POPULATION DYNAMICS, MOVEMENT AND
HOME RANGE OF BLACK-TAILED JACKRABBITS (*LEPUS*
CALIFORNICUS) IN CURLEW VALLEY, NORTHERN UTAH

MASTER

Progress Report
for Period October 1, 1975 - September 30, 1976

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Abstract

The long-term objective of the jackrabbit study in Curlew Valley, Utah and on the Idaho National Engineering Laboratory is to describe observed changes in rabbit density in terms of mortality and natality rates and to relate changes in these two population parameters to variation in environmental factors. Spring rabbit density in Curlew Valley has been observed to change by a factor of 60; changes appear to be largely determined by variation in mortality rates, as shown with K-factor analysis. Mortality of the population from fall-spring is correlated with the coyote/rabbit ratio. Spring-fall adult mortality and birth-fall loss of juveniles are correlated with coyote numbers. Coyote numbers in the relationships are modified to reflect variation in coyote feeding behavior with changes in rabbit and rodent numbers as indicated by coyote food habits studies in Curlew Valley. Coyote predation rates have varied markedly between years as a result of functional and numerical responses in the coyote population.

1. Introduction

Population ecology of the black-tailed jackrabbit population on a 250-square-mile area in Curlew Valley, Utah has been studied from 1962-1976. In spring 1975 the studies were expanded to include a 450-square-mile portion of the Idaho National Engineering Laboratory, INEL. The main objective is to describe observed changes in jackrabbit density in terms of mortality and natality rates, to relate changes in these two parameters to variation in environmental factors, and to integrate the results into a mathematical model describing population change. Controlled experiments are now being designed to investigate genetic and/or behavioral changes associated with observed high rates of juvenile mortality. In addition studies have been initiated this year to observe the effect of food supply on jackrabbit population dynamics.

The jackrabbit study in Curlew Valley is dependent on the U.S. Fish and Wildlife Service's Predator Ecology and Behavior Project for rodent and coyote density estimates and coyote food habits data for Curlew Valley. Conversely the rabbit project is providing the Fish and Wildlife Service with important data for its coyote ecology and coyote population modeling studies. On the INEL site, the rabbit project is also supplying the estimates of coyote and rodent density. Coyote food habits data on the INEL will be provided by Colorado State University under contract with the ERDA.

The present document describes findings from the 1975-1976 contract period along with some data obtained since the initiation of the project. In this way data obtained this year can be kept in perspective and demonstration made of their contribution to the long-range objectives of the study.

2. Population Measurement

Curlew Valley rabbit density indexes.-- October 1975 and March 1976 density indexes for the 250-square-mile study area in Curlew Valley were obtained using 68 one-mile foot transects. As in previous years, flushing angles and flushing distances of observed rabbits were recorded. Since flushing behavior of jackrabbits changes with density and between spring

and fall, the absolute number of jackrabbits seen on the transects cannot be used as an index to density. Instead, we have utilized the flushing angles and distances and an equation derived by Gates (1969) to correct the transect results for observed changes in flushing behavior (Stoddart 1972).

Transect results over the years of study (Table 1 and Fig. 1) show a slow, continuous decline in density from an index to 61 in fall 1963 to 21 in fall 1967. In the following 3 years density increased rapidly to 190 in fall 1970, an increase over the 3-year period of 9-fold. The next 3 years saw a very rapid decline in density to a low in October 1973 of 15. The fall 1974 index of 25 indicated an increase in density over fall 1973, however, the population decline resumed in 1975 with a fall density of 11, the lowest fall density yet observed. The spring 1976 density of 2.4 was approximately unchanged from spring 1975.

Rates of change from one census period to the next are indicated in the last 2 columns in Table 1. During this reporting period, the rabbit population increased 400 percent from March 1975 to October 1975. This is the second highest observed rate of increase over a breeding season. The over-summer increase was followed by an October 1975 to March 1976 decline of 78 percent, the second highest over-winter rate of loss we have observed. Demographic mechanisms underlying these rates of change will be discussed below.

INEL rabbit density index.-- A 450-square-mile portion of the INEL was selected in 1975 for the jackrabbit study area. This portion will henceforth be termed the "INEL study area". The INEL study area was selected in cooperation with the U.S. Fish and Wildlife Service which is conducting coyote studies in the same area. The INEL study area is shown in Figure 2 as the unshaded portion of the map of the INEL. Eighty one-mile foot transects were randomly located in the area (Fig. 3). For the rabbit transect locations, the study area was stratified into 6 vegetation types as determined utilizing INEL vegetation analyses of Harniss and West (1973) and McBride (1968).

