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

Progress Report
for Period October 1, 1976 - September 30, 1977

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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. Proposed coyote predation models, which account for the entire observed jackrabbit cycle, are consistent with existing predation theory.

1. Introduction

Population ecology of the black-tailed jackrabbit population on a 250-square-mile area in Curlew Valley, Utah has been studied from 1962-1977. 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.

During the 1976-1977 contract period data collections were initiated on two new aspects of the jackrabbit study: (1) controlled experiments to investigate genetic and/or behavioral changes in the jackrabbit population associated with observed high rates of juvenile mortality, and (2) field studies to observe the effects of food supply on jackrabbit population dynamics. In addition, data collections designed to investigate habitat preferences of rodents on the INEL were completed.

The present document describes findings from the 1976-1977 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.

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 ERDA.

2. Population Measurement

Curlew Valley rabbit density indexes. -- October 1976 and March 1977 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 of 26 in spring 1964 to 7.4 in spring 1967. In the following 4 years density increased rapidly to 130 in spring 1971, an increase over the 4-year period of nearly 18-fold. The next 4 years saw a very rapid decline in density to a

Fig. 1. Spring jackrabbit population trend ($\pm$ one standard error) and fall coyote population trends in Curlew Valley.

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	
Oct. 1976	23	20		733
March 1977	9	7.0	-65	

low in spring 1975 of 2.2, a factor of nearly 60 below the peak density. In the last 2 years spring densities have increased somewhat to 7.0 in spring 1977.

Rates of change from one census period to the next are indicated in the last 2 columns of Table 1. During this reporting period, the rabbit population increased 733 percent from March 1976 to October 1976. This is the highest observed rate of increase over a breeding season. The over-summer increase was followed by an October 1976 to March 1977 decline of 65 percent. Demographic mechanisms underlying these rates of change are discussed below.

INEL rabbit density index. -- The 80 rabbit transects on the INEL study area (see 1976 Progress Report) were walked in October, 1976. Six rabbits were observed (Table 2). As with transects in Curlew Valley, flushing angles and distances were recorded and Gates' method used to calculate a density index. The fall 1976 index of 7.6 is slightly below, but not significantly different from the fall index of 9.1. These values compare with a fall 1976 index in Curlew Valley of 20. Jackrabbit tracks in the coyote scent stations were also recorded. The frequency of these tracks may be a reasonably good index to rabbit numbers. This index is included with the transect results in Figure 2. The jackrabbit transects on the INEL were not walked in spring 1977. Extremely frequent rain storms during the month of May greatly hampered our field efforts, and time and money allocated for the INEL field work were exhausted on the rodent and coyote index lines. This is not a big loss however, since with the very low jackrabbit density that now exists on the INEL, the standard error of a transect density estimate would be relatively large and the usefulness of such an index somewhat in question.

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 3), age of fetuses, and conception dates. 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 3, 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 1976 mean litter sizes (Table 3, column C) for the four littering periods were 1.4, 4.2, 6.8, and 3.5 respectively. This compares with means over all years of study of 1.6, 4.6, 5.7, and 3.9. The mean number of fetuses produced per female surviving the breeding season (column D) was 14.7 compared with the mean of 14.0.

Table 2. Results of INEL Jackrabbit Population Transects

Census Date	No. Rabbits Observed	Density Index
May 1975	1	1.0
Oct. 1975	2	9.1
May 1976	0	0
Oct. 1976	6	7.6

Fig. 2. Jackrabbit and Coyote density indexes for the INEL Study Site.

Table 3. Percentage of January 1 female population alive, percentage littering, mean litter size, and number of fetuses per female.

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 3. 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	14.5
1976	1	53	100	1.4	1.4
	2	40	100	4.2	4.2
	3	40	100	6.8	6.8
	4	40	66	3.5	2.3
Totals				15.9	14.7

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 4, 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 15 fall-spring periods was 60 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 1976-March 1977 mortality rate was 65 percent.

