A POPULATION PERSPECTIVE OF SUCCESSFUL MOUNTAIN GOAT TRANSPLANTS

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ABSTRACT: The mountain goat (Oreamnos americanus) has been introduced into at least 29 areas. Eleven of these transplants were evaluated to determine what effects the demographic characteristics of the introduced stock had on population growth. The average rate of increase for introduced populations up to 20 years post-introduction was compared to the following parameters using simple and multiple regressions: the number of individuals released, the number of different populations from which the introduced goats were taken, the sex ratio of the animals released, the number of introductions, the average number of goats released per introduction, and the average time interval between subsequent introductions. Significance of these regressions was tested using an F-test. For all parameters, either alone or in combination, no significant correlations were found. This may indicate that other factors related to habitat quality and environment may be more important in influencing population growth than the demographic properties of the individuals released. On average, 13.5 goats were released in 2.1 introductions per population. The average male-to-female ratio was 0.622. The mean number of populations from which transplanted goats were taken was 1.6. It was noted that the three populations having the highest rates of increase had some factor such as salt which may have encouraged the population to stay together rather than disperse.

Of all the North American ungulates, the mountain goat is one of the least studied and understood. The natural distribution of the mountain goat during historical times has been restricted to the mountainous regions of North America, principally west of the Continental Divide (Fig. 1). There are many areas of potential habitat beyond the native range of the mountain goat, especially in the Central and Southern Rocky Mountains (Rutherford 1972a). Mountain goats have been introduced into many areas where seemingly unoccupied niches occur in order to help meet the increasing demands for hunting and non-consumptive uses of wildlife. Since the early-to-mid 1920's, more than 278

Figure 1. Distribution map for the mountain goat in North America showing the native (striped) and introduced (solid) range of this species (after Johnson 1977a).


DISTRIBUTION
OF THE
MOUNTAIN GOAT
IN
NORTH
AMERICA
NATIVE
INTRODUCED

goats have been introduced in at least 29 areas (Table 1).

Though many reports have addressed the procedures used in trapping and transplanting mountain goats (Couey 1948, McDowell and Stockstad 1952, Rutherford 1972b, Rideout 1974), few have looked at the demographic parameters of the groups of individuals which have been released. The purpose of this paper is to evaluate the performance of successful mountain goat transplants with respect to the characteristics of the goats which were released. For this discussion, a "successful" mountain goat transplant is defined as an introduction in which the population increased and is still in existence. Knowledge of what effect these parameters have on population growth would be useful in formulating guidelines for future introductions.

It is obvious that the habitat to which the goats are released must be suitable. Otherwise, the new population cannot establish itself regardless of the quality or quantity of individuals released. The following analyses presuppose the above to be true, though relative differences among habitats of different populations may occur as well as vary through time. It is also apparent that these environmental differences may influence the population response of introduced herds.

METHODS

Riney (1967) identified 5 types of population responses for introduced species in new habitats: (1) size of the animal, (2) age structure, (3) sex ratios, (4) population density, and (5) physical condition. I have chosen aspects of types 3 and 4 for analyses based upon published

Table 1. Summary of reported mountain goat introductions.

POPULATION	YEAR	NUMBER OF GOATS RELEASED[a]	MALES	FEMALES	PARENT POPULATION	SOURCE
ALBERTA						
Shunda Mountains	1972	7	2	5	Alberta	Hall 1977
BRITISH COLUMBIA						
Vancouver Island	1924	4	-	-	Banff, Alberta	Lloyd 1925
ALASKA						
Baranof Island	1923	18	-	-	Tracey Arm, AK	Burris & McKnight 1973
Chichagof Island	1953	22(25)	-	-	-	"
Kodiak Island	1952	2	2		Seward, AK	"
		1	1		Cooper Lake, AK	"
		2	2		Seward, AK	"
		2	1	1	Eagle River, AK	"
	1953	10	1	9	Seward, AK	"
		17	7	10		
COLORADO						
Sawatch Range						
Mt. Shavano	1948	8(9)	3(4)	5	Montana	Denney 1977
Sheep Mountain	1950	6	2	4	"	"
		14(15)	5(6)	9		
Mount Evans	1961	14(15)	5(6)	9	Idaho & South Dakota	"

(continued)

Table 1 (continued). Summary of reported mountain goat introductions.