The 80 rabbit transects on the INEL study area were first walked in April 1975. Only 1 jackrabbit was observed. In fall 1975, 2 rabbits were seen and in April 1976, no rabbits were observed. Using Gate's equation for transect data, indexes of 1, 9.1, and 0.0 were obtained for the 3 census periods respectively. These values compare with a recorded low spring density of 2.2 and a recorded fall low of 11 in Curlew Valley. The INEL rabbit indexes are shown graphically in Figure 4, along with rabbit indexes obtained using 6 scent post stations (see later section). The agreement between these two index methods is good. Spring 1976 scent posts indicate jackrabbits still do exist on the INEL site.

3. Natality

Each month approximately 50 adult rabbits are collected from the Curlew Valley study area. An autopsy is performed on each female to determine percent females breeding; litter size (Table 2), age of fetuses, and conception dates.

Table 1. Results of Curlew Valley Jackrabbit Population Transects.

Census date	No. Rabbits observed	Density index	Percent Density Change	
			Oct.-March	March-Oct.
Oct. 1962	29	40		
March 1963	19	14	-65	
Oct. 1963	66	61		336
March 1964	26	26	-57	
Oct. 1964	49	42		62
March 1965	30	18	-57	
Oct. 1965	28	33		83
March 1966	15	12	-64	
Oct. 1966	20	24		100
March 1967	9	7.4	-69	
Oct. 1967	12	21		184
March 1968	15	9.2	-56	
Oct. 1968	81	65		606
March 1969	75	43	-34	
Oct. 1969	192	120		179
March 1970	173	67	-44	
Oct. 1970	268	190		184
March 1971	181	130	-32	
Oct. 1971	191	160		23
March 1972	107	87	-46	
Oct. 1972	68	64		-26
March 1973	17	18	-72	
Oct. 1973	8	15		-17
March 1974	5	5.5	-63	
Oct. 1974	16	25		355
March 1975	2	2.2	-91	
Oct. 1975	7	11		400
March 1976	2	2.4	-78

Fig. 1. Spring jackrabbit population trends and fall coyote population trends in Curlew Valley. The broken line indicates coyote density index obtained using 4 scent post lines in spring and fall.

Fig. 2. INEL jackrabbit study area indicated by the unshaded portion of the INEL maps.

Fig. 3. Location of 80 one-mile jackrabbit transects within 6 major vegetation types in the INEL study area.

Fig. 4. INEL jackrabbit and coyote density indexes obtained using transects and scent posts.

Table 2. Percentage of January 1 female population alive, percentage littering, mean litter size, number of fetuses per female, and number of fetuses per female alive January 1 in each littering period for each year

Year	Littering period	(A) Percentage of Jan. 1 female pop. alive	(B) Percentage littering	(C) Mean litter size	(D) Fetuses per female (BXC)
1963	1	66	13	1.0	0.1
	2	49	95	4.8	4.6
	3	39	100	5.2	5.2
	4	30	70	5.1	3.6
	Totals			16.1	13.5
1964	1	66	100	2.1	2.1
	2	49	100	4.3	4.3
	3	33	100	5.5	5.5
	4	23	100	3.4	3.4
	Totals			15.3	15.3
1965	1	66	100	1.6	1.6
	2	54	100	4.5	4.5
	3	43	100	5.2	5.2
	4	33	50	3.5	1.8
	Totals			14.8	13.1
1966	1	66	100	1.6	1.6
	2	51	100	4.2	4.2
	3	41	100	5.8	5.8
	4	33	16	3.8	0.6
	Totals			15.4	12.2
1967	1	59	100	1.4	1.4
	2	45	100	5.2	5.2
	3	37	100	6.8	6.8
	4	30	100	4.5	4.5
	5	25	29	3.5	1.0
	Totals			21.4	18.9
1968	1	69	100	1.8	1.8
	2	60	100	5.3	5.3
	3	60	100	6.3	6.3
	4	59	100	4.2	4.2
	5	58	40	2.5	1.0
	Totals			20.1	18.6
1969	1	88	94	1.6	1.5
	2	76	100	5.3	5.3
	3	64	100	6.4	6.4
	4	56	24	3.8	0.9
	Totals			17.1	14.1

Table 2. Cont'd.

