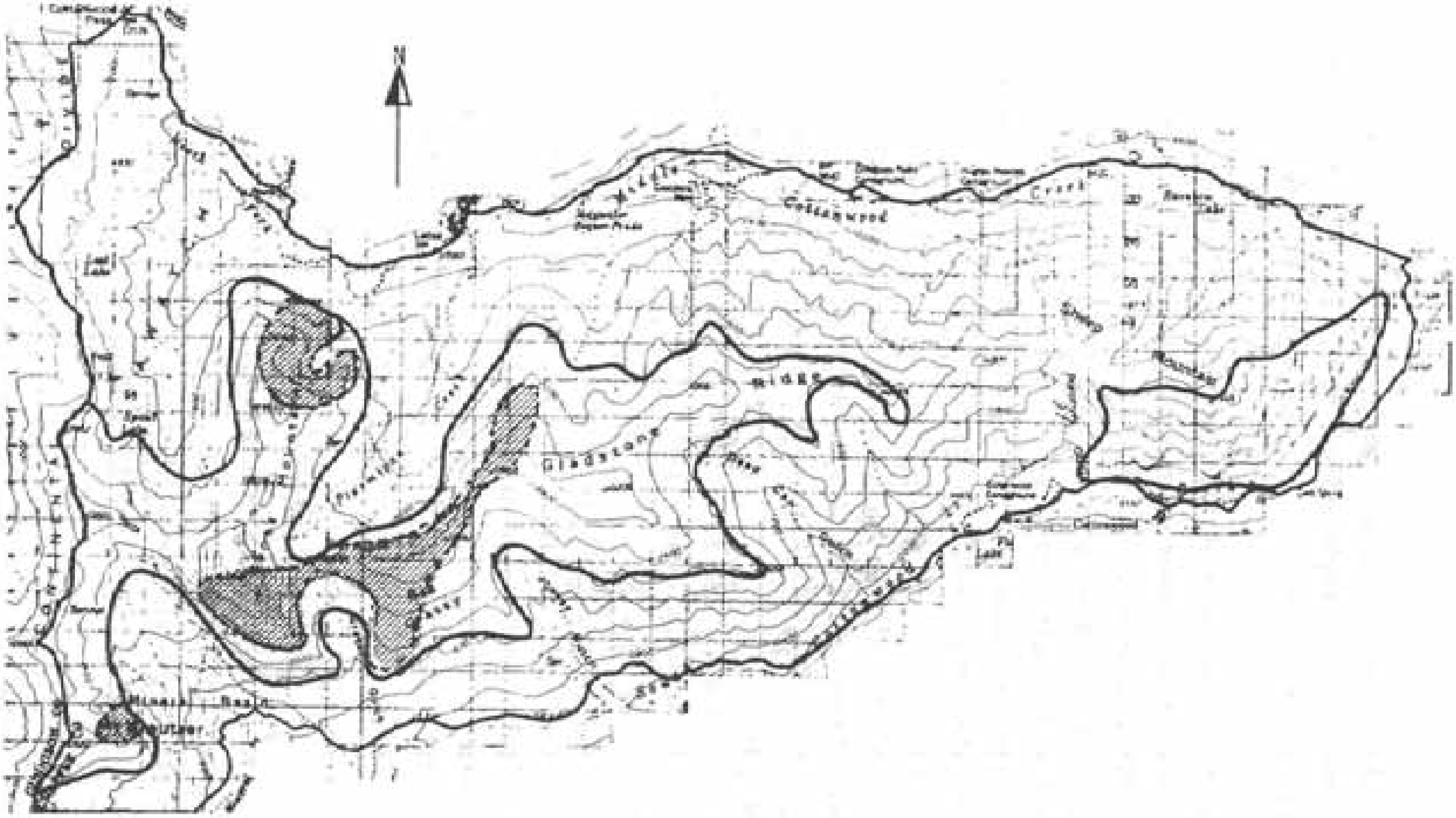

Fig. 1. Sheep Mountain-Gladstone Ridge study area, Sawatch Range, Colorado. Outer solid lines indicate study area boundary. Inner solid lines indicate areas available to mountain goats in winter. Shaded areas are alpine tundra ranges used by goats in winter. All available subalpine winter range on Sheep Mountain was used by goats.

Ridge was considered available to goats in winter. In the subalpine zone, the predominantly southfacing slopes of Sheep Mountain were considered available (Fig. 1). This area was also used by goats in summer.

Vegetation types were delineated on aerial photographs using a stereoscope and type boundaries were adjusted to fit ground observations (Kuchler 1955). Vegetation types were:

1. Mountain shrub: A mix of shrubs and herbaceous vegetation found primarily on southfacing slopes of Sheep Mountain below 3500 m.
2. Sparse conifer: Stands of trees with more than 50% coniferous species where tree crowns covered less than 50% of the ground as determined from aerial photographs.
3. Dense conifer: Similar to the sparse conifer type except that tree crowns covered more than 50% of the ground
4. Aspen: Any stand of trees that was more than 50% aspen (Populus tremuloides).
5. Willow: Any area with at least 50% of the ground covered by willow.
6. Rock: This type included cliffs, outcrops, scree, talus, and boulder fields.
7. Alpine tundra: All areas above 3600 m not included in a previous type, including fellfields, intermittent rock and grass, alpine turf, alpine meadows, and alpine marshes.

The percent vegetation compositions of the available alpine and subalpine winter ranges (Fig. 2) were used to quantify habitat availabilities in calculating habitat preference indices (PI):

$$PI = \frac{\text{\% of goat observations in a habitat type}}{\text{Habitat type as \% of available winter range}}$$

The subalpine winter range was also classified into percentages in each of three elevation classes (Fig. 6). Preference indices for elevation were calculated from these percentages and the percentages of goat observations in each elevation class.

RESULTS

Over 3 winters, 133 groups of mountain goats, with 647 individuals

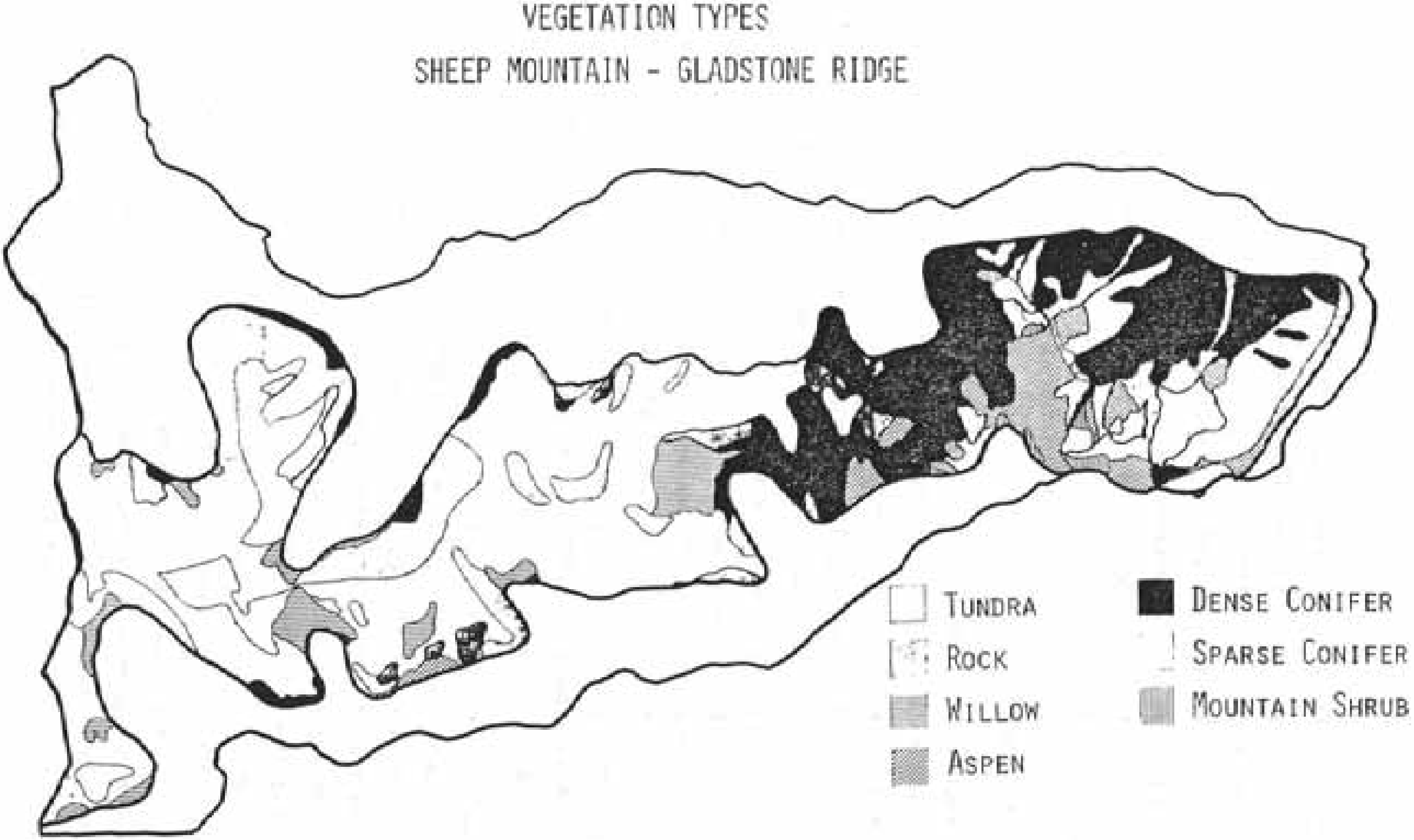

Fig. 2. Vegetation types within mountain goat summer range on the Sheep Mountain-Gladstone Ridge study area, Sawatch Range, Colorado.

(including repeated observations), were observed. Thirty-three groups were seen above treeline and 100 groups were seen in the more frequently observed range below treeline (Fig. 1). Habitat preferences in these 2 ranges will be discussed separately.

Based on the 22 January 1980 helicopter survey, more goats may have been wintering above treeline than below. Sixty-three of the 69 goats observed were above treeline. However, goats were easier to observe in the open tundra and cliffs above treeline than they were in the forested zone.

Alpine Winter Range

Alpine winter ranges were located on Gladstone Ridge, Jones Mountain, and Mount Kreutzer on the west half of the study area (Fig. 1). Areas used were characterized by windblown alpine tundra ridgetops and northfacing cliffs and outcrops. Elevation ranged from 3700 m to 4031 m.

Mountain goats showed a preference for the alpine tundra type and rock type (preference indices of 1.3 and 1.1, respectively), which were also the most abundant of available vegetation types above treeline (Fig. 3). Other available types, willow, sparse conifer, and dense conifer, tended to collect and hold snow and were not used. Sixty-six % of the 33 groups of mountain goats were observed on predominantly northfacing slopes (Fig. 4).