B. Spring-fall mortality of adults. Adult jackrabbit mortality rate from March-October (Table 4, 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 5) 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 14 summer periods of 49 percent. Adult mortality for the March-October 1974 period and the March-October 1976 period was calculated at 0 percent. These estimates are obviously low and will be discussed in a following section.

C. Mortality of juveniles from birth to October census. Mortality of juveniles from birth to October 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 4, 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 5). 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 6, column C). Birth-October mortality rates varied from 7-88 percent with a mean of 59. Birth-October mortality in 1976 was 7 percent, the lowest observed during this study.

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 largely due to annual variation in mortality rates and that changes in natality have had little effect on density trends. Table 6 shows the relative contribution of natality rate (column C) 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

Table 4. 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		
1976		0	7
1976-1977	65		
Unweighted means	60	49	59

Table 5. Percentage of Adults in October Rabbit Collection from
1963-1976

Year	% Adults
1963	7
1964	8
1965	14
1966	15
1967	12
1968	13
1969	14
1970	28
1971	40
1972	45
1973	16
1974	22
1975	17
1976	15

Table 6. 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 1963-76

Year	(A) Ova/ female	(B) Fetuses/ female	(C) Fetuses per Jan. 1 female (ΣAXD Table. 3)	(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
1976	16.2	14.7	6.0	5.7	35
Means	15.9	13.9	6.8	2.8	17

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. The relative importance of mortality and natality in the dynamics of the jackrabbit population will be demonstrated graphically in the following analysis.

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.

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 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 3. 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

Fig. 3. Jackrabbit mortality during 5 life stages expressed in terms of k-values. See text.

both the adult and juvenile generations). It is clear from Figure 3 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. 4) as a function of the effective coyote to rabbit ratio, $(\text{coyote/rabbit})_E = (\text{coyote/rabbit})_F$. 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. 4), 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 4 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 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 over summer adult mortality estimate was 0, obviously a low estimate (cf. Table 4). 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.

Fig. 4. Linear regression of instantaneous rabbit mortality rate from October-March on the effective Coyote/rabbit ratio over the study area.

The coyote/rabbit ratio used in the calculation of (coyote/rabbit)_E in Figure 4 was calculated for each October-March period by dividing the coyote index on the study area in October by the October rabbit index. Coyote indexes (Fig. 1) were obtained from studies contracted with the U.S. Fish and Wildlife Service in Curlew Valley. Since 1967 the coyote index has been calculated from a composite of a trap line index and a scat line index (Fig. 5). These two indexes, in general, have been in good agreement except over the last 2 years. In addition, starting in 1973 4 scent post lines have been operated in the Utah study area in order to get a comparison of all 3 indexes. The scent post results are not included in the composite coyote index.

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). The evolution of the following model is described in the 1976 Progress Report. 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 proportional 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. 6). This model is very encouraging and explains 76% of the observed variation in juvenile mortality (excluding 1976). 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.

C. Reduced natality, k_3 . Production of fetuses per female surviving the breeding season (Table 3, 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 7 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 . With the 1974 and 1975 points excluded an r^2 value of only 0.41 was obtained. Because the 1974 and

Fig. 5. Curlew Valley Coyote Indexes from a Trap line, Scat line and Scent post lines.

Fig. 6. Regression of Juvenile mortality on the coyote index X F.
See text.

Fig. 7. Linear regression of reduction in jackrabbit natality on the spring jackrabbit density index.

1975 points were so extremely different from the values expected from the model (See 1976 Progress Report), our thinking concerning March-October adult mortality was also revised. The same independent variable, coyote index $\times F$, 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. 8). 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 $\times F$, was multiplied by a buffering term B , where $B = e^{-.012d}$ and d is spring rabbit density. The variable, coyote index $\times F \times B$ was then plotted against March-October adult mortality (Fig. 9). 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.