Year	Littering period	(A) Percentage of Jan. 1 female pop. alive	(B) Percentage littering	(C) Mean litter size	(D) Fetuses per female (BXC)
1970	1	78	93	1.4	1.3
	2	67	100	4.8	4.8
	3	64	100	5.4	5.4
	4	61	45	3.6	1.6
	Totals			15.2	13.1
1971	1	85	96	1.4	1.3
	2	76	100	3.3	3.3
	3	67	100	4.9	4.9
	4	59	52	3.5	1.8
	Totals			13.1	11.3
1972	1	74	100	1.7	1.7
	2	63	100	4.3	4.3
	3	48	33	4.6	1.5
	Totals			10.6	7.5
1973	1	52	92	2.1	1.9
	2	36	100	4.9	4.9
	3	26	93	6.2	5.8
	4	21	14	3.5	0.5
	5	12	12	1.0	0.1
	Totals			17.7	13.2
1974	1	66	100	2.0	2.0
	2	55	100	4.7	4.7
	3	55	100	5.5	5.5
	4	55	86	3.7	3.2
	Totals			15.9	15.4
1975	1	.31	100	1.3	1.3
	2	.25	100	5.3	5.3
	3	.25	100	6.7	6.7
	4	.23	29	4.3	1.2
	Totals			17.6	14.3

Female jackrabbits in Curlew Valley generally produce four synchronized litters spaced about 40 days apart during the breeding season. Usually the breeding season ends during the conception period of the fourth litter so that not all females produce this last litter (Table 2, column B). In two years, 1968 and 1969 all females produced the fourth litter and some produced a fifth. In 1972 for the first time during the study not all females bred for the third litter, and none produced a fourth. The end of the breeding season was not well defined in 1973 as in previous years. Essentially all females produced the first three litters, 14 percent produced a fourth, but then 12 percent went on to produce a fifth. In 1975 mean litter sizes (Table 2, column C) for the four littering periods were 1.3, 5.3, 6.7, and 4.3 respectively. This compares with means over all years of study of 1.6, 4.6, 5.7, and 3.9.

4. Mortality

Mortality rates for three stages of the jackrabbits' life history were calculated:

A. Fall-spring mortality of total population. Mortality of the total population from October-March (Table 3, column 2) was calculated by dividing the spring density index by the preceding fall index, subtracting the quotient from 1, and multiplying by 100. October-March mortality rates have varied from 32 percent in 1970-71 to 91 percent in 1974-75. The unweighted mean for the 14 fall-spring periods was 59 percent. There are some indications (see below) that the estimated population mortality over the October 1974-March 1975 period of 91 percent was higher than that actually sustained by the population. The October 1975-March 1976 mortality rate was 78 percent.

B. Spring-fall mortality of adults. Adult jackrabbit mortality rate from March-October (Table 3, column 3) was estimated for each year by dividing the fall adult density index by the spring index, subtracting the quotient from 1, and multiplying by 100. The fall adult index was obtained by multiplying the fall population index by the fraction of adults (Table 4) in a collection of 100 rabbits made in October of each year. March-October adult mortality rates have varied from 0-87 percent with a mean over the 13 summer periods of 52 percent. Adult mortality for the March-October 1974 period was calculated at 0 percent. This estimate is obviously low and will be discussed in a following section. The March-October 1975 adult mortality rate was 14 percent.

C. Mortality of juveniles from birth to October census. Mortality of juveniles from birth to October census was calculated each year by dividing the fall juvenile index by the index to juveniles born into the population, subtracting the quotient from 1, and multiplying by 100 (Table 3, column 4). Fall juvenile indexes were calculated by multiplying the October population index of each year by the fraction of juveniles in the October collection (Table 4). Indexes to juveniles born were obtained by multiplying the January 1 female indexes (Stoddart 1972) by the number of fetuses born per January 1 female (Table 5, column C). Birth-October mortality rates varied from 22-88 percent with a mean of 63. Birth-October mortality in 1975 was 48 percent.

5. Population Density Change

The pattern of events observed so far during the study of jackrabbit population dynamics in Curlew Valley indicates that density changes are

Table 3. October-March Mortality Rate of Total Jackrabbit Population,
March-October Mortality Rate of Adults and Birth to October
Mortality Rate of Juveniles

Year	Percentage mortality		
	Oct.-March	March-Oct.	Birth-Oct.
1962-1963	65		
1963		70	22
1963-1964	57		
1964		87	69
1964-1965	57		
1965		74	69
1965-1966	64		
1966		70	67
1966-1967	69		
1967		65	67
1967-1968	56		
1968		9	38
1968-1969	34		
1969		60	61
1969-1970	44		
1970		23	68
1970-1971	32		
1971		50	85
1971-1972	46		
1972		67	88
1972-1973	72		
1973		87	85
1973-1974	63		
1974		0	56
1974-1975	91		
1975		14	48
1975-1976	78		
Unweighted means	59	52	63