Subalpine Winter Range

Subalpine winter range was located on the southfacing slopes of Sheep Mountain (Fig. 1). The area is characterized by steep, broken terrain with cliffs, outcrops, and talus slides intermixed with forested and mountain shrub vegetation. Elevation on the subalpine winter range varied from 2800 to 3640 m.

Mountain goats showed preference for the mountain shrub and sparse conifer types (preference indices of 2.8 and 2.0, respectively, Fig. 5). The rock type was used frequently (34% of the 100 groups observed) but, due to the abundance of this type on the range, was not preferred (preference index of 0.7). The eastern half of Sheep Mountain winter range (Fig. 2) is primarily the rock type with little interspersion of

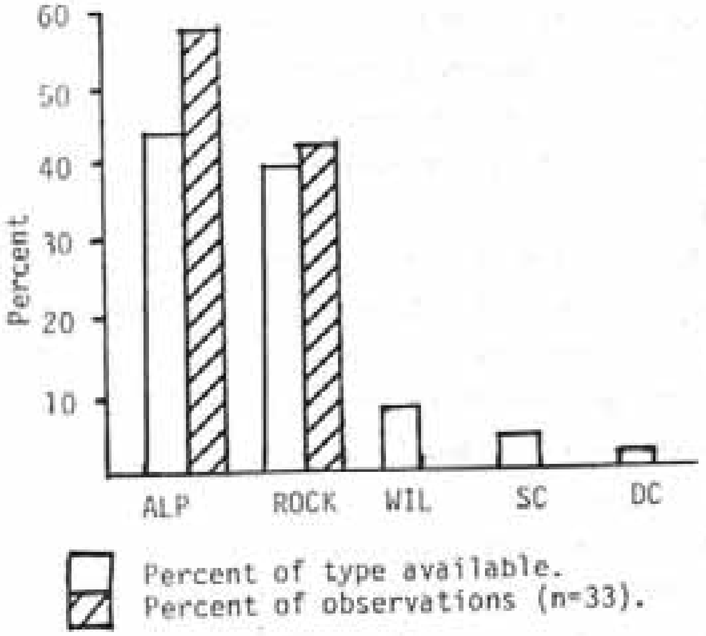

Fig. 3. Habitat selection by mountain goats on alpine winter ranges, Sheep Mountain-Gladstone Ridge study area. Vegetation types are alpine tundra, rocks, willow, sparse conifers and dense conifers.

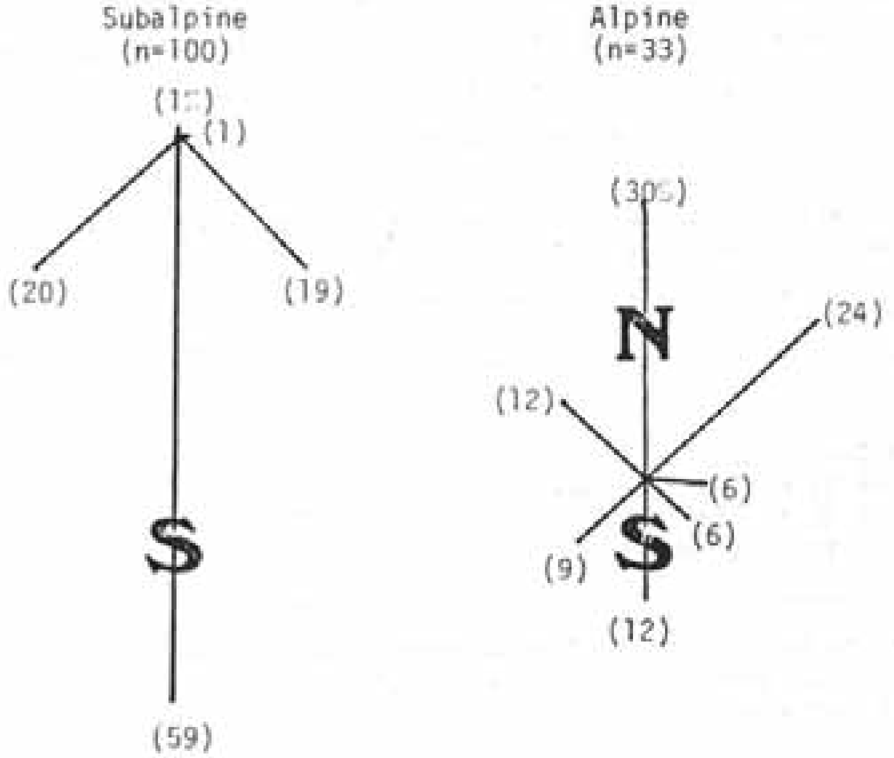

Fig. 4. Use of aspects on subalpine and alpine winter ranges by mountain goats on the Sheep Mountain-Gladstone Ridge study area.

the preferred mountain shrub and sparse conifer types and provides little forage. Only 15% of the observed groups of goats were on this area. In contrast, units of the rock type are interspersed with preferred vegetation types on the western half of the available winter range and were used heavily by goats.

Ninety-eight % of the observed groups were on predominantly southfacing slopes of Sheep Mountain (Fig. 4). The northfacing slopes of Sheep Mountain are covered by the dense conifer type. They accumulate as much as 2 m of snow and therefore were unavailable to goats.

In 1979, when there was about 15% more snow on the winter range than in 1978 (based on a snow survey course observed by the U.S. Soil Conservation Services at Monarch Pass, 25 km south of Sheep Mountain), goats preferred the lower slopes of Sheep Mountain and avoided areas above 3354 m. In contrast, in 1978, with less snow, use of the Sheep Mountain winter range was evenly distributed across all elevation classes (Fig. 6).

Winter Group Size

Data on mountain goat group sizes can be presented in at least 7 ways, including a frequency distribution of observed group sizes. Six methods are illustrated in Table 1. Group sizes were larger during winter on alpine winter range than on subalpine winter range.

Table 1. Observed group sizes for mountain goats during winter on the Sheep Mountain-Gladstone Ridge Study Area, 1978-1980.

Observed Group Size	Alpine Winter Range	Subalpine Winter Range
Mean	10.4	3.1
Range	1-37	1-12
Standard Deviation	10.5	2.7
Percent of Groups as Solitary Goats	12	36
Percent of Goats, Solitary	1	12
Group Size for "Average Goat"[1]	20.6	5.5

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[1] These averages are computed by weighting group sizes by the number of goats in each group, summing the products, and dividing by the number of goats observed.

had more affect on habitat selection by mountain goats than did availability of forage. Snow crusting has also been indicated as influencing winter habitat selection by goats. Smith (1976) found goats using parkland colluvial slopes early in winter when snow was fluffy, but moving to steeper slopes that shed snow when it had consolidated elsewhere. Snow depth, hardness, and density affect habitat selection by many other ungulate species (Peek 1971, Formozov 1946, Skogland 1978, Pruitt 1959).

Mountain goat winter ranges on windswept slopes above treeline and on south-facing slopes below treeline have been recorded elsewhere (Hebert and Turnbull 1977, Rideout 1978, Brandborg 1955, Casebeer et al. 1950, Lentfer 1955, Vaughan 1975). In studied populations in Idaho (Brandborg 1955) and Montana (Smith 1976) most animals wintered at lower elevations. This is in contrast to the Sawatch Range where most goats wintered above treeline, based on numbers seen during the 22 January, 1980 helicopter survey.

Results of this study and reports of DeBock (1970), Brandborg (1955) and Smith (1977) indicate that average mountain goat group sizes during winter are larger on alpine tundra range than on subalpine forest range. Lentfer (1955) reported that mountain goat group sizes were "somewhat" larger during winter than during summer. On our study area, average group sizes were similar for winter and summer but maximum group sizes were much larger during summer (83 and 34 on alpine and subalpine ranges, respectively; unpublished data).

Average group size in mountain goats appears to be a function of season, population size in relation to habitat resources, steepness of terrain, vegetation density as it affects opportunities for visual communication, and snow conditions. Hebert and Turnbull (1977), Smith (1977) and Chadwick (1976) discussed some of these factors. Larger groups may occur above treeline because goats are less restricted in movements and may have access to more forage than do goats wintering below treeline. In addition, visual communication among goats is unrestricted by trees on the tundra. Lastly, much winter range below treeline is on relatively steep slopes where goats may be dispersed to avoid danger of agonistic behavior causing a fatal fall.

We suspect that behavioral mechanisms are important in regulating populations of mountain goats, as suggested by Kuck (1977), and that group size is therefore a parameter of goat behavior deserving more study. We hypothesize that larger group sizes will be characteristic of recently introduced goat herds because these herds have abundant forage resources supporting high reproduction (Bailey and Johnson 1977) and allowing goats to congregate without severe competition and abundant agonistic behavior. The very large groups sometimes observed on our study area support this hypothesis.

However, it is difficult to compare data on group size reported in the literature. Comparisons should be made within seasons and within habitat types (alpine tundra and subalpine forest). This information is not provided with some data in the literature. Further, average group size alone is an inadequate statistic for comparing populations. We suggest the reporting of group-size statistics as presented in Table 1. In addition, spacing of individuals within groups, the frequency of interactions among goats, and forage density and quality should be recorded. Results of such research could shed light on population-regulating mechanisms in mountain goats.

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QUESTIONS - RESPONSES

John Youds: What is the range of productivity?

Layne Adams: We had upwards of 70-80 kids per 100 older animals and since then it has dropped to around 40, quite a bit lower than that. Over the three years that I've been in field work, it ranged from about 32 kids per 100 older animals to around 28 or so.

John Youds: What do you mean by older animals?

Layne Adams: Yearlings and adults. The problem with that is that we don't feel that we can identify yearlings after about the middle of August. There is some problem with that anyway due to the fact that a lot of times they move long distances. Late in summer, first couple weeks in August the yearlings are pretty large in the study area.

Jim Bailey: They don't have yearling classification in the early years.

Layne Adams: That's the other thing, this is based on trend counts, aerial trend counts and those are just kids and others.

Jim Ellis: Do you have any ideas about potential differences either in body condition or productivity between alpine and subalpine group?

Layne Adams: No, we sure don't. There is quite a bit of interchange between the two. We only had collared animals for one winter, but these animals were all trapped at the same spot and that was in close proximity to the subalpine winter range. Over the summer we saw large movements, 8 to 10 miles a day back and forth from alpine to subalpine. We don't really know is it's two seperate populations.

Jim Bailey: Although they don't exchange animals in mid winter.

Layne Adams: Right.

Rolf Johnson: I'm interested in the relationship between hunting on the growth rate of the population; now you indicated that before hunting you had a 17% growth rate and after you initiated hunting you had a decreased growth rate, but you also think that the animals may be nearing carry capacity?