The above 4 models were all calculated with data collected previous to the 1976-1977 field season. After a few more years data, new models will be generated and new k -values, as shown in the following section, will be calculated.

Analysis of k -values. -- The regression for October-March mortality in Figure 4 can be used to partition k_1 into 2 k -values, k_{12} and k_{11} (Fig. 10). 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 10 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. As shown above, 1974 was a year with high mortality due to unknown factors and/or high experimental error.

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_{21} (Fig. 10). Again this figure indicates that most of the variation in March-October mortality of adult jackrabbits is a result of changes in coyote predation rate.

In the same manner, birth-October mortality of juveniles, k_5 , was partitioned (Fig. 11). The figure clearly indicates that the general trend of juvenile mortality is a result of coyote predation.

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. 12) 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. This relationship of

Fig. 8. Regression of jackrabbit flushing distances in fall on the jackrabbit density index.

Fig. 9. Linear regression of summer adult mortality on the effective coyote index multiplied by B (see text).

Fig. 10. 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. 11. Birth-October mortality, k_5 , partitioned into mortality due to coyote predation, k_{52} , and unknown factors plus experimental error, k_{51} .

Fig. 12. Plots showing relationship of rate of coyote predation and rabbit density.

decreasing predation loss with increasing prey numbers is consistent with some recent predator/prey concepts as discussed by Keith (1974). This relationship exists in the case of the jackrabbit study because, in general, when October-March jackrabbit density was high, the coyote/rabbit ratio was low (Fig. 1 and 4).

The relationship of March-October predation loss of adults is not so obvious. However, a relationship somewhat as that shown in Figure 12 probably exists. It has the indicated parabolic form as a result of the action of the 2 functions, F and B, as discussed in connection with Figure 9. This type of parabolic form is similar to that described by Holling (1959) in his study of functional and numerical responses of vertebrate predators to changes in prey numbers.

In contrast with the October-March predation loss, a positive relationship exists between predation loss of juveniles from birth-October and rabbit density (Fig. 12). The relationship is a result of the numerical response of the coyote population to increased jackrabbit density and the observed relationship that juvenile mortality is a positive function of coyote density (Fig. 6). This result is consistent with the Lotka-Voltara predator/prey equations and Holling's (1959) model as discussed below.

The Lotka-Voltara equations state:

$$\frac{dN_1}{dt} = N_1(B_1N_2 - D_1) \text{ and } \frac{dN_2}{dt} = N_2(B_2 - D_2N_1)$$

Where N_1 and N_2 are predator and prey numbers respectively, and B and D are birth and death rates. The total number of prey lost to predation is then DN_1N_2 or the number of prey lost per predator is DN_2 , i.e.,

This says that the number of prey taken per predator increases linearly with prey density or that each predator takes a constant percentage, D , of the prey species regardless of prey density. It follows from the above equations that the percentage, D_2N_1 , of the prey population taken by predators increases linearly with prey density, i.e.

Holling (1959), however, described the following functional response for vertebrate predators:

Where d = % prey killed/predator

Holling also found that if the numerical response of the predator were included, the relationship of D_2N_1 to N_2 was of the form:

The ascending portion of this curve is essentially the same as that described by the Lotka-Voltara equation. In words, the equation says that the percentage of the prey population killed increases linearly as the predator population increases. This is precisely what is indicated in the model (Fig. 6) for juvenile mortality from birth to October.

The reason Holling's functional response curve levels off at the top is that the predator runs out of time or interest in killing more prey. In order for coyotes to stop an increasing jackrabbit population, as our data would suggest, it is necessary that DN_1 equal B (from the Lotka-Voltara equation) and that it does so on the ascending portion of Holling's model. This requires that coyotes do not lose interest or run out of time in killing juvenile rabbits.