Table 4. Percentage of Adults in October Rabbit Collections from 1963-1973

	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
% Adults	7	8	14	15	12	13	14	28	40	45	16	22	17

Table 5. Mean number of ova and fetuses produced per female in the population surviving the breeding season, mean number of fetuses produced and mean number of juveniles alive at fall census per female alive January 1, and percent of potential juveniles actually observed at time of fall census from 1963-73

Year	(A) Ova/ female	(B) Fetuses/ female	(C) Fetuses per Jan. 1 female (AXD Table)	(D) Observed juv. in fall per Jan. 1 female	(E) Percent potential juv. obser. (D/Ax100)
1963	15.4	13.5	5.4	4.1	27
1964	19.1	15.3	6.1	1.9	10
1965	14.6	13.1	6.3	2.1	14
1966	13.2	12.2	5.8	1.9	14
1967	19.3	18.9	7.3	2.4	12
1968	19.8	18.6	11.2	6.9	35
1969	16.1	14.1	9.9	3.9	24
1970	14.2	13.1	8.7	2.8	20
1971	13.4	11.3	8.0	1.2	9
1972	8.1	7.5	4.7	0.6	7
1973	16.6	13.2	4.4	0.7	4
1974	17.8	15.4	8.7	3.9	22
1975	18.9	14.5	3.7	1.9	10
Means	15.9	13.9	6.9	2.6	16

largely due to annual variation in mortality rates and that changes in natality have had little effect on density trends. Table 5 shows the relative contribution of natality rate (column A) and combined mortality rates to the production of fall juveniles by females alive at the beginning of the breeding season, January 1 (column D). Natality rate as measured by the number of ova produced per female surviving the breeding season has varied from 8.1-19.8 with a mean over all years of 15.9. Except for the low value of 8.1 in 1972, the range in natality rate has been less than ± 30 percent of the mean. Fall 1972 density index was 64, a decrease of 60 percent from the fall 1971 index of 160. Had the 1972 natality rate been an average value of 15.9 the fall 1972 index would have been approximately 90, still a decrease of 44 percent from 1971. Though the low natality rate in 1972 did affect density, the basic trend of decreasing density would not have been greatly altered by a mean natality rate for that year.

The number of ova produced per female is reduced through prepartum mortality to give the number of fetuses produced per female surviving the breeding season (column B). This number is further reduced by mortality of females during the breeding season to give an estimate of the number of young born per female starting the breeding season (column C). Finally, the number is reduced through juvenile mortality from birth to October to produce the number of juveniles at times of fall census per female starting the breeding season (column D). This number varied from 0.6-6.9, a range of about ± 200 percent of the mean 2.7. Therefore, through changes in mortality rates, variation in the number of ova produced per female compared to variation in the number of juveniles in fall per female starting the breeding season has increased from 30 percent to 200 percent of the respective means. The conclusion is that in most cases annual changes in mortality rates have overshadowed variation in natality. A multiple regression analysis (Fig. 5) indicates that 91 percent of the variation in population change from October-October is accounted for by changes in adult mortality rate from October-October and changes in juvenile mortality rate from birth-October.

K-factor Analysis.-- Changes in jackrabbit density from generation to generation, as indicated in Figure 1 by spring density indexes, occur only through mortality or natality in the population. Since variation in natality rate has had little effect on trends of population change, we have concentrated mainly on mortality in the analysis of population change. However, because variation in natality has affected rates of change in some years, natality is also included in the analysis. The purpose of K-factor analysis is to learn in which temporal period of a jackrabbit generation, i.e. spring-spring, mortality is most important in determining population numbers (cf. Varley et al. 1973).

A k-value for any time period is defined as the $\log_{10}$ of the population density at the beginning of the period divided by the density at the end of the period or stage. Thus k-values express mortality on the basis of a life stage rather than as a function of time. The greater the percentage loss during the period, the larger will be the k-value. Generation mortality, K, is defined as the sum of the k-values for all periods into which the generation has been divided.

Since the jackrabbit population has overlapping generations, the population was divided into 2 generations. The first is adults from spring-spring and

Fig. 5. Multiple regression of October-October instantaneous rate of jackrabbit density change on the October-October population mortality and the percent juvenile mortality from birth-October.

$$y = 4.2066 - 0.0254X_1 - 0.0333X_2$$

$$r^2 = 0.91$$

the second is juveniles from maximum-potential-number born to the following spring. Adult generation mortality, K_1 , and juvenile generation mortality, K_2 , are plotted in Figure 6. The adult generation was divided into 2 periods: spring-fall mortality, k_2 , and fall-spring mortality, k_1 . It is apparent from the figure that the 2 mortality periods, i.e. k_2 and k_1 , have contributed about equally over the years to the generation mortality, K_1 , and are thus both important in the analysis of adult mortality,

The juvenile generation was divided into 4 periods: loss due to natality being below the maximum potential, k_3 , prenatal mortality, k_4 , birth-fall mortality, k_5 , and fall-spring mortality, k_1 (k_1 is the same for both the adult and juvenile generations). It is clear from Figure 6 that prenatal mortality has been insignificant over the years in terms of the juvenile generation mortality and thus is not considered any further in the analysis of mortality. Both k_1 and k_5 have been important through all years of study in determining K_2 , while k_3 has had some importance some of the years. All three of these factors will be analyzed.