Layne Adams: We think it's an interchange of two factors. The herd was harvested prior to that period we had that big growth spurt and they were harvested at about the same level, 8-10% of the late summer population, and there was a slight increase. They took the harvest off and got this big boom in the population and then it leveled off at that harvest rate of about 8% which didn't amount to the same amount of growth that occurred over those 3 years. When we look at our age ratio data in comparison to snow depths, we get that decrease in productive, pretty significant decrease. So we feel that it's an interplay of two factors, they are reaching carrying capacity, they're starting to impact their range. We don't know what the affect of that will be; if they will shift to other areas or what will happen.

Mike Sullivan: Did you get all of your available forage transects in the summer time?

Layne Adams: Right.

Mike Sullivan: Doesn't that skew your preference data then?

Layne Adams: Correct, I'm sure it does. That was just due to ease of doing it?

Lynn Burton: I'm just curious at what point on that sigmoid curve is the Fish and Game going to try and maintain the population? Are they going to maintain at the top or what do you think?

Layne Adams: I don't think right now that there is much of a management plan as far as locally; the field personnel, what they plan to do here. Last year due to this information, we got the impression they were being held at that level. In 1978 they allowed 16 permits on the study area, this last year they allowed 10. So right now it seems indications are that they are going to harvest at a lower level and allow them to increase somewhat, but who knows what will happen in the next few years.

PRELIMINARY DATA ON MOUNTAIN GOAT POPULATION GROWTH

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Abstract

Mountain goat survey and harvest data from southeastern British Columbia and western Alberta was examined using a population projection simulation model. Preliminary results indicated an approximate intrinsic rate of increase (r_m) of 0.10 for mountain goats in the present study area. As a result of this low r value, simulated mountain goat populations were sensitive to changes in population parameter values. In regard to harvest policies, it is predicted that rates of increase are sensitive to relatively minor changes in adult mortality and that, in order to avoid overharvesting, harvest rates must be tied to the rate of increase.

Mountain goat population dynamics are poorly documented. Quantitative studies on reproductive biology and mortality are completely lacking, while census studies have failed to obtain accurate counts and classification of animals. Consequently, rates of increase for mountain goat populations are not adequately understood, and impacts of activities, such as harvest, on population growth are presently difficult to predict. Despite this lack of basic knowledge many monitoring programs continue to collect and compile crude population statistics, consisting of age ratios based kids per 100 females and number of yearlings per 100 adults. However, without specific knowledge of mountain goat population dynamics these statistics are difficult to interpret (Caughley, 1974).

This paper examines relationships which exist between population growth and various measurable population parameters using a population projection simulation model. It is a preliminary analysis based primarily upon harvest and survey data from southeastern British Columbia and western Alberta. Objectives include compilation of a preliminary set of population parameter values, establishment of a preliminary range of r values based upon estimated parameter values, examination of the potential impacts of harvest on population growth, and establishment of preliminary qualitative and quantitative relationships between population parameter values and rate of increase.

Study Areas

Data used for simulation was drawn from two areas: the East Kootenay area in southeastern British Columbia and the Willmore Wilderness Park area in Alberta (Figure 1). Harvest data was drawn from both areas, while survey data was primarily from the Willmore area.

The East Kootenay study area encompasses an area of approximately 10,000 square kilometers situated in the Rocky Mountains of southeastern British Columbia. This area supports the largest number of goats in southern British Columbia (Jamieson, 1978). During the 1960's, goat populations severely declined primarily due to overharvesting which resulted from uncontrolled access (Phelps et al., 1975). Mountain goat hunting seasons were closed in the area in 1971,

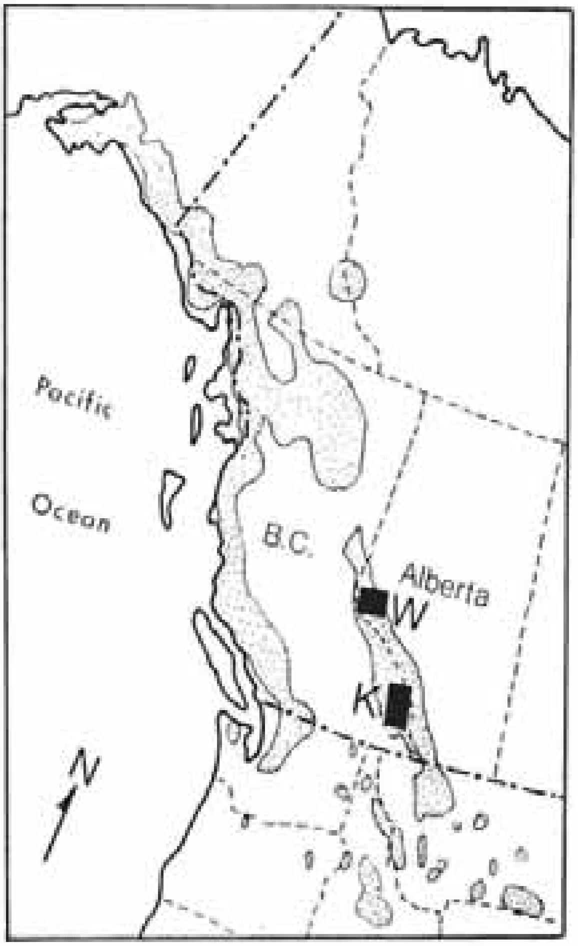

Figure 1. Location of study areas in terms of present mountain goat distribution (adapted from Johnson, 1977). W indicates the Willmore area, while K indicates the East Kootenay area.

and then opened again in 1976 under a limited permit system. Preliminary population estimates have been made for smaller land units within the total area (Warkentin and McLellan, pers. comm.). Present harvest rates among these units vary from 0 to 2 percent.

The Willmore study area is an area of approximately 3,000 square kilometers situated north of Jasper National Park in the Rocky Mountains of western Alberta. The hunted portion of this area, from which most of the survey data was collected, has been divided into six zones. Population estimates are available for each zone from 1974-1979. Hunting is on a limited permit system, and harvest rates among the zones vary from 5 to 10 percent (dependent on hunter success).

Methods

Data Collection

The survey and harvest data utilized in this paper was collected and compiled by employees of the Alberta Wildlife Division (Willmore study area) and Region 4 of the British Columbia Fish and Wildlife Branch (E. Kootenay study area). Survey data was collected using total (best) count aerial census techniques which classified adults, yearlings and kids. No information is available on the proportion of uncounted animals using this technique. Surveys were generally restricted to relatively small land unit areas (i.e. mountain blocks) and repeated on an annual basis in early summer. Harvest data, consisting of numbers, sex and age, were obtained for generally the same land units as flown for survey.

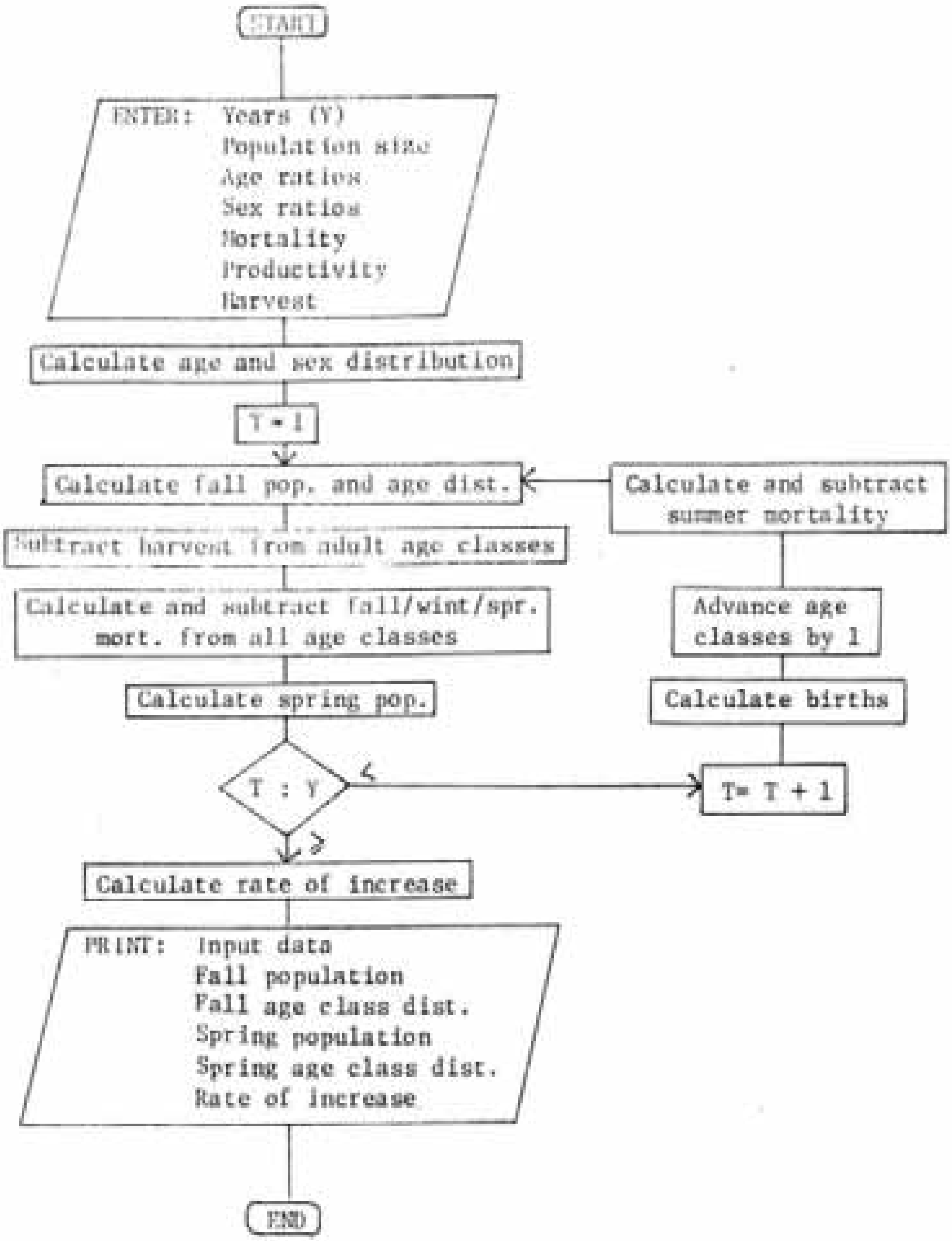

Figure 2. Flowchart of computer program used to project populations.

Population Parameters

The available survey and harvest data was examined to establish preliminary population parameter values which could be used in the population projection model. Productivity was estimated from Willmore data using a mean of 52 separate kid per 100 female ratios. Age ratios (K:Y:A) were calculated from survey data as a percentage of 100. Kid mortality was estimated in two ways, using yearling: kid ratios and Y/100A: K/100A ratios. Yearling and adult mortality estimates were based upon harvest data and the literature.