We can make a few simple calculations to estimate the number of juvenile rabbits a coyote must have killed in order to have stopped the last jackrabbit increase. At the rabbit high, B for the rabbit population was 6. Thirty percent of the juveniles born were lost to other causes (indicated by the intercept in the juvenile mortality model). This leaves an effective B of approximately 4; therefore DN_1 must equal 4. At the rabbit high, N_1 , the coyote density, was about 1.5 per square mile. Therefore d was approximately 2.5. The spring rabbit density at the rabbit high was 150 per square mile. Then:

$$150 \text{ rabbits/mile}^2 \times 2.5 = 400 \text{ juveniles/1.5 coyotes}$$

and since coyotes have about 200 days in which to kill juveniles:

$$\frac{400 \text{ juveniles/1.5 coyotes}}{200 \text{ days}} = 1.3 \text{ juveniles/coyote day}$$

indicating coyotes could easily have stopped the increasing rabbit population.

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 jackrabbit "cycle" can be accounted for by coyote predation alone.

6. Controlled Studies

The penned studies seek (1) to assess the role of behavior in the mortality of young jackrabbits and (2) to develop behavioral "signatures" of jackrabbit populations as indicators of environmental status.

The procedures include stocking four 2-ha enclosures with jackrabbits from Curlew Valley where the current population density is low. Two of the enclosures are stocked with two pair each, and the other two enclosures are stocked with six pairs each. Blood samples were taken from the rabbits to obtain electrophoretic patterns of serum protein.

The data acquisition system is designed to collect information on the frequency and form of activity and spatial and social relationships. Special attention is directed toward recording reproductive, maternal and antipredator behavior. The information is recorded in coded or numeric form to facilitate machine processing. The long-term plan is to replicate the penned studies using rabbits from the Curlew Valley population when the population is at its peak numbers.

The first objective will be met by a broad comparison of the behavior and performance of jackrabbits. The comparison will be of animals taken from a low population density and studied under conditions of high and low density and of animals taken from a high population density and studied under conditions of high and low density. The second objective will be met by statistically defining the performance of behavior of jackrabbits living under various conditions.

Approximately 15,000 observational units (1 unit = 1 computer card) have been collected on the rabbits thus far. Since the observations are continuing, the data have not been processed. However, a partial, manual reduction of information on several parameters produced some interesting results.

The jackrabbits in the high-density pens move more, fight more, and behave sexually less than jackrabbits in the low-density pens.

	High Density	Low Density
Movement Index	5.23	2.90
Sexual Encounters (no./indivi./hr.)	0.22	0.29
Agressive Encounters (no./indiv./hr.)	0.52	0.36

Jackrabbits in the high-density pens also maintain a shorter individual distance than do animals in the low-density pens, and they frequently aggregate in one area of the pen. This pattern of dispersion is symptomatic of a breakdown in social organization associated with high density. Currently, as the vegetation increases in height the rabbits cluster less than before. Presumably, the vegetation decreases sensory contact among the animals and reduces the apparent density. The high level of activity of jackrabbits in the high-density pens may suggest a general readiness to disperse -- a behavioral characteristic common to animals living under conditions of high density. The relationship between these behaviors, the environmental situations, and reproduction has yet to be assessed.

7. INEL Coyote Density Index

Originally 6 coyote scent post lines were established on the INEL study area (See 1976 Progress Report). In order to increase the precision of the coyote estimate, in fall 1976 we increased the scent posts to 10 lines, 4 in the grazed and 6 in the ungrazed portions of the study area. In addition, we established a standard coyote trapline of 150 steel traps operated for 30 nights. Also, 6 scat lines, each consisting of 8 1-mile samples, were initiated in Fall 1976. The six lines were each operated for a 2 week period.

Coyote scent post results (Fig. 2 and Table 7) indicate the coyote population over the study area increased 154 percent from fall 1975 (index 26.2) to fall 1976 (index 66.5). The spring 1977 index of 10.1 is midway between the indexes of the two previous springs. These values compare with a fall 1976 index of 23 and a spring 1977 index of 2 in Curlew Valley.