Analysis of Mortality.-- It is apparent from the above section that analysis of environmental factors affecting k_1 , k_2 , k_3 , and k_5 is necessary to obtain an understanding of jackrabbit population change.

A. Fall-spring population mortality, k_1 . Jackrabbit instantaneous mortality rates (instantaneous rate = $\log_e$ of the survival) for the October-March periods were plotted (Fig. 7) as a function of the effective coyote to rabbit ratio, $(\text{coyote/rabbit})_E$, where $(\text{coyote/rabbit})_E = (\text{coyote/rabbit})_F$. The term $(\text{coyote/rabbit})_F$ is the observed coyote to rabbit ratio and $F = 1 - e^{-kd^x}$. F is a variable that relates the rate at which a single coyote eats jackrabbit as a function of rabbit density, d . The other terms, k and x , are constants which are determined empirically from coyote food habits studies. The rate at which F changes with rabbit density is determined by x , where k moves the curve up or down the F axis as a function of density of rodents or other buffer species. We have used values of 0.3 and 0.45 for k and x respectively. The values were determined from food habits studies in Curlew Valley under contract with the U.S. Fish and Wildlife Service, Predator Ecology and Behavior Project. The food habits studies are as yet incomplete.

The regression (Fig. 7), excluding the 1974-1975 data point, accounts for 87 percent of the observed variation in October-March mortality. October-March mortality in 1974-1975 was 91 percent, by far the highest so far observed (cf. Table 1). It is apparent from Figure 7 that the close relationship between rabbit mortality and coyote predation will not account for this high mortality in the 1974-1975 period. There are two possibilities: (1) some other factor was accounting for a large part of the rabbit mortality during that winter, or (2) random experimental error in the density estimates during that period of low density (cf. Fig. 1) resulted in erroneous mortality estimates. The latter possibility is most likely. If the fall 1974 density estimate were too high (a good possibility since it broke the downward trend in density which we actually still seem to have, Figure 1) we would expect to over estimate the October-March loss since it is calculated from $1 - (\text{spring density/fall density})$. Also, if the fall 1974 density estimate were too high we would expect to under estimate March-October 1974 mortality. In fact, this was the case since the

Fig. 6. Jackrabbit mortality during 5 life stages expressed in terms of k-values. See text.

Fig. 7. Linear regression of instantaneous rabbit mortality rate from October-March on the effective Coyote/rabbit ratio over the study area.

over summer adult mortality estimate was 0, obviously a low estimate (cf. Table 3). Another possibility which would explain the observed results, i.e. the 91 percent mortality over winter 1974-1975 and the 0 percent loss over summer 1974, would be March 1974 and March 1975 density estimates that were too low. This could easily have occurred with the low densities existing during 1974 and 1975 (Table 1). Observation of just one rabbit more or less on the transects would have made substantial difference in the density estimates. The potential for large experimental error was great.

The coyote/rabbit ratio used in the calculation of (coyote/rabbit) c in Figure 7 was calculated for each October-March period by dividing the estimated number of coyotes/square mile on the study area in October by the October rabbit index. Coyote densities (Fig. 1) were obtained from studies contracted with the U.S. Fish and Wildlife Service in Curlew Valley.

B. Birth-fall juvenile mortality, k_5 . Mortality of juveniles has been of particular importance because of the great effect it has had on density change (discussed above). Juvenile survival in the past has been plotted as a function of two variables, the coyote/rabbit ratio multiplied by F and the mean rabbit index for the March-October period (Fig. 8). The multiple regression equation, represented by the surface in Figure 8, was calculated using data from 1964 through 1970 only. Almost 80% of the observed variation was explained by the two independent variables. The 1971-1973 data did not fit the model well. Even though density had decreased in 1971-1973, mortality remained high. The assumption was that in those years we were observing some "cumulative" and/or "carry-over" effect of density on juvenile survival which Christian and Lemunyan (1957), Chitty (1967), and Krebs et al. (1973) have postulated might result from changes in behavior and/or genetic composition. In 1974 and 1975, even though the coyote/rabbit ratios were by far the highest observed during the study (Fig. 8), survival rates of juveniles were high. Each year it was becoming more evident that the model was not a good representation of the real world. Thus a major change in our thinking concerning juvenile mortality has evolved this year.