Population Model and Simulation

The model used for this analysis was a simple population projection model, capable of projecting a population of a given size and age distribution, with given age class mortality rates, productivity rates, adult sex ratio, and harvest rates, for n number of years. Figure 2 illustrates the basic structure and function of the model. An assumption incorporated into the model was that all forms of mortality are additive. In all simulations rate of increase (r) was calculated from the fifth year of simulation onward (to approximate stable age distribution) using the formula,

$$r = \frac{\mathrm{loge}\ N_t - \mathrm{loge}\ N_o}{t}$$

Results

Parameter Values

Number of kids per 100 females, as measured through surveys, was used as a measure of productivity. Table 1 presents data collected in the Willmore area from 1974-1979, stratified by hunting zone. The

	Zone A	Zone B	Zone C	Zone D	Zone E	Zone F
1974	--	28.6	97.5	68.6	59.5	20.5
1975	43.8	57.9	87.4	57.9	117.2	--
1976	50.0	58.0	41.9	26.3	104.8	--
1977	54.5	97.1	75.0	53.3	32.3	--
1978	70.6	53.8	45.7	91.9	91.9	60.0
1979	87.2	46.2	56.3	37.3	55.6	43.9
$\bar{\bar{X}}$	61.2	56.9	67.3	55.9	76.8	41.5

61.6
s = 24.3

Table 1. Kid per 100 female values collected in the Willmore area 1974-1979 (assuming 1:1 sex ratio).

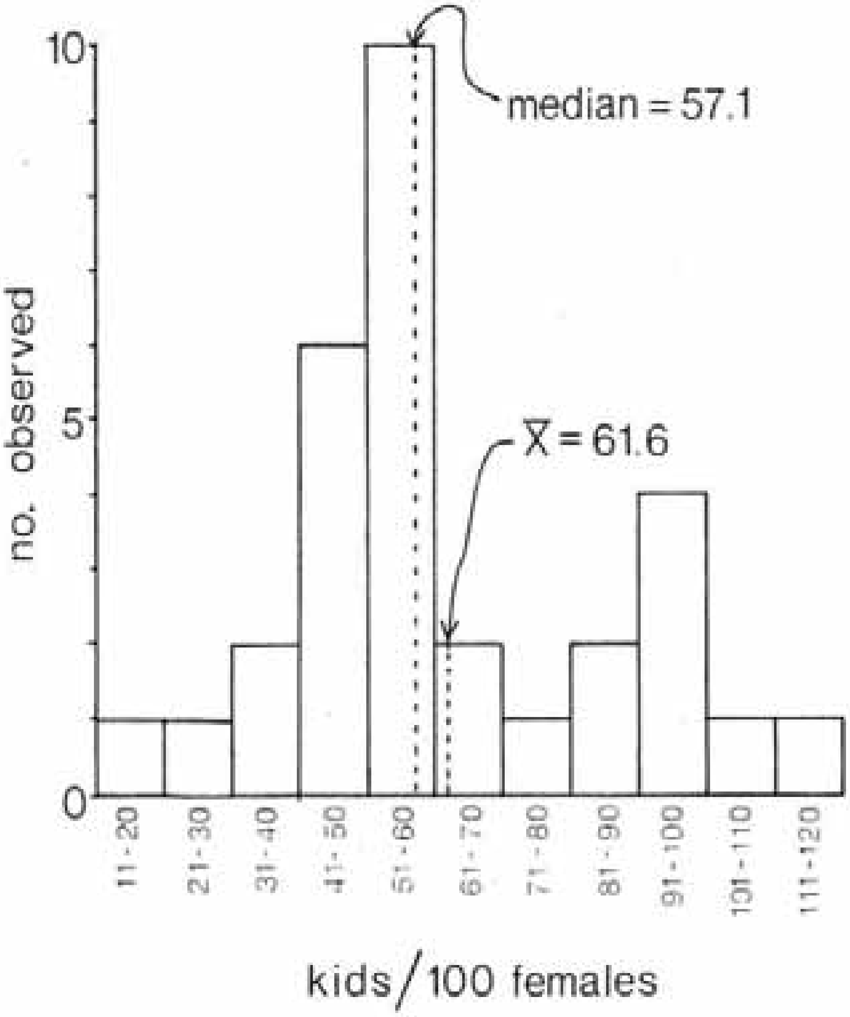

Figure 3. Frequency histogram of kid per 100 female values collected in the Willmore area from 1974-1979.

values range from a minimum of 20.5 to a maximum of 117.2 kids per 100 females (based on the assumption of an even sex ratio). A frequency histogram (Figure 3) of these kid per 100 female values (distributed by arbitrary class intervals) indicates the median (57.1) may be more representative of an average productivity value than the mean (61.6, s.d. = 24.3); the histogram also suggests a possible bimodal distribution of kid per 100 female values. Recent productivity estimates are not available for the East Kootenay area, however, an estimate of 73.3 kids per 100 females was established for a part of this area during a major goat decline in the 1960's (Hebert and Turnbull, 1977).

Mortality estimates were made for three age classes: kids, yearlings, and adults. Kid mortality estimates were made from yearling:kid ratios and Y/100A : K/100A ratios, while yearling and adult mortality estimates were derived from a range of guesses, based on harvest data and the literature.

Table 2 presents yearling:kid ratios and Y/100A : K/100A ratios collected in the Willmore area from 1975-1979. It is assumed that these ratios provide rough estimates of kid survival (p). An estimate of kid mortality was obtained by calculating 1-p. The mean kid mortality estimate was calculated as 53 percent from yearling:kid ratios (n=21, s.d. = 20), 55 percent from Y/100A : K/100A ratios collected in the same year (n= 21, s.d. = 19), and 60 percent from Y/100A : K/100A ratios collected in consecutive years (n = 18, s.d. = 22).

Yearling mortality rates could not be estimated from age ratios because two year olds were not classified in surveys. However,

Table 2. Estimates of kid survival in the Willmore area using various age ratios.

a) Yearling: Kid Ratios

Year	A	B	C	D	E
1975	.29	--	.50	.50	.63
1976	.82	.29	.44	.18	.29
1977	.42	.40	.36	--	.77
1978	.53	.30	.88	.28	.79
1979	--	.33	--	.33	.55

n = 21

$\bar{x}$ = 0.47

s = 0.20

b) Y/100A: K/100A ratios (from same year)

Year	A	B	C	D	E
1975	.29	--	.30	.46	.65
1976	.80	.30	.46	.20	.27
1977	.50	.44	.38	--	.80
1978	.42	.29	.87	.29	.48
1979	--	.33	--	.36	.65

n = 21

$\bar{x}$ = 0.45

s = 0.19

c) Y/100A: K/100A ratios (from consecutive years)

Year	A	B	C	D	E
1975	--	--	.27	.38	--
1976	.91	.30	.22	.09	.24
1977	.54	.73	.68	--	.25
1978	.54	.16	.53	.51	--
1979	--	.29	--	.15	.40

n = 18

$\bar{x}$ = 0.40

s = 0.22

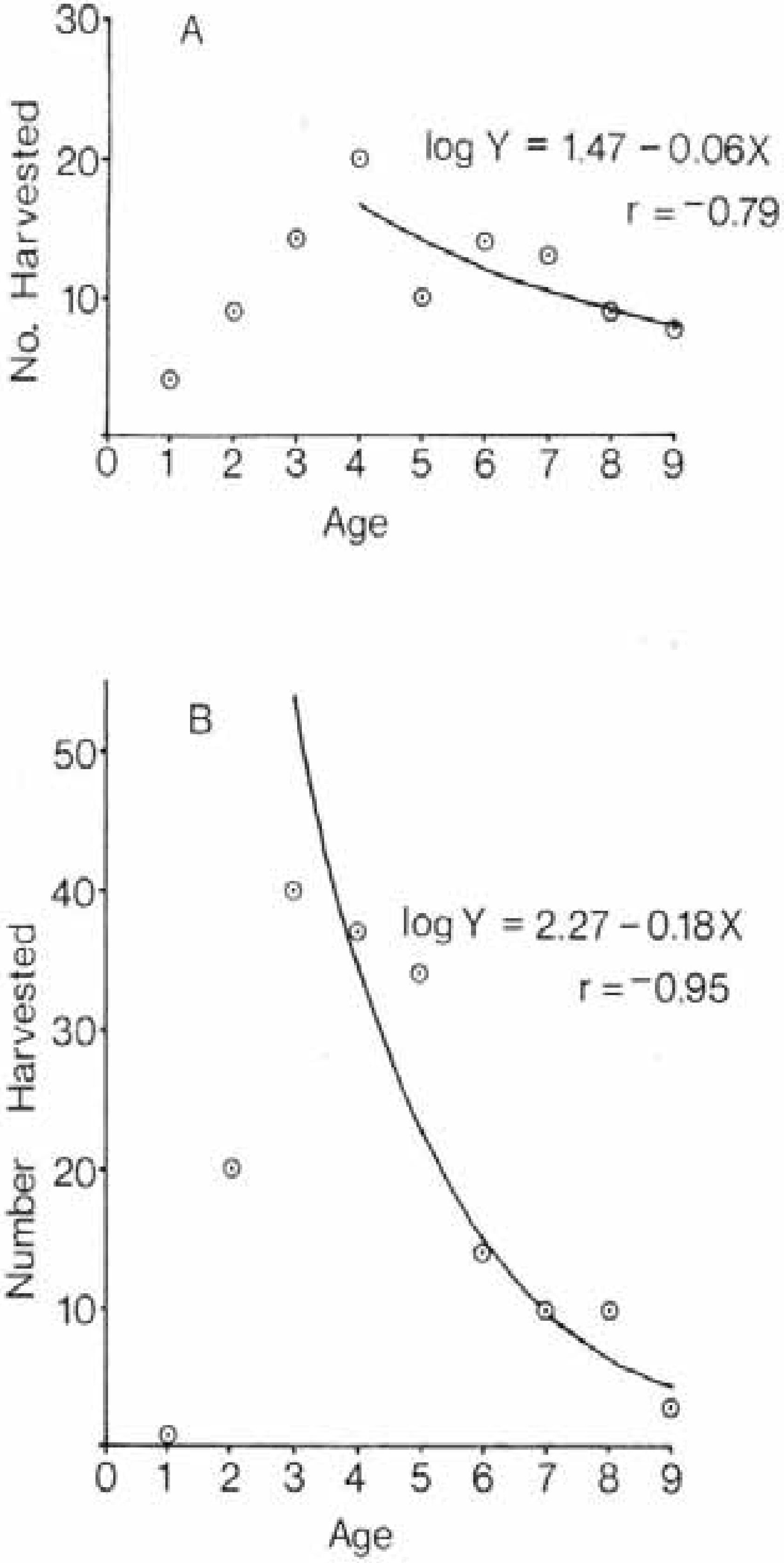

Figure 4. Harvest data from the Willmore area (A) and the East Kootenay area (B) collected from 1974-1979 and from 1976-1979, respectively. (⊙) symbols represent actual harvest numbers. The Willmore ages are based on tooth annuli, whereas the Kootenay ages are based on horn rings.