POPULATION	YEAR	NUMBER OF GOATS RELEASED[a]	MALES	FEMALES	PARENT POPULATION	SOURCE
COLORADO (continued)						
Needles Mountains						
San Cristobal	1964	8(10)	4(6)	4	South Dakota	Denney 1977
Chicago Basin	1971	4	1	3	British Columbia	"
		12(14)	5(7)	7		
Gore Range	1968	5	2	3	South Dakota	"
	1970	3(4)	1(2)	2	British Columbia	"
	1970	1		1	"	"
	1971	1	1		"	"
	1972	1	1		Mt. Shavano, CO	"
	1972	2		2	"	"
	1972	2	2		"	"
		15(16)	7(8)	8		
Marcellina Mountains	1975	4	2	2	Sheep Mountain, CO	"
IDAHO						
Lake Pend Oreille	1960	20	-	-	Snow Peak & Black Mountains, ID	Kuck 1977
Seven Devils Mountains	1962	8	4	4	-	"
	1974	9	2	7	-	"
		17	6	11		

(continued)

Table 1 (continued). Summary of reported mountain goat introductions.

POPULATION	YEAR	NUMBER OF GOATS RELEASED[a]	MALES	FEMALES	PARENT POPULATION	SOURCE
IDAHO (continued)						
Palisades						
Reservoir	1969	5	3	2	-	Kuck 1977
	1970	4	2	2	-	"
		9	5	4		
MONTANA						
Crazy Mountains	1941	4	2	2	-	Lentfer 1955
	1941	6	2	4	-	"
	1943	11	4	7	-	"
		21	8	13		
Rock Creek	1942	12	-	-	-	Stoneberg & Foss 1977
Stillwater Canyon	1945	2	-	-	-	"
	1946	7	-	-	-	"
		9				
East Rosebud						
Canyon	1948	5	-	-	-	"
	1952	10	-	-	-	"
	1953	7	-	-	-	"
	1956	5	-	-	-	"
		27				

(continued)

Table 1 (continued). Summary of reported mountain goat introductions.

POPULATION	YEAR	NUMBER OF GOATS RELEASED[a]	MALES	FEMALES	PARENT POPULATION	SOURCE
MONTANA (continued)						
Pine Creek	1957	10	-	-	-	Stoneberg & Foss 1977
	1958	6	-	-	-	"
		16				
NEVADA						
Ruby Mountains	1964	-	-	-	-	Johnson 1977a
OREGON						
Eagle Creek Wilderness	-	-	-	-	-	"
Tanner Butte	-	-	-	-	-	"
SOUTH DAKOTA						
Black Hills	1924	6	-	-	Rocky Mountain Park, Alberta	Harmon 1944
UTAH						
Wasatch Plateau	1967	-	-	-	-	Johnson 1977a
WASHINGTON						
Cascades						
Mt. St. Helens & Mt. Margaret	1972 & 1973	8	-	-	Mt. Angeles, Olympic Mountains, WA	Johnson 1977b

(continued)

Table I (continued). Summary of reported mountain goat introductions.

POPULATION	YEAR	NUMBER OF GOATS RELEASED[a]	MALES	FEMALES	PARENT POPULATION	SOURCE
WASHINGTON						
Cascades (continued)						
Mt. Pilchuck	1975	-	-	-	Olympic Mountains, WA	Johnson 1977b
	1976	-	-	-	"	"
Olympic Peninsula	1926	4	-	-	Selkirks, Alberta	"
	1927-30	7	-	-	Alaska	"
		11				
Selkirk Mountains	1965	7	-	-	-	"

[a] Numbers in parentheses indicate the number released prior to known mortality of the introduced stock.

accounts. Specifically, I examined the effects of the following parameters on population growth:

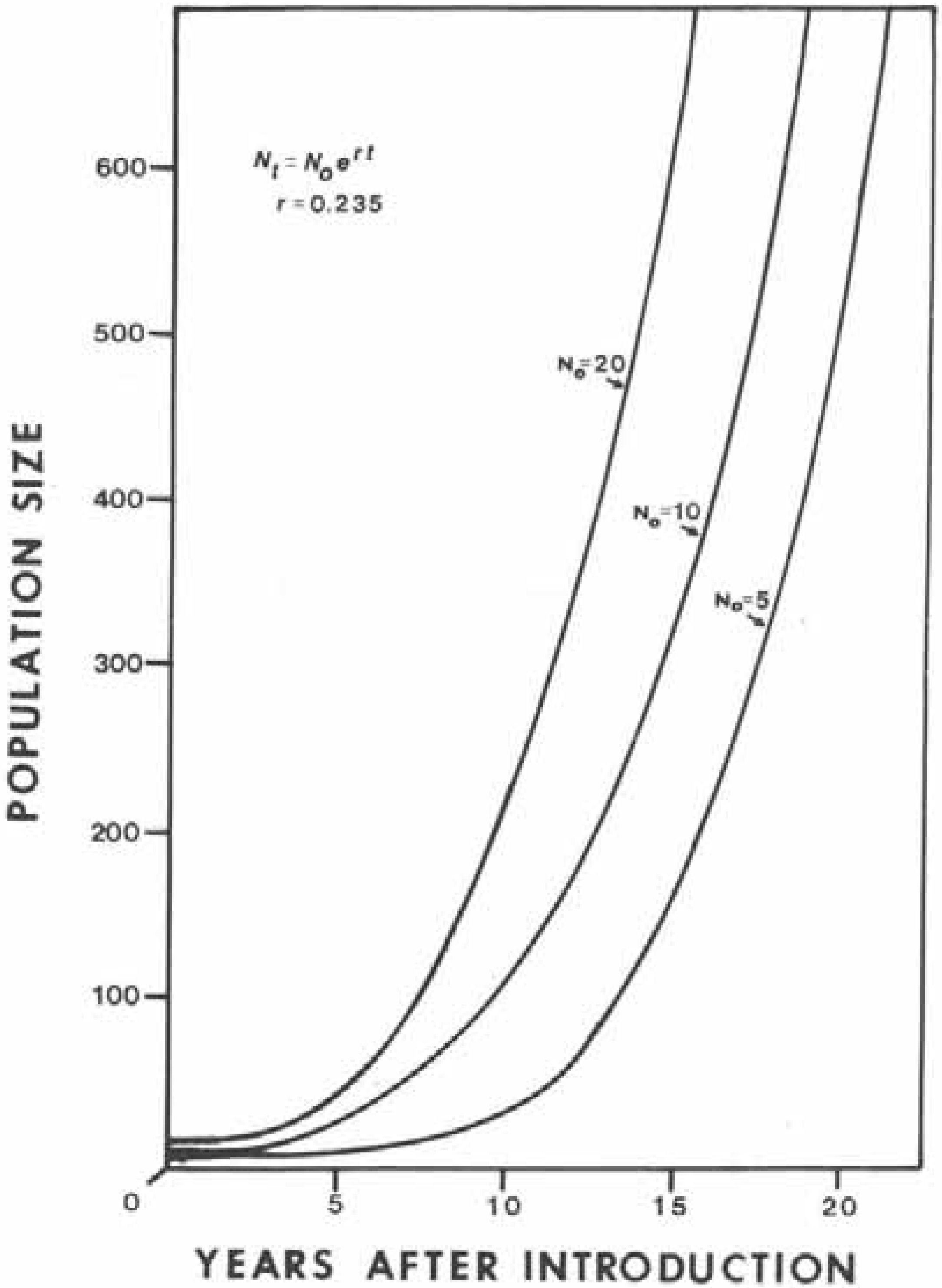
(1) number of individuals released.
(2) number of different populations from which the transplanted stock was taken.
(3) sex ratio of the introduced animals.
(4) average number of goats released per introduction.
(5) number of introductions.
(6) average time interval between introductions.