Our new thinking is based on two factors: (1) the main defense for juvenile jackrabbits against predation by coyotes is hiding and (2) it is behaviorally sound thinking that coyotes will continue to kill juvenile rabbits as they encounter them in the field, more or less independent of the number, as long as the effort expended is not great (Frederick Knowlton, David Balph, pers. com.). Therefore, it is reasonable that the fraction of the juvenile population killed by coyotes is proportioned to the coyote density and not the coyote/rabbit ratio. Also, the functional response of coyotes to food supply would dictate that as density of jackrabbits declined feeding behavior would change. This may mean that coyotes would spend their time in areas of rodent or livestock abundance and thus preclude their coming in contact with jackrabbits at the expected rate. With these thoughts in mind, juvenile jackrabbit mortality was plotted against the coyote index multiplied by the function F as defined above (Fig. 9). This model is very encouraging and explains 76% of the observed variation in juvenile mortality. The model is extremely interesting since it does not require any density effect or "carry-over" effect and allows coyote predation alone through functional and numerical responses to account for the observed variation in mortality.

$$y = 1.0068 - 0.002308X_1 - 0.0002211X_2$$

$$r^2 = 0.78$$

Fig. 8. Multiple regression of percent juvenile survival from birth-October on the effective coyote/rabbit ratio and mean rabbit index during the March-October period.

Fig. 9. Regression of Juvenile mortality on the coyote index X F.
See text.

C. Reduced natality, k_3 . Production of fetuses per female surviving the breeding season (Table 2, column D) has varied from 18.9 to 7.5. Annual weather patterns undoubtedly account for some of this variation, however, an inverse relationship exists between spring density and natality rate. This relationship is shown in Figure 10 where the log of the maximum potential natality rate divided by observed natality is regressed on the log of the spring jackrabbit density. The relationship is significant at the 5% level and accounts for 37% of the observed variation between years in the number of fetuses produced per female surviving the breeding season.

D. Spring-fall adult mortality, k_2 . In the past the model for March-October adult mortality described mortality as a function of the coyote/rabbit ratio multiplied by F (Fig. 11). With the 1974 and 1975 points excluded an r^2 value of only 0.41 was obtained. Because the 1974 and 1975 data points were so extremely different from the values expected from the model, our thinking concerning March-October adult mortality was also revised. The same independent variable, coyote index XF, as utilized in the model for juvenile mortality was used; this variable was modified, however, to incorporate an observed density related change in jackrabbit behavior. Fall flushing distances were found to increase with density (Fig. 12). It may be that this change in behavior has some survival value. With long flushing distances and with high juvenile numbers to act as a buffer, adult jackrabbits may essentially escape predation at high rabbit densities. Therefore, the independent variable, coyote index XF, was multiplied by a buffering term B, where $B = e^{-.012d}$ and d is spring rabbit density. The variable, coyote index XFXB was then plotted against March-October adult mortality (Fig. 13). If the 1974 point, which is thought to be erroneous (see above), is excluded, an r^2 value of 0.72 is obtained with the model.

Analysis of k-values.-- The regression for October-March mortality in Figure 7 can be used to partition k_1 into 2 k-values, k_{12} and k_{11} (Fig. 14). k_{12} represents mortality due to coyote predation while k_{11} is a combination of a constant mortality indicated by the intercept of the regression equation and experimental error at each of the data points. The straight, broken line in Figure 14 is the constant mortality of the intercept; the deviation of the dashed line, k_{11} , from this line is the experimental error. The figure depicts graphically our best estimate of the contribution of coyote predation, unknown mortality factors, and experimental error to the total October-March mortality, k_1 . It also shows that for most years change in October-March mortality is a result mainly of change in the rate of coyote predation.

The same procedure was used to partition k_2 into mortality due to coyote predation, k_{22} , and mortality due to unknown factors plus experimental error, k_2 , (Fig. 14). Again this figure indicates that most of the variation in March-October mortality of adult jackrabbit is a result of changes in coyote predation rate.

In the same manner, birth-October mortality of juveniles, k_5 , was partitioned (Fig. 15). The figure clearly indicates that the general trend of juvenile mortality is a result of coyote predation.

Fig. 10. Linear regression of reduction in jackrabbit natality on the spring jackrabbit density index.