Parameter	Mean Value Estimate	Range of Values
Productivity	.57 kids/adult female	.40 - .90
Kid Mortality	.53 (53%)	.36 - .67
Yearling Mortality	.24 (24%)	.14 - .34
Adult Mortality	.07	.05 - .12
Sex Ratio	100 (males/100 females)	57 - 148
Age Ratios (K,Y,A)	N/A	.16 .10 .75
(some examples)		.167 .042 .792
		.19 .12 .69
		.20 .10 .70
		.20 .14 .65
		.212 .069 .719

Table 3. Summary of parameter value estimates used for simulation.

Chadwick (1977) classified two year olds in a study in Glacier National Park, and from this data two year old to yearling ratios provide mortality estimates that range from 0 to 44 percent, with a mean of 24 percent (n = 3, s.d. = 22).

Adult mortality rates were estimated to range from 5 to 12 percent. The oldest reported age of a mountain goat (dead) is 13 years (Chadwick, 1977). If it is assumed that all animals in a cohort are extinct by year 14, then average annual mortality for all age classes must be approximately 7 percent; this figure becomes less for adult mortality when it is considered that juvenile mortality is usually substantially higher than 7 percent. Harvest data from the East Kootenay area and the Willmore are, adjusted using an age class frequency smoothing formula of log Y = a + bX (where Y = frequency and X = age class), indicate average annual adult mortality rates of approximately 15 percent and 10 percent, respectively (Figure 4). These mortality estimates include both harvest and natural mortality.

A summary of parameter value estimates used in simulation is presented in Table 3.

Simulation

Simulation of population growth produced a range of r values as presented in Table 4. Using the previously established range of parameter values, the maximum r attained was .1024 (λ = 1.1078) with a productivity rate of .90 (90 kids per 100 females) and kid, yearling and adult mortality rates of 53, 14, and 5 percent, respectively. The value of r calculated using mean parameter value

(k/100F) Productivity	Kid	Mortality Yearling	Adult	r	λ
57	.50	.20	.05	.0559	1.0575
57	.43	.14	.07	.0534	1.0548
57	.43	.14	.10	.0281	1.0285
57	.43	.14	.12	.0111	1.0112
57	.53	.14	.07	.0404	1.0412
57	.53	.14	.10	.0343	1.0349
57	.53	.14	.12	-.0031	0.9969
84	.36	.22	.07	.0950	1.0997
73	.36	.22	.07	.0793	1.0826
56	.36	.22	.07	.0519	1.0533
56	.60	.20	.07	.0241	1.0244
42	.60	.20	.07	.0043	1.0043
57	.53	.24	.05	.0490	1.0503
57	.43	.24	.035	.0736	1.0764
90	.53	.14	.05	.1024	1.1078
30	.53	.14	.05	.0131	1.0132
90	.53	.24	.05	.0738	1.0766
30	.53	.24	.05	-.0116	0.9885

Table 4. Range of r and λ values produced using a range of productivity and mortality rates as interpreted from data (refer to Table 3 and text).

estimates (productivity, .57; kid mortality, 53 percent; yearling mortality, 24 percent; adult mortality, 5 percent) was 0.0490 (λ = 1.0503).

Impacts of harvest were investigated by imposing three levels of adult harvest (3, 5, and 8 percent) on different survival and fecundity schedules. Figure 5 illustrates the impact of these harvest levels on four fecundity and survival schedules (a, b, c, d), defined as follows:-

	Productivity Rate	Mortality Rate		
		Kid	Yearling	Adult
a	.73	.36	.22	.07
b	.56	.36	.22	.07
c	.73	.60	.20	.07
d	.56	.60	.20	.07

The near constant difference in r values between harvest regimes (there are minor deviations from this constancy due to rounding errors introduced by using a decimal number for age class projections, but a whole (rounded) number for a population figure in r calculations, and also because of calculating the r after the fifth year of projection when a completely stable age configuration has not in all cases been reached) illustrates that, within the model, harvest mortality is additive. Each 1 percent change in harvest results in a change in r of approximately 0.008. In this example in three out of the four survival and fecundity schedules modeled an 8 percent harvest rate produces a negative rate of increase. This result has important harvest management implications.

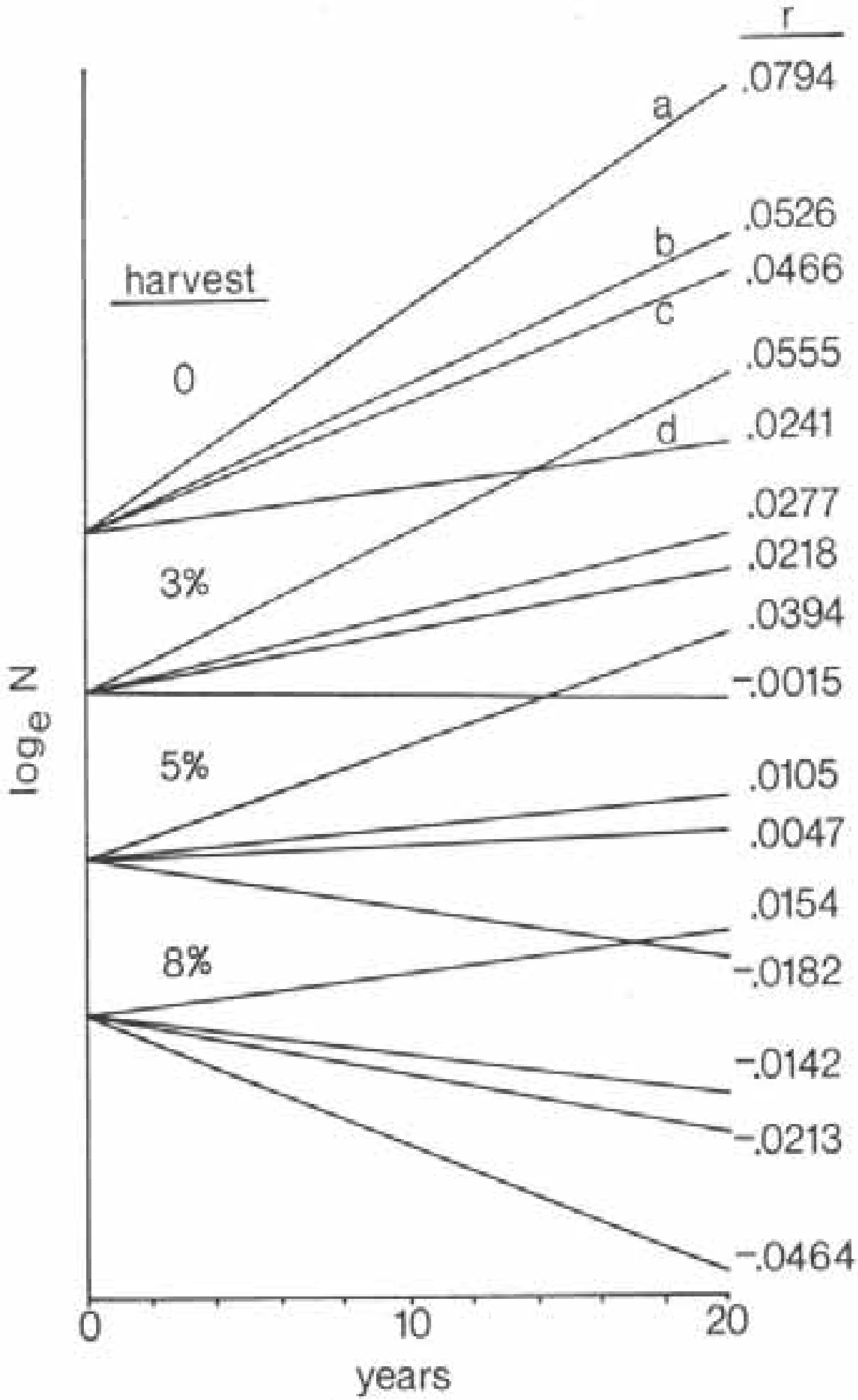

Figure 5. Population projections showing changes in r due to changes in adult harvest rate. Refer to text for mortality and productivity rates used in a,b,c and d.

The impact of harvest varies if the harvest is distributed disproportionately between sexes. Table 5 provides a numerical illustration of this result. It is shown that if the proportion of males in the harvest is greater than the proportion of females then a higher sustainable harvest can be achieved. In this example the highest net 10 year harvest, maintaining a positive rate of increase, is realized with a 30 percent male harvest and 0 percent female harvest. However, under such a harvest regime the number of adult males in the population drastically declines, with a resultant decline in actual harvest (even though a constant percent is harvested). Regardless, these results indicate that a harvest regime selecting for males has the least impact on population growth.

Relationships between parameters and rates of increase within the present model were investigated by varying one parameter value while keeping all other parameter values constant over a number of projections (>2). Using this procedure, changes in the stable rate of increase could be directly correlated to changes in the selected parameter value.

Within this model the influence of an initial age ratio on r is negligable. Variations in age ratios result in initial differences in the rate of increase, but under constant schedules of survival and fecundity age ratios converge to a stable form and produce a stable rate of increase. Table 6 provides an example of age ratio stabilization. However, it should be stressed that age ratio stabilization is probably more of a model phenomenon than a real phenomenon, as under natural conditions survival and fecundity are rarely constant over an extended time period.

Harvest Rates			Actual Harvest (Years After Imposing Harvest Regime)											
Male	Female	r	1	2	3	4	5	6	7	8	9	10	Net 10-Yr. Harvest	
0	0	0.0528	0	0	0	0	0	0	0	0	0	0	0	(0)
.03	.03	0.0277	2.1	2.2	2.3	2.4	2.4	2.5	2.6	2.6	2.7	2.8	24.6	(20)
.05	.05	0.0105	3.6	3.6	3.7	3.8	3.8	3.8	3.9	3.9	4.0	4.0	38.1	(32)
.08	.08	-0.0142	5.7	5.7	5.7	5.6	5.5	5.4	5.3	5.2	5.2	5.1	54.4	(50)
.25	.25	-0.1748	17.8	14.9	12.9	10.8	9.1	7.7	6.5	5.4	4.6	3.9	93.6	(87)
.25	.05	-0.0023	10.7	9.2	8.4	7.6	7.0	6.7	6.5	6.4	6.3	6.3	75.1	(71)
.30	0	0.0462	10.7	8.4	7.0	6.0	5.5	5.2	5.1	5.2	5.3	5.5	63.9	(61)
0	.30	-0.0848	10.7	8.4	7.0	5.6	4.4	3.6	2.9	2.3	1.8	1.5	48.2	(43)

Table 5. Numerical illustration of differences in r and actual harvest when the sex ratio of the harvest is manipulated.

Initial Age Ratios			Age Ratios After 12 Yrs.			Productivity	Mortality			r
K	Y	A	K	Y	A		K	Y	A	
.19	.12	.69	.17	.11	.72	.56	.36	.22	.07	.055
.20	.14	.65	.17	.11	.72	.56	.36	.22	.07	.055
.212	.069	.719	.17	.11	.72	.56	.36	.22	.07	.055
.167	.042	.792	.17	.11	.72	.56	.36	.22	.07	.055
.16	.10	.75	.17	.11	.72	.56	.36	.22	.07	.055

Table 6. Example of the principle of stable age distribution occurring when productivity and mortality schedules are constant through time.