Age ratios for the introduced animals were omitted from the analyses since these were seldom reported.

One would expect the number of goats introduced to have an effect on how rapidly a population attained a particular size (Fig. 2), even though the rate of increase would be independent of the number of goats introduced during the initial growth phase of the population. It appears that many introduced mountain goat populations may increase exponentially until density-dependent factors become more influential. Exponential growth phases have been demonstrated for mountain goat populations on Kodiak Island in Alaska (Hjeljord 1971) and the Gore Range in Colorado (Thompson and Guenzel 1978). Hjeljord (1971) noted that mountain goat populations do not appear to overshoot their carrying capacity as drastically as some other ungulates (Klein 1968, Caughley 1970).

Introducing goats from different populations might increase the likelihood that some of these individuals could better exploit the new habitat and increase the chances for a successful transplant. Generally, introduced populations result from the release of relatively few individuals which might cause problems associated with inbreeding. Selecting animals for transplant from more than one population might alleviate some of these potential problems.

Figure 2. The effect of the number of animals introduced on population growth assuming an exponential rate of increase of 0.235.



$N_t = N_0 e^{rt}$
$r = 0.235$
$N_0 = 20$
$N_0 = 10$
$N_0 = 5$
600
500
400
300
200
100
0
5
10
15
20
POPULATION SIZE
YEARS AFTER INTRODUCTION

The ratio of males to females in the introduced stock may influence the rate of increase by affecting the potential number of offspring that may be produced. This assumes that these animals survive and reproduce. Since age-specific fertility can influence population growth, age ratios cannot be neglected. The number and frequency with which additional animals are released into the population might also be an important factor.

Published accounts of mountain goat introductions were examined and the 6 parameters above were tabularized for comparison with population growth data. Perhaps the best measure of actual performance of an introduced population with respect to population growth would be the amount of time it took to reach a specified population size following release. By this approach, one could evaluate population growth as a function of time after release. Unfortunately, very little continuous data on population sizes exist for introduced mountain goat herds and so this method was abandoned.

Instead, I selected the average (observed) rate of increase, $\bar{r}$, as the measure of population growth for comparison with the introduction parameters. This was determined for each population by the following equation:

$$\bar{r} = \frac{\ln\left(\frac{N_t}{N_o}\right)}{t} \qquad \text{(equation 1)}$$

where: N_o = initial population size (usually the number of goats introduced).

N_t = population size t years later.