Fig. 11. Linear regression of instantaneous adult rabbit mortality rate from March-October on the effective coyote/rabbit ratio over the study area.

Fig. 12. Regression of jackrabbit flushing distances in fall on the jackrabbit density index.

Fig. 13. Linear regression of summer adult mortality on the effective coyote rabbit ratio multiplied by B (see text).

Fig. 14. October-March mortality, k_1 , and March-October mortality, k_2 , partitioned into mortality due to coyote predation and mortality due to unknown factors plus experimental error.

Fig. 15. Birth-October mortality, k_5 , partitioned into mortality due to coyote predation, k_{52} , and unknown factors plus experimental error, k_{51} .

Since coyote predation mortality rates, k_{12} , k_{22} , and k_{52} , have been partitioned from the total mortalities k_1 , k_2 , and k_5 , they can be plotted against rabbit density (Fig. 16) to determine the relationship of coyote predation to rabbit density. A strong inverse relationship exists for the October-March period, indicating that loss due to coyote predation increases as rabbit density declines. No density related relationship is evident for March-October predation loss of adults. On the other hand a positive relationship exists for juvenile mortality from birth-October, indicating increased loss to coyote predation with increased jackrabbit density.

In summary the above analysis shows that with the observed functional and numerical response of the coyote population to jackrabbit density and with jackrabbit behavioral changes the general trend of the observed jack-rabbit "cycle" can be accounted for by coyote predation.

6. Controlled Studies

Four 5-acre pens of 4-foot chain link fence were constructed in 1974-1975 and equipped with water and electrical power. An observation tower has now been constructed at the center of the pens.

The objective is to observe changes in jackrabbit behavior as a function of density of the natural population from which the pens are stocked. Particular emphasis is to be placed on behavioral factors which may affect population size. The basic problem is to test the hypothesis (c.f. Krebs et al. 1973 and Chitty 1967) that genetic shifts occur within the population as a function of density which affect subsequent mortality rates. The first phase of the study is to obtain a behavioral profile of jackrabbit from a low density population such as exists in Curlew Valley at the present time. Later as densities change in Curlew Valley the pens will be restocked and the behavioral observations repeated.

In addition to the behavioral studies, blood proteins will be analyzed using electrophoretic techniques in an attempt to detect shifts in genetic frequencies within the rabbit population.

In September of 1975 a graduate student started the first phase of these studies. The pens were stocked and electrophoretic patterns of the plasma proteins made. However, the behavioral observations did not progress as they should have and it was finally necessary to dismiss the student. A new student has just recently taken over the project; his study proposal is found in the 1976-1977 renewal proposal for the rabbit project.

7. INEL Coyote Density Index

In spring 1975, 6 coyote scent post lines were established in the INEL study area. Three were located in the part of the area grazed by domestic livestock and 3 in the ungrazed portion (Fig. 17). The scent post lines have now been operated 3 times for a total of 4500 scent station nights. The results (Fig. 4; Table 6) indicate the coyote population over the study area

Fig. 16. Plots showing relationship of rate of coyote predation and rabbit density.

Fig. 17. Location of 6 coyote scent post lines (numbered solid lines) on the INEL study area. Shading indicates portion of study area grazed by domestick livestock.

Table 6. Coyote index values for the 6 scent-post line on the INEL study area.

Date	Line						Ungrazed mean	Grazed mean	Grand mean
	1	2	3	4	5	6			
Spring 1975	4	12	4	0	20	5	6.7	8.3	7.5
Fall 1975	44	12	20	0	45	36	25.3	27.0	26.2
Spring 1976	21	5	5	16	21	11	10.3	16.0	13.2

increased approximately 76% from spring 1975 to spring 1976. The mean fall 1975 and spring 1976 INEL index values of 26.2 and 13.2 respectively compare with 5.5 and 8.9 for Curlew Valley for the same periods. It is interesting to note that index values on the grazed portion of the INEL have tended to be somewhat higher than on the ungrazed portion.

A conversion of scent-post indexes to estimates of absolute density was made by comparing absolute estimates of coyote density in Curlew Valley (J. J. Knudsen 1976) with scent post indexes taken the same years. An index of 20 is approximately equal to 1 coyote per square mile. Our best estimate of the coyote density on the INEL is then 1.3 and .67 per square mile for fall 1975 and spring 1976 respectively.

8. INEL Rodent Biomass

Twenty-five rodent snap-trap transects were located along each of the 6 15-mile coyote scent post lines (Fig. 17). Each transect consists of 10 trap stations 10 meters apart with 2 traps at each station. The lines are run for 3 consecutive nights. The lines have now been operated 3 times; spring 1975, fall 1975, and spring 1976; for a total of 27,000 snap-trap nights.