A total of 32 coyotes was trapped in fall 1976 on the INEL coyote trap line, producing an index of 6.6 coyotes/1000 trap nights. The index has been corrected for sprung or otherwise disturbed traps. This compares with an index of 5.5 coyotes/1000 trap nights in Curlew Valley. The 6 scat lines on the INEL sight produced a fall 1976 mean index of 2.1 with a standard error of 0.46 compared with a mean in Curlew Valley of 1.4. After the 3 indexing procedures on the INEL site have been carried out for a few years a composite index can be established.

Table 7. Coyote index values for the 10 scent post lines on the INEL study area.

Date	Line										Ungrazed Mean	Grazed Mean	Grand Mean
	1 ¹	2 ¹	3 ¹	4	5	6	7 ¹	8 ¹	9 ¹	10			
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	16.3	13.2
Fall 1976	80	41	102	20	100	0	40	80	100	102	73.8	55.5	66.5
Spring 1977	0	0	0	0	24	0	-	20	24	24	8.8	11.8	10.1

¹ Transects on ungrazed portion of the study area.

8. Impact of Vegetation Parameters on Curlew Valley Jackrabbits

Studies were conducted in three parts over the past year with the objective of analyzing the part vegetation parameters might play in jackrabbit population changes. Data were collected on stomach contents from rabbits shot on the study area and data were also collected on the availability of plant food resources in the collection areas. The third part of these studies was designed to measure the impact of herbivory on selected plant species on plots exclosed from livestock.

Preliminary results. -- Stomach analysis has been completed by a technician using microscopic techniques (Sparks and Maleček 1968). Detailed data analysis has not begun but some preliminary observations of the data indicate seasonal use patterns similar to those found by Westoby (1973). Grasses and forbs are most frequently eaten in spring and summer, small shrubs in fall and large shrubs in winter. Unlike Westoby's data, gray molly (*Kochia americana*) was not a highly preferred species based on frequency of occurrence in stomachs.

Vegetation availability data were collected concurrently with rabbits for stomach analysis. Methods employing clustered plots to measure cover by species and then ratio estimators to convert cover estimates to biomass were used to measure availability (see Cochran 1963). Data analysis to date has consisted only of statistical evaluation of sampling procedures. Estimates of mean biomass are comparable to those obtained on similar sites by the Desert Biome. Coefficients of variation for the composite estimates of dry biomass (Kg/ha) ranged from 5-10 percent for dominant shrubs to 100-200 percent for rare, clumped or variably shaped species.

Study of impact of jackrabbit utilization on gray molly and squirrel-tail grass (*Sitanion hystrix*) was continued using ocular calibration techniques (Tadmor et al. 1975). Statistical evaluation of the techniques showed that good results are obtained after enough practice by observers. Rabbits only chew on roughly 10 percent of the molly plants and even a smaller percentage of the squirrel-tail grass clumps. Average removal of material on those plants that were chewed was 15 percent for molly and less than that figure for the grass. The combined data show that removal by jackrabbits amounts to less than 5 percent of standing crop of the two species measured.

Projected work for the next year will be the complete and detailed analysis of the data from the three parts of the vegetation studies.

9. INEL Rodent Biomass

Twenty-five rodent snap-trap transects were located along each of the 6 15-mile coyote scent post lines (see 1976 Progress Report). 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 5 times for a total of 54,000 snap-trap nights.

A total of sixteen 12 x 12 live-trap grids designed to obtain absolute density estimates, has been operated for 5 days each on the INEL site. 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.

In the 1976 Progress Report, estimates of the conversion factors for the 6 most accessible species on the INEL were presented. These conversion factors, multiplied by the mean number of animals of the respective species caught per transect on the snap-trap transect lines, produced an estimate of the mean number of animals of that species per hectare along the lines. Density estimates were then multiplied by the observed mean weight per animal of the respective species to obtain estimates of biomass per hectare.

