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

Progress Report

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Abstract

The main objective of the jackrabbit study on a 250-square-mile area in Curlew Valley, Utah is to describe observed changes in rabbit density in terms of mortality and natality rates and to relate changes in these parameters to variation in environmental factors. Rabbit density has been observed to change by a factor of 13; changes appear to be largely determined by variation in mortality rates. Mortality of the population from fall-spring and of adults from spring-fall are correlated with the coyote/rabbit ratio. Juvenile loss from birth to fall is correlated with the coyote/rabbit ratio and some yet unknown density related mortality factor(s). There is also evidence of "carry-over" effect in adult and juvenile mortality.

1. Introduction

The long-term objective of the jackrabbit study in Curlew Valley has been 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. Since the inception of the study, considerable progress has been made toward meeting this objective. Findings through 1970 concerning jackrabbit population biology and dynamics are documented in a 150-page manuscript which has now been accepted by the editor of Wildlife Monographs and sent to the publisher. A substantial amount of time was spent this year in revising the manuscript after it was returned from reviewers. We are now initiating another manuscript in which we will describe our knowledge at the present time of jackrabbit population ecology.

The present document describes findings from the 1973-1974 report period along with some data gathered 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

October 1973 and March 1974 density indexes for the 250-square-mile study area were obtained using 68 one-mile transects. As in previous years flushing angles and flushing distances of rabbits were recorded. Since flushing behavior of jackrabbits changes with density and between spring and fall, the absolute number of rabbits 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 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 lowest fall density we have measured. Spring density indexes have followed the same trend and, like fall 1973, the March 1974 index of 5.5 was the lowest we have observed and is less than one third that of spring 1973.

Rates of change from one census period to the next are indicated in the last 2 columns in Table 1 and are represented by the slopes (instantaneous rates of change) of the solid lines in Fig. 2. (Dashed and broken lines in Fig. 2 indicate rates of change from fall-fall and spring-spring respectively). During this reporting period the population declined 17 percent from March 1973 to October 1973 despite the intervening breeding season, and then declined another 63 percent from October 1973 to March 1974. Demographic mechanisms underlying these rates of change will be discussed below.

3. 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 to March (Table 2, column 2) was calculated by dividing the spring 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 72 percent in 1972-73. The un-weighted mean for the 12 spring-fall periods was 55 percent. Population mortality over the October 1973-March 1974 period was 63 percent.

The jackrabbit instantaneous mortality rates (the instantaneous rate = $-\log_e$ of the survival) for the October-March periods were plotted as a function of the independent variable, coyote/rabbit ratio (Fig. 3). Rates of population change from October-March are synonymous with October-March mortality rates since there is no reproduction during this period. It is apparent from the regression then that 72 percent of the observed variation in October-March density change is associated with variation in the coyote/rabbit ratio.

The coyote/rabbit ratio 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. The coyote/rabbit ratio for the October 1973-March 1974 period was the highest observed during the study and was a factor of 16 higher than the observed low value during the October 1968-March 1969 period.

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	-65	
March 1963	19	14		336
Oct. 1963	66	61	-57	
March 1964	26	26		62
Oct. 1964	49	42	-57	
March 1965	30	18		83
Oct. 1965	28	33	-64	
March 1966	15	12		100
Oct. 1966	20	24	-69	
March 1967	9	7.4		184
Oct. 1967	12	21	-56	
March 1968	15	9.2		606
Oct. 1968	81	65	-34	
March 1969	75	43		179
Oct. 1969	192	120	-44	
March 1970	173	67		184
Oct. 1970	268	190	-32	
March 1971	181	130		23
Oct. 1971	191	160	-46	
March 1972	107	87		-26
Oct. 1972	68	64	-72	
March 1973	17	18		-17
Oct. 1973	8	15	-63	
March 1974	5	5.5		

Fig. 1 Spring and fall jackrabbit population trends and fall coyote population trends in Curlew Valley. Closed dots indicate fall density, open dots spring density. Closed and open triangles indicate coyote density indexes in fall and spring respectively.

Fig. 2 A plot of the log of rabbit density in March and October for 12 years of study, 1962 - 1974. The slopes of the lines are the instantaneous rates of density change between census periods.