The influence of adult sex ratio (males per 100 females) on r is minimal. Variations in sex ratio result in only minor changes in r. The direction of change in r is negative as males per 100 females is increased, and positive as males per 100 females is decreased. Population projection series C in Figure 6 illustrates this graphically. The slope of each of these population trends plotted on a $\log_e$ scale is equal to r. The relationship between adult sex ratio and r is illustrated in a more quantitive manner in Figure 7. Lines A and B represent sex ratio values regressed against r values (correlations = -1) for two different sets of survival and fecundity, as indicated below:

	Productivity Rate	Mortality Rate		
		Kid	Yearling	Adult
A	.57	.53	.14	.05
B	.56	.36	.22	.07

The slope of both A and B equals -0.00015, and consequently a shift in sex ratio in either direction results in only a minor change in r. Different schedules of survival and fecundity produce a shift along the y-axis only (indicating basic differences in rates of increase between schedules). Therefore, within the present model the regression, $r = -0.00015X + b$ (where X = sex ratio and b = y - intercept), approximates the relationship between r and sex ratio for all schedules of survival and fecundity. The dotted line included in Figure 7 is intended to indicate that this relationship probably only holds for sex ratios above a critical level where there are enough males to fertilize all potentially productive females. The critical level(s) at which this relationship breaks down, and the manner in which r falls to 0, are not known.

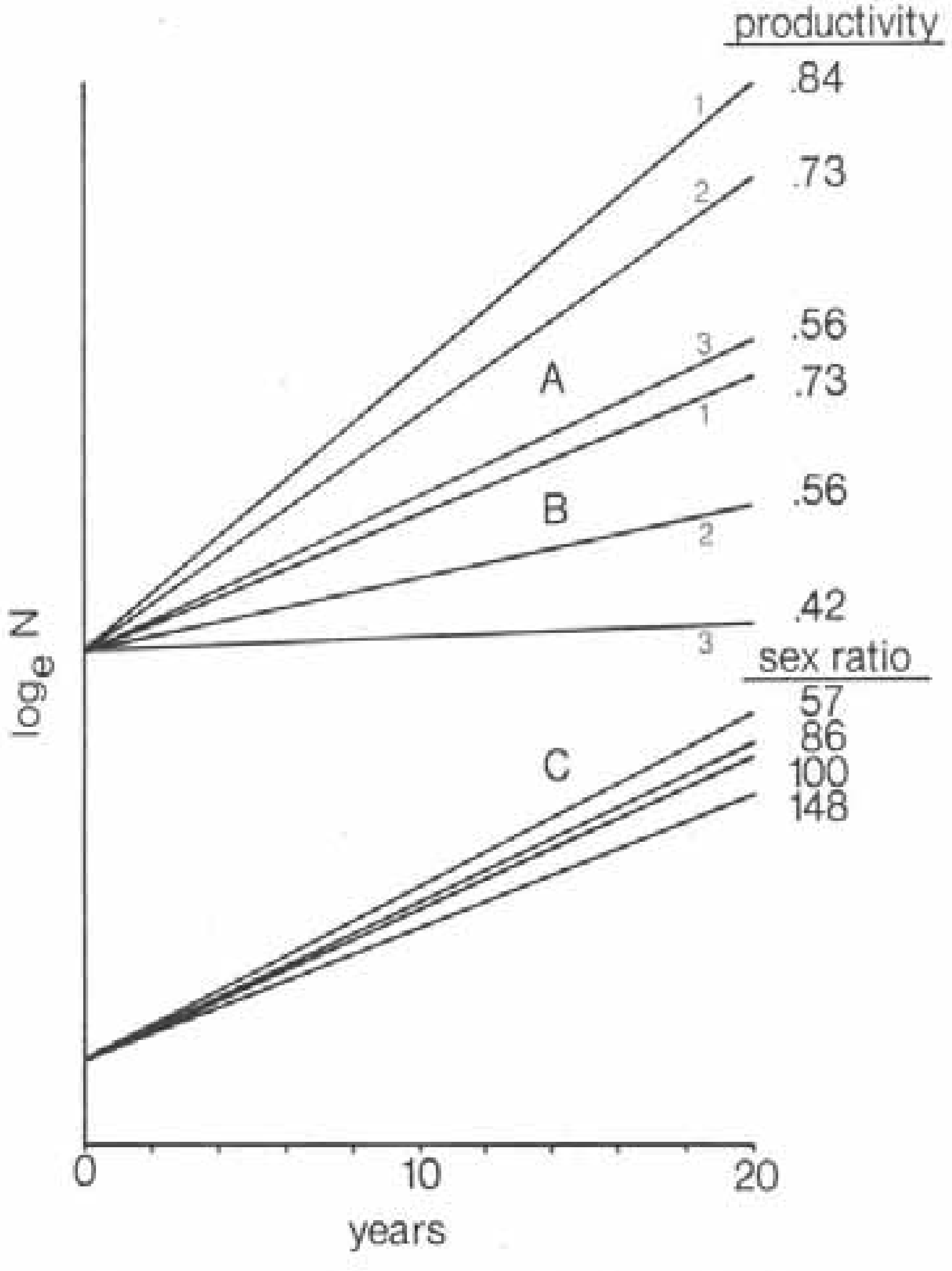

Figure 6. Population projections showing the changes in r due to changes in productivity (A,B) and sex ratio (C). Note changing sex ratio has minor effect on r in comparison to changing productivity. Refer to text.

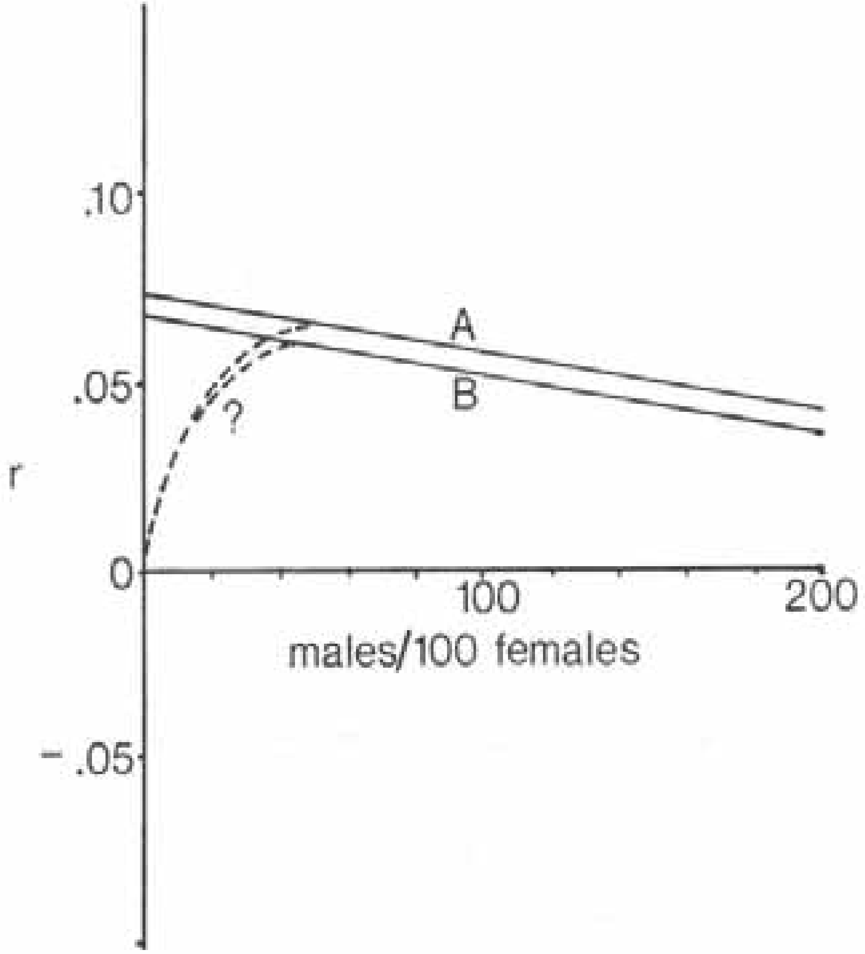

Figure 7. Relationships between adult sex ratio and r for two different survival and fecundity schedules (refer to text).

The influence of productivity on rate of increase is far greater than the influence of sex ratio. Minor changes in productivity rates have major impacts on r. Population projection series A and B in Figure 6 illustrate this result. The sets of mortality values used for A and B are indicated below:

	Mortality Rate		
	Kid	Yearling	Adult
A	.36	.22	.07
B	.60	.20	.07

Population projections of series A have higher values than projections in series B, due to lower kid mortality rates. However, the magnitude of changes in r resulting from changes in productivity are similar. Regressions of productivity rate against r (correlations equal 1) have similar slopes. Figure 8 indicates three such lines (a, b, c) which differ in mortality rates as indicated below:-

	Mortality Rate		
	Kid	Yearling	Adult
a	.53	.14	.05
b	.36	.22	.07
c	.60	.20	.07

The mortality rates influence the positioning of these lines vertically on the y-axis (r), but have only a minor influence on the slope of the lines. Thus, a general relationship between r and productivity rate in the present model can be described such that $r = 0.14X + b$ (where X = productivity rate, b = y - intercept). In Figure 8 a series of lines with identical slopes (parallel to a, b and c) could

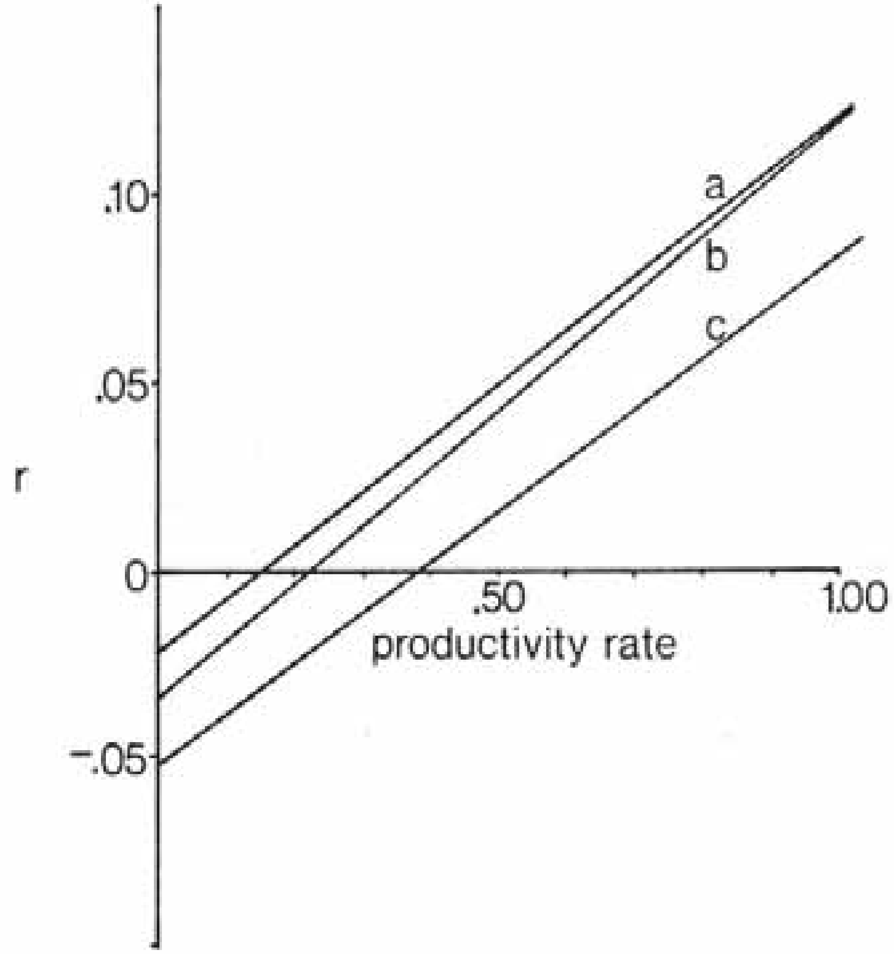

Figure 8. Relationships between productivity rate and r for three different mortality regimes (refer to text).

conceivably be drawn vertically along the r axis, ad infinitum, to represent the relationship between productivity rate and r for all possible mortality regimes.