This procedure has now been modified somewhat. Catch per unit of effort is considered a better index to rodent density than simply the number of animals caught per transect as was used previously. The catch per-unit-of-effort equation is derived in the following manner:

Let N = number of operable traps at any time, t ,

$$\text{then } \frac{dN}{dt} = -\lambda N \text{ and } \lambda = cN$$

where c is a catchability constant for each species and N is the number of rodents having access to the N traps.

$$\text{Then } \int dN/N = -\lambda \int dt$$

$$\text{or } \ln N/N_0 = -\lambda t$$

or $N = N_0 e^{-\lambda t}$ where N_0 is the initial number of traps in a transect, i.e. 20, and t goes from 0-1, the over-night time period.

Total effort is then:

$$E = \int_0^1 N dt = N_0 \int_0^1 e^{-\lambda t} dt$$

or
$$E = N_0 \left[\frac{e^{-\lambda} - 1}{-\lambda} \right] \quad (1)$$

where $\lambda = -\ln N_1/N_0$ and N_1 is the number of unsprung traps at the end of the overnight time period. Substituting for λ in equation (1) we have:

$$E = \left[\frac{N_1/N_0 - 1}{\ln N_1/N_0} \right] N_0$$

The density index for any rodent species, s , is then C_s/E where C is the number of a particular species caught. These density indexes have all been calculated; however, the new conversion factors have not yet been determined so rodent biomass estimates are not presented here. Rodent density indexes of the 5 most accessible species on the 6 snap-trap lines over 4 trapping periods are shown in Figure 13.

10. Rodent density and species frequency as a function of soil and vegetation types on the INEL.

Data collection for this project is now complete and funding of the research assistantship will end in September 1977. A final report will be submitted in the form of a thesis within the year.

Six areas visually distinct in vegetation and soil were sampled both spring and fall. Habitats 1-6 were as follows: ungrazed: (1) sagebrush (*Artemisia tridentata*)-hard substrate, (2) grass-sandy substrate, and (3) sagebrush/winterfat (*Eurotia lanata*)-hard substrate; grazed: (4) sagebrush-hard substrate, (5) grass-sandy substrate, and (6) chained and seeded crested wheatgrass (*Agropyron cristatum*). Soil and vegetation parameters were measured on 3 grids within each habitat. Soil parameters measured were bulk density, particle size, strength, and depth. Vegetation parameters measured were percent crown cover by species and horizontal density (MacArthur and MacArthur 1961).

In each habitat, rodent data were collected using three 6x6 snap-trap grids with two traps per station. Grids were operated for only 2 nights to reduce the chance of catching transient animals moving into the area

Fig. 13. Rodent density indexes for 5 species over 4 trapping periods on the INEL site.

after the resident animals were removed (Gier, per. comm.). Catch per unit of effort per species was calculated according to Stoddart (1977).

A selected sample of means for the different parameters is presented in Table 8. A 2 x 2 factorial analysis of variance with 6 habitats (treatments) was utilized to test all parameters for differences due to treatment, season, and the interaction of these two. An example of this analysis for percent cover data is shown in Table 9. Complete analysis will be presented in the final report.

Preliminary analysis of the habitat parameters indicated that significantly different habitats were chosen. However, the six habitats are not completely separated from each other. For example, bulk density in habitats 1, 3, and 5 are not significantly different from each other. Least significant difference (Ostle and Mencint 1975) tests are presently being performed on all other parameters.

From the field data a total of 35 variables has been generated and a Pearson's correlation matrix (NIE 1975) will be used to eliminate 1 of each pair of variables that are correlated with each other. A multiple regression will be used to determine the most important variables correlated with each rodent species; also principle component analysis (Isebrands and Crow 1975) will be utilized.