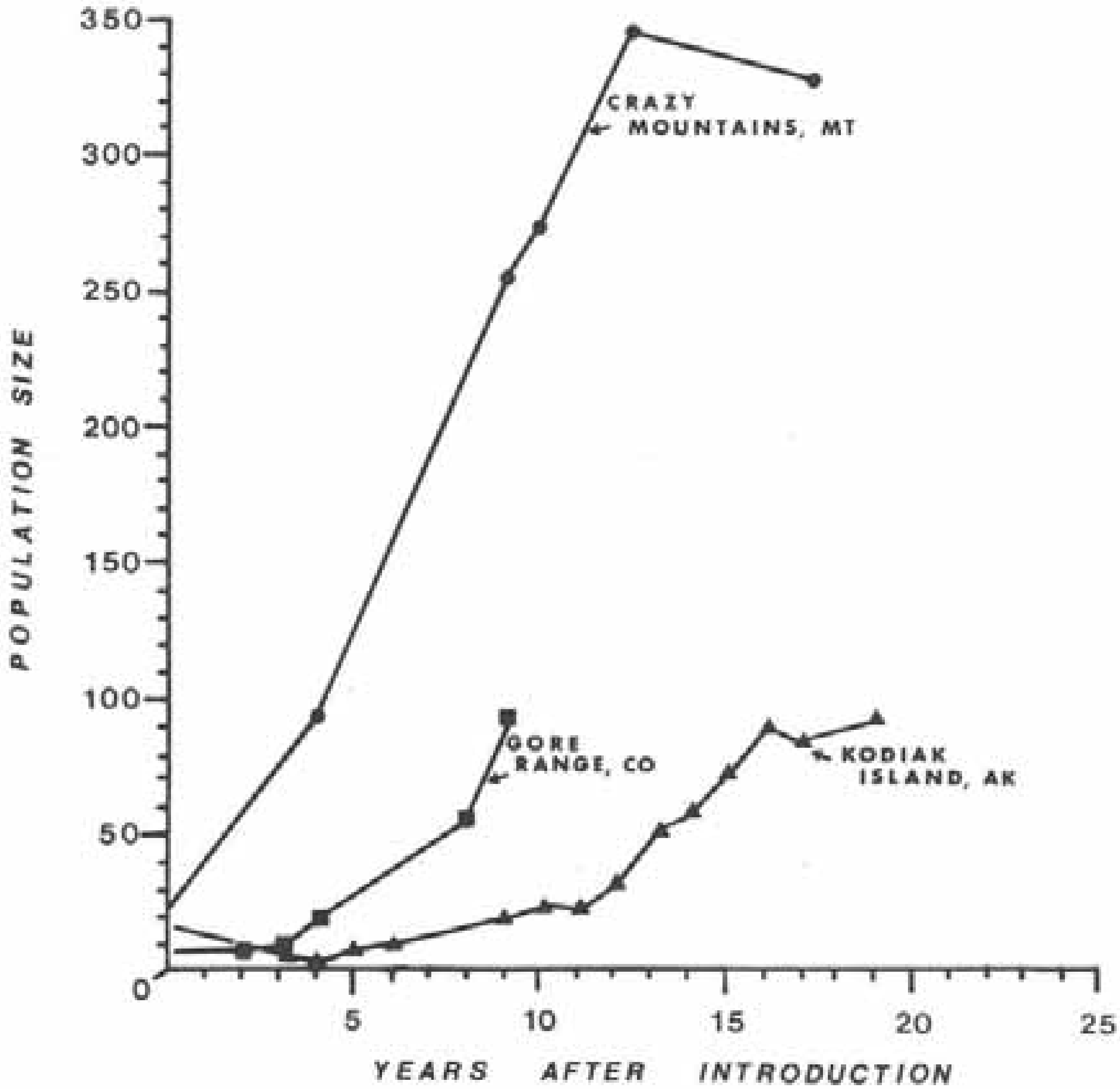
t = time interval in years from N_o to N_t.

However, the average rate of increase must be used cautiously when comparing populations as discussed below.

The rate of increase may be considered as some function between the difference in birth and death rates. For any given value of $\bar{r}$, there are a variety of combinations of birth and death rates. Each population has an intrinsic rate of increase which may be subsequently reduced through density-dependent and density-independent factors. Frequently, $\bar{r}$ may decline as higher population densities are reached. Density-dependent kid production has been observed in many mountain goat populations (Hjeljord 1971, Bailey and Johnson 1977, Stoneberg and Foss 1977).

When comparing $\bar{r}$'s, one must be careful to compare similar time periods. Average rates of increase for older, stabilized populations may be lower than $\bar{r}$'s for younger, expanding populations although an older population may have had a higher $\bar{r}$ when it was that young. Presumeably, once an introduced mountain goat population has reached its habitat's carrying capacity and equilibrated, $\bar{r}$ would be averaged with zero over time, unless some perturbation disrupted the equilibrium. For this reason, only $\bar{r}$'s determined for mountain goat populations up to 20 years post-release were used in the analyses. This period would be comprised mostly of the growing phase of the population (Fig. 3). Where multiple introductions occured over several years, a population estimate taken after the introduction period was used as the initial population size, N_o, in equation 1. The accuracy of the $\bar{r}$ determined for these populations depends on the reliability of the population estimates used. Much of the data on introduced mountain goat populations could not be included in the analyses because of the sketchiness of the information.

Figure 3. Population growth for 3 introduced mountain goat herds.


350
300
250
200
150
100
50
0
POPULATION SIZE
5
10
15
20
25
YEARS AFTER INTRODUCTION
CRAZY MOUNTAINS, MT
GORE RANGE, CO
KODIAK ISLAND, AK

There are few mountain goat populations where consecutive population data have been collected, particularly for early years following introduction.