The influence of mortality on r was investigated using three mortality classes; kids, yearlings and adults. Variation of adult mortality had the greatest impact on r. This result is indicated in Figure 9, where population projection series A, B, and C, represent adult, kid, and yearling mortality variations, respectively. It is shown that a 2 percent change in adult mortality results in a net change of 0.017 in r; a 10 percent change in kid mortality results in a net change of 0.014 in r; and a 10 percent change in yearling mortality results in a net change of only 0.010 in r. Changes in adult mortality have the greatest impact on r largely because the adult age class in the present model constitutes more than one age class, and therefore changes impact on more than one age class.

Regressions for r and mortality rate (correlations = -1) were calculated for each mortality class (Figure 10). Survival and fecundity schedules for lines a through f are indicated below:

	Productivity Rate	Mortality Rate		
		Kid	Yearling	Adult
a	.57	varied	.24	.05
b	.57	.53	.20	.07
c	.57	.53	varied	.05
d	.57	.53	varied	.07
e	.57	.43	.14	varied
f	.57	.53	.24	varied

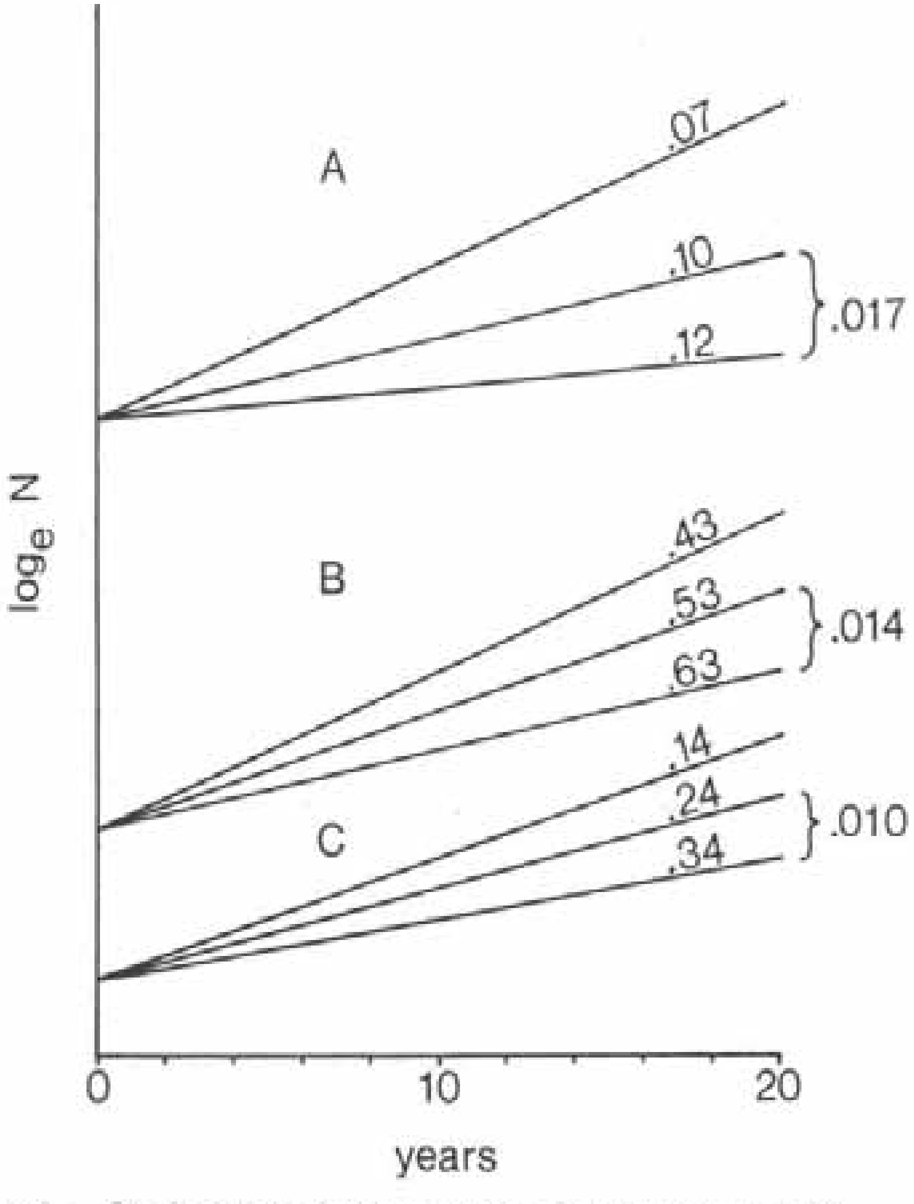

Figure 9. Population projections showing the changes in r due to changes in adult mortality (A), kid mortality (B), and yearling mortality (C). Refer to text for productivity and mortality schedules.

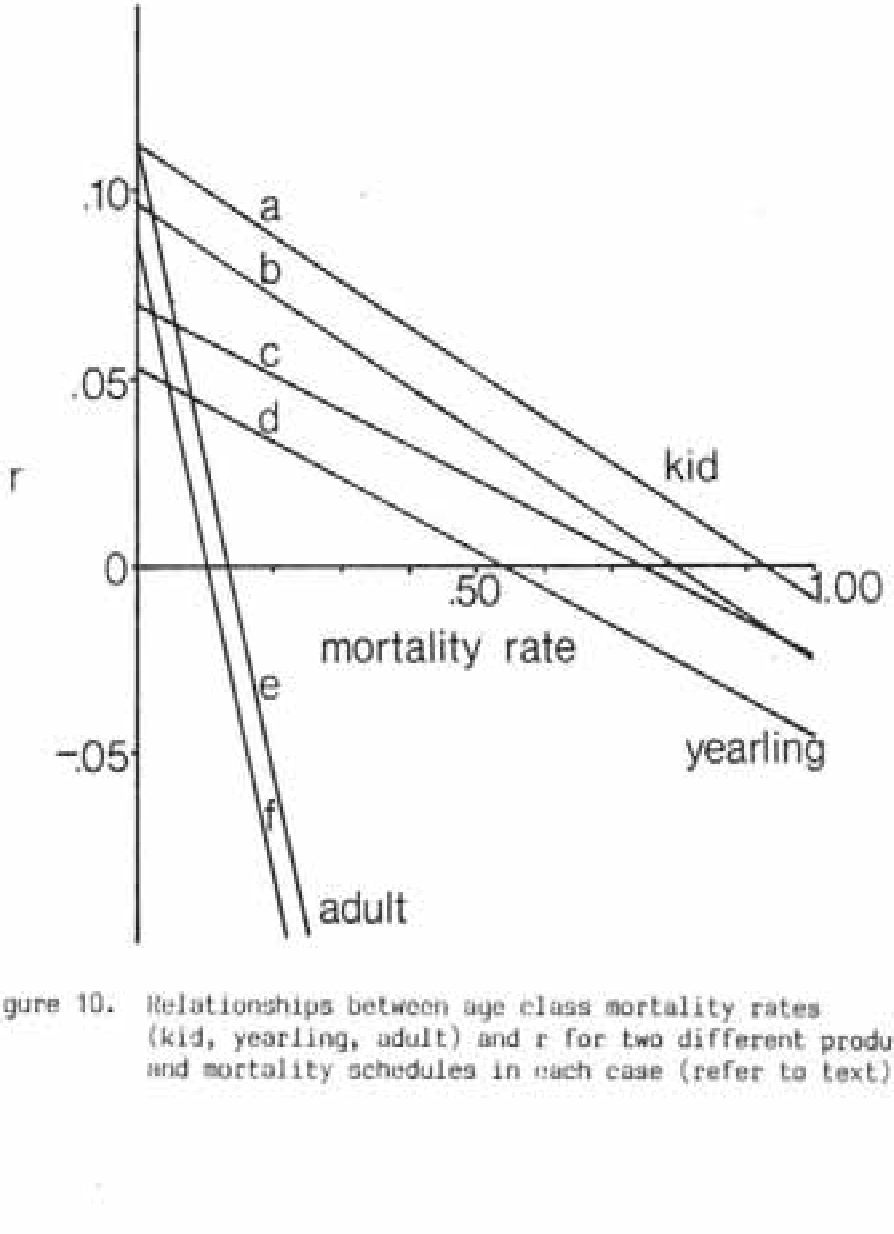

Figure 10. Relationships between age class mortality rates (kid, yearling, adult) and r for two different productivity and mortality schedules in each case (refer to text).

A general relationship describing the kid mortality class lines (a,b) is $r = -0.12X + b$; the yearling mortality class lines (c,d), $r = -0.09X + b$; and the adult mortality class lines (e,f), $r = -0.85X + b$. The comparatively greater slopes of lines e and f indicate the potential major impacts of small changes in adult mortality on rate of increase.

Discussion

Parameter Value Estimates

Productivity estimates used for simulation fall within the range of literature values. The median kid per 100 female value from the Willmore area compares well with intensive data collected in two other areas (Chadwick, 1977; Foster, 1978):

Area	Author	K/100F
Willmore	This paper	57
North Central B.C.	Foster	55
Montana	Chadwick	57

The appearance of two modes in the frequency histogram of Willmore kid per 100 female values (Figure 3) suggests the possibility of two average productivity values; one average at approximately 50-60 K/100F and a second average at approximately 90-100 K/100F. Cursory examination of the Willmore productivity estimates suggests that herd productivity may fluctuate on an annual basis.