11. Comments

Probably the most critical comment of last years review read: "Work with natural populations is almost worthless without some estimate of confidence intervals . . . I feel that the investigator is ignoring these problems." This investigator appreciates very well the importance of statistical analysis. In general we have not emphasized the statistical problems for the following reason: In most cases we know very little about the distributions, behaviors, and resultant biases associated with the animals we are trying to census. For example there are some indications which would suggest that our coyote census methods may be measuring transient animals rather than resident animals; the same thing may be occurring with the rodent census (we have thus proposed this year to investigate a new method of rodent census). In the face of these real problems, that we know very little about, it would seem that applying conventional analysis to obtain estimates of error is little more than an exercise.

Instead of looking at individual parameter estimates and the error associated with each, we are looking at trends over a number of years. Though the errors attached to estimates of a particular parameter over a number of years may be so large as to make the estimates not significantly different, relationships of the parameter to another variable, if they exist, should begin to appear. Thus we have stressed such relationships as over winter mortality of the rabbit population as a function of the coyote/rabbit ratio. These are the functional relationships we are after, and these are the realtionships we will get regardless of the estimates of error we might come up with.

TABLI		HABITATS					
		1	2	3	4	5	6
Fol. ht. Indexes Spr/Fall	% Shrub Cover	22.819	8.278	15.097	9.583	2.292	5.833
	% Grass Cover	21.472	35.208	8.708	6.583	19.778	24.222
	Ht. 1	0.1046/0.0989	0.0836/0.1908	0.0780/0.1082	0.0670/0.1013	0.0975/0.1390	0.2209/0.1990
	Ht. 2	0.1311/0.1345	0.0843/0.1852	0.0960/0.1208	0.0988/0.1185	0.1032/0.1361	0.3017/0.2527
	Ht. 3	0.0803/0.0881	0.0323/0.0624	0.0403/0.0563	0.0518/0.0563	0.0336/0.0435	0.1412/0.0995
	Ht. 4	0.0513/0.0553	0.0215/0.0270	0.0204/0.0260	0.0294/0.0244	0.0192/0.0153	0.0497/0.0346
	Ht. 5	0.0280/0.0306	0.0168/0.0180	0.0146/0.0151	0.0202/0.0153	0.0153/0.0153	0.0184/0.0170
	Ht. 6	0.0166/0.0183	0.0155/0.0158	0.0153/0.0154	0.0170/0.0153	0.0153/0.0153	0.0153/0.0153
	Ht. 7	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153
	Ht. 8	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153	0.0153/0.0153
	% Sand	71.43/71.77	86.93/85.27	57.93/61.47	43.13/50.07	81.83/81.03	46.07/51.47
	% Silt	19.50/19.23	8.03/8.83	15.67/17.47	27.07/29.33	6.50/11.67	40.07/37.83
	% Clay	9.07/9.00	5.03/5.90	26.40/21.07	27.80/20.60	8.37/10.60	13.87/10.70
	% Sand	65.53/71.06	84.50/87.77	57.87/64.60	44.87/47.07	61.40/63.53	45.27/48.27
	% Silt	17.07/18.20	9.93/7.00	14.13/20.00	28.07/28.87	18.40/17.87	38.67/39.00
	% Clay	16.07/10.73	5.63/5.23	28.00/19.40	27.10/24.07	20.20/18.60	16.07/12.73
Fall	$\bar{X}$ SD ¹ Spr/Fall	13.28/13.42	16.39/17.11	18.00/18.00	18.00/18.00	18.00/18.00	17.47/15.97
	$\bar{X}$ SS ² 0/10/20	0.32/1.60/2.80	0.00/0.74/2.19	1.60/1.95/3.72	1.60/2.43/3.63	0.63/1.38/3.14	1.02/2.20/2.26
	$\bar{X}$ BD ³ Spr/Fall	1.5421/1.1563	1.5773/1.4706	1.3189/1.1770	1.2991/1.0656	1.4410/1.2477	1.2072/1.0211

1 Mean soil depth for spring and fall

2 Mean soil strength for spring at ground level, 10 cm, and 20 cm below surface

3 Mean bulk density for spring and fall

Table 9.