A total of twelve 12 x 12 live-trap grids have been operated for 5 days each on the INEL site this year. After 5 days of live trapping on the grids, 3 snap-trap transects, identical to those on the snap-trap lines, were located in and near each of the grids. The purpose was to get a conversion factor for each rodent species whereby we could convert transect results to estimates of absolute density. Since trappability varies between rodent species, each species will have a different conversion factor. It is also likely that trappability within each species will be found to vary between habitat types, therefore grids have been placed in a number of habitat types.

Conversion factors for the 6 most accessible species on the INEL have been found. The conversion factors (Table 7), multiplied by the mean number of animals of the respective species caught per day on the snap-trap transect lines, will produce an estimate of the mean number of animals of that species per hectare along the lines. The density estimates are then multiplied by the observed mean weight per animal of the respective species to obtain estimates of biomass per hectare (Table 8). Biomass estimates are generally higher on the grazed portion of the site than on the ungrazed portion as was the case with the coyote density estimates. The total number of rodents trapped of the 5 most accessible species on the six snap-trap lines over the 3 trapping periods are shown in Figure 18.

9. Jackrabbit-Vegetation Subproject

As part of the overall Curlew Valley studies, we initiated this year investigations of the jackrabbit-vegetation interactions. The goal is to understand the effects of vegetation factors on jackrabbit population dynamics.

Table 7. Conversion factors for converting mean number of rodents caught on snap-trap transects to estimate of numbers per hectare.

	Species code ¹					
	1	2	3	4	7	8
Conversion factor	0.81	6.27	2.24	2.63	1.2	1.54

¹ Code	Species
1	<i>Peromyscus maniculatus</i>
2	<i>Perognathus parvus</i>
3	<i>Dipodomys ordii</i>
4	<i>Eutamias minimus</i>
7	<i>Onychomys leucogaster</i>
8	<i>Spermophilus townsendii</i>

Table 8. Estimates of rodent biomass per hectare by species and by snap-trap line on the INEL study site.

Spring 1975 Line	Species code ¹						Total
	1	2	3	4	7	8	
1	32.5	27.8	61.9	82.8	4.9	23.3	233.2
2	26.2	4.0	49.0	132.3	7.4	66.5	285.4
3	32.7	25.3	77.7	96.6	2.2	62.0	296.5
4	34.4	7.8	80.5	94.9	9.6	87.5	314.7
5	38.4	8.0	101.3	48.5	1.9	93.4	291.5
6	50.3	7.8	345.3	151.6	1.9	365.2	1073.7
Mean	35.8	13.5	119.3	101.1	4.7	116.3	390.7
% by number	40.8	2.6	17.7	21.8	2.1	13.7	98.7
% by weight	9.1	3.4	30.5	25.9	1.3	29.8	100.0
Fall 1975 Line	Species code ¹						Total
	1	2	3	4	7	8	
1	69.5	8.7	18.5	102.6	11.6	0	210.9
2	30.8	32.6	43.2	117.9	13.1	0	210.9
3	58.1	0	32.8	79.9	3.9	0	174.7
4	28.3	26.3	108.4	77.8	13.3	0	254.1
5	29.9	69.0	145.1	43.8	3.5	0	291.3
6	45.1	5.0	155.2	54.1	5.1	0	264.5
Mean	43.6	23.6	83.9	79.4	8.4	0	238.9
% by number	53.8	4.8	13.9	21.3	4.8	0	98.6
% by weight	18.3	9.9	35.1	33.2	3.5	0	100.0

¹See Table 7

Fig. 18. Number of rodents caught during 3 trapping periods on the INEL site. See Table 7 for species code.

In order to examine the effects of jackrabbits on the vegetation two 1 ha livestock-proof exclosures were built. Ocular estimation of available biomass and percent utilization of two preferred species, a perennial grass, *Sitanion hystrix*, and a half-shrub, *Kochia americana* was made in mid-June. A preliminary look at the data indicated that utilization of both species was less than 1% of peak standing crop.

Stomach contents of rabbits were taken from the monthly collections to gain dietary composition data by microscopic analysis. Plant materials were collected in order to develop a reference collection of available species. Grinding and slide preparation is about 50% completed on plant materials taken during the winter and spring seasons. Sampling of cover and biomass of the plant community in the vicinity of rabbit collecting sites was also completed through the June collections of rabbits.

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Principal Investigator's Time:

As of June 30, 1976, the principal investigator had spent approximately eight months of 1/2 time on the project. Approximately two months of 1/2 time will be spent during the remainder of the contract period.