The maximum productivity value used for simulation (90 K/100F) is exceeded by several values reported in the literature (Stevens and Driver, 1978; Hibbs, 1965, Thompson and Guenzel, 1978). However, each of these values have been from introduced herds, and it has been suggested that such herds experience a density-dependent decline in reproductive success as they grow larger (Bailey and Johnson, 1977).

Area	Author	K/100F
Olympics, Washington	Stevens	97
Eagles Nest, Colorado	Thompson	125
Colorado	Hibbs	150

It must also be noted that in each of these cases it is not known whether the reported K/100F value represents an average value. High K/100F values have also been observed in the Willmore area (eg. 117, 105, 97), but these high values did not represent long term trends, for this reason they were not used as maximum values in simulation.

Kid mortality estimates used for simulation are generally higher than those that have been reported in the literature, though the minimum estimate (36 percent) compares well with literature values:

Source		Kid Mortality Estimates(%)	
This paper: Minimum est.		36	
: Mean est.		53	
: Maximum est.		67	
Stevens and Driver (1979)		33	
Chadwick (1977)	a	41	(74-75)
	b	27	(75-76)

The difference between maximum estimates and literature values is possibly an artifact of kid mortality calculation techniques; yearling:kid ratios and Y/100A : K/100A ratios may provide biased estimates if sampling techniques are not consistent. However, values calculated for the entire Willmore area from 1973-1977 indicate that mortality estimates can fluctuate substantially, and a mean estimate for this area of approximately 50 percent may not be wrong (Hall and Bibaud, 1978).

Year	Kid Mortality Estimate(%)
1973-1974	37
1974-1975	19
1975-1976	76
1976-1977	42

Yearling mortality estimates have rarely been reported in the literature. Cahdwick (1977) has reported estimates of 44 percent and 15 percent for two consecutive years. Vaughan (1975) worked out a hypothetical model to fit the observed growth of a specific goat herd with an estimated yearling mortality rate of 20 percent. Estimates used for simulation (14-34 percent) compare well with these estimates, however, it must be stressed that quantitative data on this parameter is limited.

Adult mortality estimates, outside of guesses, are completely lacking in the literature. More intensive research on the value(s) of this parameter is required. Estimates used for simulation cover a broad range (5-12 percent), but as indicated in simulation results small changes in adult mortality can have major impacts on r. More realistic estimates of rate of increase require more precise estimates of adult mortality.

Generally, the parameter value estimates, or their respective ranges, approximately fit available literature values. As noted for productivity estimates, there are undoubtedly specific sets of circumstances under which these estimates are either too low or too high. However, it is believed that such circumstances arise rarely and are of a short duration.

Simulation

Preliminary rates of increase calculated through simulation

(Table 4) are based on constant survival and fecundity schedules, and results must be interpreted in this light. Population projections simulate an expected rate of population growth given a specific set of population parameter values; they do not predict how population parameter values will change over time. Rates of increase in this instance, must be interpreted as instantaneous measures of growth. As an example, given inventory results which indicate a stable age distribution, an even sex ratio, a productivity value of 56 kids per 100 females, an adult mortality rate of 7 percent, a yearling mortality rate of 22 percent, and a kid mortality rate of 36 percent, the expected rate of population growth will be approximately 5.3 percent annually ($r = 0.0519, \lambda = 1.0533$), until these parameter values change. The potential management value of such a measure of population growth is that, given sufficient data, the manager is able to know the direction of population growth, and able to assess impacts on this growth, in the present tense and immediate future.

The maximum r value calculated using the upper range of productivity estimates and the lower range of mortality estimates ($r = 0.1024$) represents an approximate intrinsic rate of increase (r_m) for mountain goats in the present study area. This value of r_m may be exceeded under environmental conditions where productivity is greater than one kid per adult female (eg. transplants). The present estimate of r_m may over-estimate this value by considering all females 2.5 years or over as productive females. Many studies suggest that under most circumstances females do not breed until 3.5 years of age (Hibbs, 1966; Hjelford, 1971; Rideout, 1974; Stevens and Driver, 1978).

Most rates of increase reported in the literature are for transplanted goat populations, (Hibbs et al., 1969; Vaughan, 1975; Stevens and Driver, 1978; Thompson et al., 1978) with one exception being a rate of increase reported for a harvested population (Kuck 1977).

Author	Area	% Rate of Increase	λ	r	Time Span (years)	K/100F	Comments
		13.0	1.1300	0.1222	1		
Vaughan	Oregon	11.5	1.1150	0.1089	1		Transplant
Hibbs	Colorado	15.5	1.1550	0.1441	30	150	Transplant
Stevens	Washington	11.0	1.1100	0.1044	45	97	Transplant
Thompson & Guenzel	Colorado	30.0	1.3000	0.2624	9	125	Transplant
Kuck*	Idaho	-14.0	0.8597	-0.1512	5	(11-19%)	Native, harvested

* This rate of increase was presented as -0.7561 for a five year period; productivity is percentage of kids in total population

As mentioned previously, transplanted populations have been noted to have substantially higher productivity rates than native populations (Bailey and Johnson, 1977). This difference can explain differences between the observed rates of increase in the first three examples (Vaughan, Hibbs, Stevens) and the approximate r_m calculated for the present study area. However, the observed rate of increase reported by Thompson and Guenzel (1978) can not be explained in this manner. Simulations using their reported productivity estimate (125 K/100F) and low mortality estimates of 20, 10, and 2 percent for kids, yearlings and adults, respectively, could not duplicate the reported rate of increase (0.2624). It is possible that recent censuses have over-estimated the number of goats in this population.

Harvest impacts on populations vary dependent on productivity and mortality rates in a population. It has been suggested that a 5 percent harvest rate is safe (sustainable) and conservative (Hall and Bibaud, 1978). However, in light of the present results such a statement needs to be modified: 5 percent harvest of adults is safe (sustainable) given moderate productivity rates (approximately 57 kids per 100 females) and mortality rates equal to or less than 40, 10 and 7 percent of kids, yearlings and adults, respectively. As indicated from the approximation of r_m (0.1024), sustainable harvests may range as high as 8 - 10 percent under certain circumstances. Foster (1978) reports a herd in north central British Columbia, which apparently sustains a harvest level of 10 percent. From a management viewpoint, harvest rates need to be refined to respond to differences in productivity and mortality between populations, and also need to be flexible enough to respond to changes in productivity and mortality within a population. If populations are to be harvested in excess of 3-5 percent, detailed population dynamics information is a necessity.

In assessing harvest impacts it is necessary to regard the sensitivity of rate of increase to changes in adult mortality (Figure 10). As an example, Kuck (1977) reports a negative rate of increase (-0.1512) for a population which was harvested at a rate of approximately 12 - 13 percent (of the adults). If it is assumed that this mortality was additive to natural mortality, then adult mortality within this population might have totalled 20 percent. In populations with moderate to high productivity rates, an adult mortality rate as high as this would probably result in negative rates of increase, as indicated in Figure 10. However, Kuck (1977) reported low productivity rates for this population, and therefore impacts of these high adult mortality rates were even greater; the decline as reported was inevitable.

Productivity and mortality rates, if dispersal is ignored, determine the rate of population growth (Caughley, 1977). Within the present study productivity was treated as a single rate for all adult females two years and older, while mortality rates were assessed in terms of three age classes, kids, yearlings and adults. Relationships between each of these population parameters and rate of increase (Figure 8 and Figure 10) indicate that productivity and adult mortality may be the two most important parameters in terms of population growth; small changes in the values of these parameters result in large changes in r. However, it should be stressed that it is difficult to interpret relative parameter importance without knowing more about the natural variability of the parameter. For instance, it is possible that under many situations variability in adult mortality is low, and consequently changes in productivity rates would be the most important factor affecting r. It should also be noted that the relative importance of adult mortality compared to kid and yearling mortality results directly from the fact that the adult age class (in the model) constitutes a large number of single year age classes.

Quantitatively, relationships presented in Figure 8 and Figure 10 must be interpreted with caution. These figures suggest linear relationships between each parameter and r given that all other parameters remain constant. In the real world, as the reported data indicates, constancy is not the general rule. With this caution in mind, it may prove useful to test some of the predictions suggested in each of these figures. For instance, with a constant mortality regime of 60, 20, 7 percent (K,Y,A) does a productivity rate below 40 kids per 100 females result in a negative rate as predicted? Another example: if adult mortality shifts 10 percent (manipulated through harvest) does the rate of increase also drop the magnitude predicted (.085)? Examination of these questions and refinement of these predictions should be considered in the design of census studies.

Conclusions

The simulation model used in the present analysis does not predict future population directions, but merely projects established population directions through time. To restate this, the model simulates population growth given a set of constant population parameter values; it does not predict these parameter values or how they will change with density. This is important to understand in interpreting the results.

Based on a range of population parameter values estimated from field data, a maximum positive r value of approximately 0.10 ($\lambda = 1.11$) was generated. Under certain circumstances this value of r may be exceeded through higher productivity rates and lower mortality rates. Such circumstances may occur with the introduction of goats into new areas.

Population response to harvest is dependent on productivity and mortality rates within the harvested population. Potential, sustainable harvest will range from 0 to 10 percent of the adults, dependent upon these parameters. This harvest rate may be increased if more males are harvested than females. However, impacts of disproportionate harvest strategies on mountain goat social and reproductive habits are not well understood.

It is predicted that rates of increase are sensitive to changes in adult mortality. This has important implications in regard to harvest policies, suggesting that harvest rates must be tied to the rate of increase (based on parameter values) in order to avoid overharvesting. It may be possible to utilize this rate of increase sensitivity to adult mortality in population dynamics studies. Experimental manipulation of harvest rates, together with accurate population monitoring, could provide valuable information on population growth.

To sum up: the results and predictions reported in the paper are by no means profound. They are a basic restatement of the principle that mortality and fecundity are the two main processes controlling population growth. It is hoped that the present examination has pointed out a need and value, in many management situations, to know approximate values of the mortality and fecundity parameters for mountain goats. It is only with such knowledge that we will be capable of understanding, and a step closer to predicting, mountain goat population growth.

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QUESTION - RESPONSES

Rick Guenzel: I can buy that population estimates will throw off your estimates for "r" (rate of increase). What I'm wondering is like for wild populations when you take measured data, like that where they observed 130% increases in the Crazy Mountain populations; how high above, intuitively, do you think they would go comparing that mean. But, with our data, an exponential rate of increase, it seems like there was a small change in r.

John Youds: I think what you have to do first is quantify mortality rates and try an quantify your productivity rates and look at those in terms of your observed rates of increase. Right now that's probably impossible at this basis of modeling that such result can occur. Your reported productivity for that herd, 125 kids per 100 famales; with that I could not simulate such a rate of increase, even with mortality rates that are so low as to be virtually impossible. They may occur in one year, but over a 10 year period as reported, it just can't happen.