F VALUES FOR VEGETATION PERCENT COVER (14 variables)

SV	ARTTRI	DDARTT	OPTSPP	CHRVIC	EURLAN	SITHYS	AGRSPP	STICOM	BROTEC	AGRCRI	MISCGL	TOTSHR	TOTGRA	ORYHYM
HAB.	22.498 ***	36.106 ***	16.529 ***	5.250 ***	21.489 ***	8.256 ***	1.113 NS	58.081 ***	7.469 ***	66.319 ***	1.183 NS	73.586 ***	5.673 ***	12.819 ***
SEA.	5.118 *	7.919 ***	0.927 NS	1.641 NS	0.319 NS	0.022 NS	0.423 NS	2.619 NS	0.597 NS	0.827 NS	0.032 NS	5.295 *	0.454 NS	0.551 NS
H x S	2.534 NS	15.719 ***	2.147 NS	2.201 NS	0.440 NS	1.887 NS	1.199 NS	3.640 **	0.597 NS	0.827 NS	1.022 NS	2.238 NS	1.018 NS	1.119 NS
GRD/H	1.254 NS	0.512 NS	0.870 NS	1.986 ***	5.355 ***	3.168 ***	1.064 NS	1.583 *	1.080 NS	2.843 ***	4.517 ***	0.817 NS	1.324 NS	5.524 ***

*** significant at .01

** significant at .025

* significant at .05

NS nonsignificant

SV - source of variation

HAB. habitat (5,24 df)

SEA. season (1,24 df)

H x S interaction (5,24 df)

GRD/H grids within hab. (24,828 df)

ARTTRI - Artemisia tridentataDDARTT - Dead Artemisia tridentataOPTSPP - Opuntia polyacanthaCHRVIC - Chrysothamnus viscidiflorusEURLAN - Eurosia lanataSITHYS - Sitanian hystrixAGRSPP - Agropyron spp.STICOM - Stipa comataBROTEC - Bromus tectorumAGRCRI - Agropyron cristatumMISCGL - MiscellaneousTOTSHR - Total shrubsTOTGRA - Total grassesORYHYM - Oryopsis hymenoides

The real point of criticism which none of the reviewers seemed to have picked up is that the variables in some of the relationships are not independent. For example an estimate of overwinter jackrabbit mortality contains the same estimate of the jackrabbit index as does the coyote/rabbit ratio. Thus there is a built-in association between these variables which may result in some bias in the functional relationships. We intend to explore this possibility with some simulation studies.

Another critical point was our use of scent stations to index coyotes on the INEL. The criticism was a result of a statement by Robert Roughton. Mr. Roughton has assured this investigator that there was a misunderstanding of this statement on the part of the reviewer. Since we are not, as yet, able to make a good estimate of the error associated with a scent station line, it is impossible to say how many lines are adequate or what size area is required. However, in addition to the scent station index we are getting additional indexes by utilizing standard scat lines and standard trap lines.

A third criticism was our use of the Daubenmire method of sampling to get biomass estimates. This problem arose because we failed to give a detailed description of our techniques in the proposal. We are using a "Daubenmire frame", ie. a 0.1 square meter frame, but we are measuring square cm. of cover rather than percent cover. In 10-15 percent of the plots biomass is measured directly. Then, using double sampling methods (Cochran 1963) biomasses of some species are estimated utilizing a regression method and others using a ratio estimator. Preliminary results show coefficients of variation in the range of 10-100 percent, good for range estimates.

The principal investigator has spent approximately 9 months of 1/2 time on the project since the beginning of the current term of the agreement and will spend approximately 1 month of 1/2 time during the remainder of the term.

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