The usable data were analyzed using simple and multiple regressions. All subsets of the set of introduction parameters were regressed against $\bar{r}$ for that population. An F-test was performed to determine the overall significance of the regression relationship.

RESULTS

The data from eleven introduced mountain goat populations used in the analysis were tabularized (Table 2). The results of the various regression analyses were consistent. None were significantly correlated ($p>0.5$), but appeared to be quite independent of $\bar{r}$. Figure 4 A, B, and C shows 3 of the simple linear regressions and the scatter diagrams for these data.

Based upon the information in Table 1, an average of 13.5 goats have been released in 2.1 introductions per introduced population. The mean male-to-female ratio for these introduced herds was 0.622. Goats for transplanting were taken from an average of 1.6 different populations.

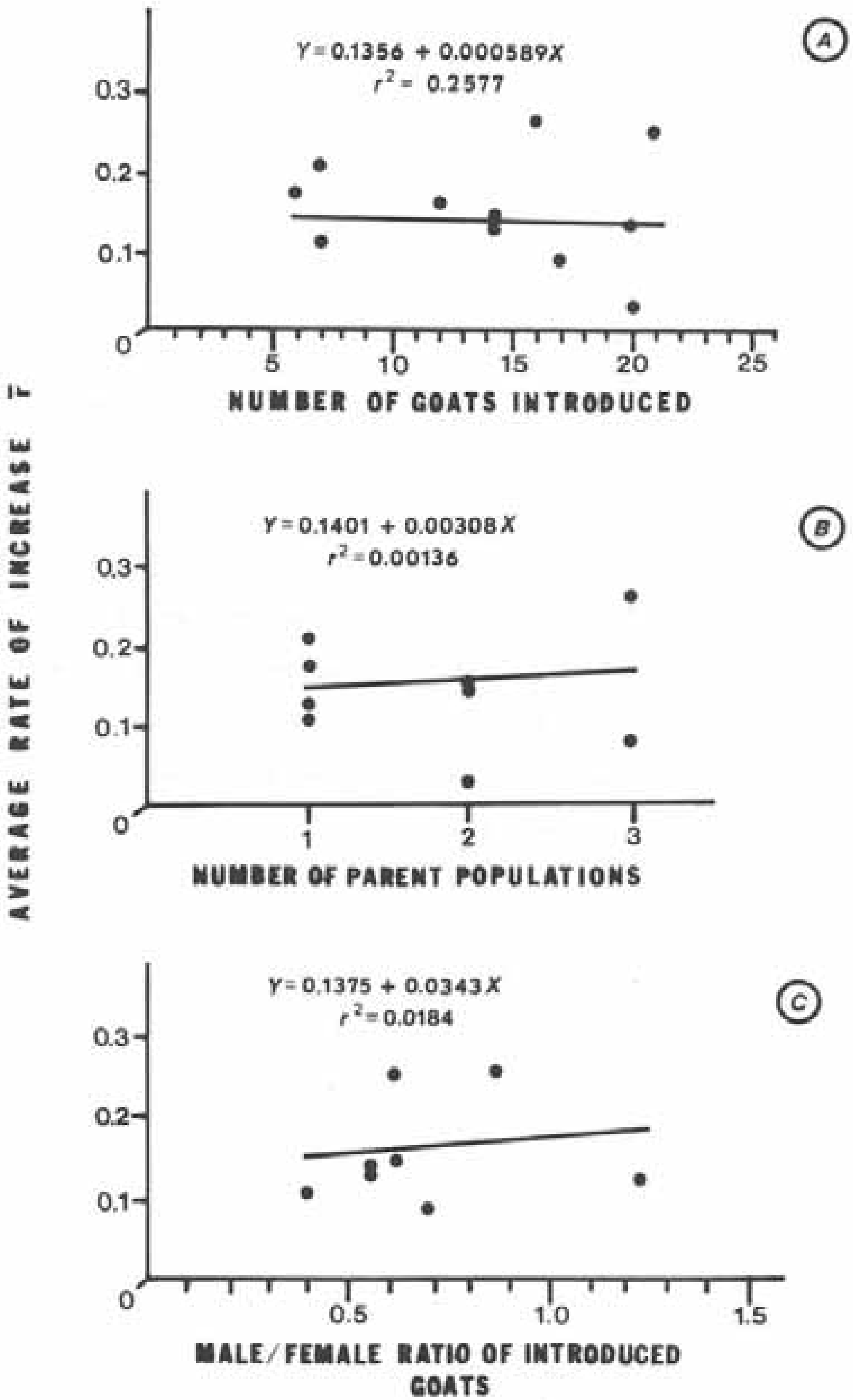
DISCUSSION

As was previously mentioned, the weak relationship between $\bar{r}$ and the number of goats transplanted would be expected (Fig. 4A). However, other factors associated with the number of goats introduced might have had some influence on population growth. One might expect the sex ratio of

Table 2. Summarization of data used in the regression analyses for introduced mountain goat populations.

POPULATION	X_1 NUMBER OF GOATS RELEASED	X_2 NUMBER OF PARENT POPULATIONS	X_3 MALE-TO-FEMALE RATIO	X_4 AVERAGE NUMBER OF GOATS PER INTRODUCTION	X_5 NUMBER OF TRANSPLANTS	X_6 AVERAGE TIME INTERVAL BETWEEN TRANSPLANTS	Y_1 AVERAGE RATE OF INCREASE $\bar{r}$
Shunda Mountains	7	1	0.4	7.0	1	0	0.113
Kodiak Island	17	3	0.7	3.4	5	0.4	0.088
Sawatch Range	14	1	0.56	7.0	2	2.0	0.149
Mount Evans	14	2	0.56	14.0	1	0	0.131
Needles Mountains	12	2	0.63	6.0	2	7.0	0.153