Table 2

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		
Unweighted means	55	60	65

Fig. 3 Linear regression of instantaneous rabbit mortality rate from October-March on the coyote/rabbit ratio over the study area

This method for calculating coyote/rabbit ratios is not the same as that reported earlier. Previously the number of rabbits used in the ratio was the mean number over the October-March period. This was not a good approach since the coyote/rabbit ratio, the independent variable in the regression equation, was a function of rabbit mortality rate, the dependent variable. Thus, as rabbit mortality rates increased or decreased, by whatever means, calculated coyote/rabbit ratios in turn increased or decreased through corresponding decreases or increases in mean rabbit number. This produced a false correlation between the two variables and likely explains why the present r^2 value is not as high as that previously reported.

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 3) in a collection of 100 rabbits made in October of each year. March-October adult mortality rates have varied from 9 - 87 percent with a mean over the 11 summer periods of 60 percent. Adult mortality for the March-October 1973 period was 87 percent, the highest recorded and equal to that in 1964.

Adult jackrabbit instantaneous mortality rates for the March-October periods were plotted again, against the coyote/rabbit ratio (Fig. 4). The number of rabbits in the ratio is the March density index and the number of coyotes is the following fall coyote index. The correlation is significant at the 70 percent level, however, the error about the regression line is large giving an r^2 value of only 0.17. Apparently other factors beside coyote predation are responsible for a large part of the observed variation in March-October adult mortality rate.

C. Mortality of juveniles from birth to October census. -- Mortality of juveniles from birth to October census, postpartum mortality, 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 2, 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 3). 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). Postpartum mortality rates varied from 22 - 88 percent with a mean of 65. Postpartum mortality in 1973 was 85 percent, exceeded only by the 88 percent value in 1972.

Survival of juveniles has been of particular importance because of the great effect it has had on density change (see following section). Two different models of juvenile survival have been constructed. First juvenile survival was plotted as a function of coyote/rabbit ratio and mean rabbit index from March-October (Fig. 5). Using data from 1964

Table 3
Percentage of Adults in October Rabbit Collections
from 1963-1973

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

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

$$y = 0.9953 - 0.9953X_1 - 0.0001875X_2$$

$$r^2 = 0.77$$

Fig. 5 Multiple regression of percent juvenile survival from birth to October on the coyote/rabbit ratio and mean rabbit index during the March-October period.

through 1970 we obtained an r^2 value of 0.77. However, when 1971-1973 data was added to the regression r^2 dropped to 0.22. The effect of mean rabbit index on juvenile survival for all years including 1971-1973 can be partitioned out of the model for better observation by plotting the difference, Δ s, between observed juvenile survival and survival calculated using only the first two terms ($y = 0.9953 - 0.9953X_1$, where X_1 is the coyote/rabbit ratio) of the above model (Fig. 6). That is, the effect of coyote predation is subtracted out so that Fig. 6 shows the relative effect of mean density only on juvenile survival. Apparently the relationship between mean density and juvenile survival is not constant between years. The smooth sequence of change in effect throughout the years of study is of particular interest. Possibly we are observing some "accumulative" 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. Numerous other possibilities exist, however, which could explain this chain of events, for example a changing pattern of disease or a change in abundance of plant species (cf. Westoby 1973) necessary for proper nutrition.

Another possibility is that juvenile survival is affected by changes in maternal care through an endocrine system response to density (Christian and Davis 1957). If this is the case the dependent variable, mean rabbit index, should probably be replaced with the variable, spring rabbit index. Juvenile survival was, therefore, plotted against the coyote/rabbit ratio and spring rabbit index (Fig. 7). With 1973 data excluded from the calculation of the regression equation, an r^2 value of 0.94 was obtained. Survival of juveniles in 1973 was considerably below that predicted by the model. Since the 1971 and 1972 data fit well with the model in Fig. 7 and poorly with the model in Fig. 5, it is of some interest to look at the relationship of the two independent variables, spring rabbit index and mean rabbit index (Fig. 8). In view of the fact that mean rabbit index from March-October is a function of adult mortality, juvenile mortality, and natality, all of which have varied to a considerable degree, the orderly sequence in the relationship of these two variables through the years of study is very curious. It would seem to point out that demographic mechanisms in the population are well attuned in their response to intrinsic and/or extrinsic factors which ultimately determine density.

4. Natality

Each month approximately 50 adult rabbits are collected from the study area. An autopsy is performed on each female to determine percent females breeding, litter size, 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 4, 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

Fig. 6 Plot of Δs against mean rabbit index during the March-October period, where Δs = difference between observed juvenile survival and survival calculated with the model: $y = 0.9953 - 0.9953X_1$ where X_1 is the coyote/rabbit ratio

$$y = 0.9920 - 0.8976X_1 - 0.0007614X_2$$

$$r^2 = 0.94$$

Fig. 7 Multiple regression of juvenile survival from birth to October on the coyote/rabbit ratio and spring rabbit index. 1973 data is excluded in the calculation of the regression equation

Fig. 8 Plot of means rabbit index from March-October against March rabbit index.