Gore Range	15	3	0.875	2.1	7	0.3	0.267
Lake Pend Oreille	20			20.0	1	0	0.025
Palisades Reservoir	9		1.25	4.5	2	1.0	0.133
Crazy Mountains	21		0.62	7.0	3	0.6	0.258
Black Hills	6	1		6.0	1	0	0.175
Selkirk Mountains	7	1		7.0	1	0	0.208

Figure 4. Least squares regressions of (a) the number of goats introduced, (b) the number of parent populations from which the transplant stock were taken, and (c) the ratio of males to females among introduced goats on the average rates of increase of populations at 20 years or less since transplant.



AVERAGE RATE OF INCREASE r̄
A
Y = 0.1356 + 0.000589X
r² = 0.2577
0.3
0.2
0.1
0
5
10
15
20
25
NUMBER OF GOATS INTRODUCED
B
Y = 0.1401 + 0.00308X
r² = 0.00136
0.3
0.2
0.1
0
1
2
3
NUMBER OF PARENT POPULATIONS
C
Y = 0.1375 + 0.0343X
r² = 0.0184
0.3
0.2
0.1
0
0.5
1.0
1.5
MALE/FEMALE RATIO OF INTRODUCED GOATS

introduced goats and the number of different populations from which these animals came to have some influence on population growth though the analyses did not support these expectations. It may be that the available data are insufficient for making comparisons between population growth and these parameters. The range in number of goats introduced is relatively narrow (4-27). Perhaps if data were available on populations where more goats had been transplanted, then some differences might have been apparent.

Although the above arguments may be true at least in part, the scattering of the data tends to indicate that there is very little tendency for these factors to correlate. Possibly, other aspects of the demography of introductions, for which little data exist, may be more important. However, it seems more likely that factors such as habitat quality and quantity or severity of the environment may be more important than these demographic considerations.

Though variations in reproductive output have been observed in introduced mountain goat herds (Hibbs 1965, Bailey and Johnson 1977), the greater proportion of the variation in rates of increase may be explained by variation in mortality rates as Caughley (1970) observed for Himalayan thar (Hemitragus jemlahicus) in New Zealand. The greater portion of this mortality may be attributable to losses in the kid and yearling age classes (Hibbs 1965). It appears that as a mountain goat population begins to grow, the major portion of kid and yearling mortality may be density-independent (Bailey and Johnson 1977), hence environmental factors may play an important role in determining $\bar{r}$'s. Adult mortality may be lower as the population begins to grow as density-dependent influences would be relatively minimal. Sinclair (1977) concluded that juvenile mortality of the African buffalo (Syncerus caffer) was probably density-independent while adult mortality was density-dependent.

Some mountain goat populations exhibited fairly high $\bar{r}$'s following introduction. The Crazy Mountains (Lentfer 1955, Stoneberg and Foss 1977), Gore Range (Sandfort 1973, Denney 1977, Thompson and Guenzel 1978) and Black Hills (Harmon 1944) populations have shown rapid growth rates which could not be explained by any of the parameters investigated. It may be that these populations were somewhat isolated so that goats did not tend to disperse far from the transplant site. Particularly noteable for the Crazy Mountains (Lentfer 1955) and Gore Range (Thompson and Guenzel 1978) populations was the use of salt to attract goats and keep them in the range. By keeping goats together, the opportunity for finding mates, even at low population densities, would be enhanced and more females would be likely to breed and bear young than if they dispersed. Survivorship and fertility in some of these introduced populations may be extremely high relative to some native goat populations. It may be erroneous to assume that mortality patterns for native herds, especially for adults, would be similar to those for increasing introduced populations. Physiologically, these high rates of increase may not be too unlikely. Woodgerd (1964) described the dynamics of a bighorn (Ovis canadensis) population where $\bar{r}$ was determined to be 0.265 (Buechner 1960). Since twinning is considered to be quite rare in bighorn populations (Geist 1971) but common in mountain goat populations (Brandborg 1955, Hibbs 1965, Bailey and Johnson 1977, Thompson and Guenzel 1978) as indicated by high kid:nanny ratios, it seems reasonable to assume that goat populations have the potential to increase more rapidly than bighorn populations.

In conclusion, I feel that demographic characteristics of the transplanted stock may have an influence on population growth, but other factors relating to the environment of the introduced population are more important in influencing population growth. Salt or other minerals may be useful in helping an introduced population become established. By evaluating the habitat of potential transplant sites, wildlife managers may be better able to determine the potential success of the transplant. Reinforcing the habitat evaluation with consideration of the quality and quantity of the individual goats selected for release, chances for a successfully established mountain goat population may be improved.

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QUESTIONS - RESPONSES

Tom Butts: Could you tell us how you calculated the rate in increase, what you labled the rate in increase?

Rick Guenzel: Yes. The rate of increase, you can look at in a couple of ways. One of them; suppose you know what the population size is at sometime, like at introduction or if your going to have multiple introductions you know what it is after the last introduction. You call that the initial population size and you know at sometime later, as far as the average rate of increase goes, what the population size is say "t" years later. You divide that population size of "t" years later by the initial population size, take the natural log of that, divide that by "t" years and that will give you an average rate of increase. If you just wanted to get just the rate of increase and you had good data year to year, you could just take the initial population size in say N_o then the population size then would be N_o+1 and so it would work out. You could plot those and that's how you could get one determinant in the intrinsic rate.

Tom Butts: One thing that you mentioned was that you couldn't; you know you can try to look at the sex ratios that were transplanted and yet you said there were problems in calculating or getting from the data the age of the animals transplanted. I would think, number one, that would enter into your rate of increase because if for instance you had a number of young or pre-breeding animals versus if you had a number that were breeding animals that would make a big difference. I think the sex ratio thing is something that a lot of people in the past haven't looked at carefully. When I've looked at population rates of increase calculated for bighorns for instance, they come up with a number, whatever you know little "r" whatever you want to call it, but, and then they compare it to another population and they say one population had this fast of a growth rate compared to the other, but I don't think they were done over a long period of time.

Rick Guenzel: Actually your right. The sex age ratio data is really important. I didn't have it so I couldn't use it. I think that even if I did it would improve these, but I think it may be intuitive that other things are influencing the rate of increase besides those as well.