Table 4

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

Table 4 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)
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
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

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. Mean litter sizes (Table 4, column C) for the five littering periods in 1973 were 2.1, 4.9, 6.2, 3.5 and 1.0 respectively. This compares with the means over all years of study 1.6, 4.6, 5.7, 3.9, and 2.3.

Production of fetuses per female surviving the breeding season (Table 4, column D) has varied independently of density during years of spring population decline (1964-1967). However, during the 4 years (1968-1971) of spring population increase, production decreased continuously from 18.9 to 11.3. The trend of decreasing production continued in 1972 to a low of 7.5 even though spring density decreased that year. This may have been due to a "carry-over" effect or have been simply a result of the record low rainfall in Curlew Valley in spring 1972. In 1973 production increased markedly to 13.2, very close to the mean for all years of study of 13.7.

5. Summary of Population 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 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 15.4. 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 15.4 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 2.6. 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 using data through 1970 indicated that 85 percent of the variation in population change from October-October

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 4)	(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
Means	15.4	13.7	7.1	2.6	16

was associated with changes in adult and juvenile mortality (Wagner and Stoddart 1972).

During the middle and late years of rabbit population decline, 1963-1967, rabbit mortality rates were high as a result of coyote predation (cf. Figs. 3, 4, 7). At the same time rabbit numbers were coming down coyote numbers were also declining at about the same rate (Fig. 1) and the spring coyote/rabbit ratios remained relatively constant (Table 6).

In spring 1968 the situation changed. Rabbit numbers were about 24 percent above the previous spring (Table 1), whereas the coyote population had continued to decline, presumably because of low rabbit numbers. The result was a reduction in the coyote/rabbit ratio to about a third that of the previous 4 years. With this reduced ratio, the rabbits were able to make a substantial density gain of over 600 percent during the March-October period (Table 1). With this rapid increase in density, the coyote/rabbit ratio was reduced still further and in 1969 and 1970 the rabbit population continued to increase, however, at a slower rate (Fig. 2). The reduced rate of increase was mainly a result of increased juvenile mortality from birth-October (Fig. 7). Factors responsible for the increase in juvenile mortality are unknown but are apparently density related. As discussed above possible factors are disease, exhaustion of necessary food items, aggressive behavior, or pituitary-adrenal stress. In 1971 juvenile mortality from birth to October had increased to 85 percent (Table 2), and the spring-fall increase in density was only 23 percent, the smallest gain so far observed. The result was a decrease in density in fall 1971 over 1970 of 15 percent. The situation got worse. Though the jackrabbit has a greater potential rate of increase, coyotes were essentially able to keep pace with them during density increase because of the rabbits' reduced rate of growth in 1969-1971. By 1972 and 1973 the coyote/rabbit ratio had increased to a point where coyote predation was again adding to adult and juvenile mortality rates and the population actually decreased over the breeding season these two years (Fig. 1). By the October 1973-March 1974 period the coyote/rabbit ratio had increased to the highest value so far observed. The result of this sequence of events was a 24-fold decrease in spring density from 1971-1974, ending with a record low density for the study.

6. Controlled experiments

The penned studies did not progress as we had expected. This was mainly a result of the considerable amount of time spent this year in two revisions of the rather lengthy manuscript for Wildlife Monographs.

The U.S. Fish and Wildlife Service, Predator Ecology and Behavior Project stationed at Utah State University is giving us use of 20 acres of land at

Table 6

Spring Coyote/Rabbit Ratios in Curlew Valley from 1963-1974

	<u>1963</u>	<u>1964</u>	<u>1965</u>	<u>1966</u>	<u>1967</u>	<u>1968</u>	<u>1969</u>	<u>1970</u>	<u>1971</u>	<u>1972</u>	<u>1973</u>
Coyote/ Rabbit Ratio	0.0710	0.0325	0.0463	0.0477	0.0553	0.0151	0.00747	0.00949	0.00499	0.0161	0.0280

their research station near Logan. Our penned experiments will be conducted there in cooperation with interests they have in coyote-rabbit relationships. The station is now just being organized and studies by the Predator Ecology and Behavior Project are still in the planning stages. The extent of our cooperation will be reported later as the studies develop.

Fencing materials for our four 5-acre pens are now being obtained and construction will start soon. Objectives for the penned studies have been modified somewhat; these modifications are explained in the 1974-75 renewal proposal.

7. References

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