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TECHNICAL PROGRESS REPORT - COO-1329-20

Project Title: Population dynamics, movement, and home range of black-tailed jackrabbits (Lepus californicus) in Curlew Valley, northern Utah

Principal Investigator: L. Charles Stoddart, Research Biologist, Department of Wildlife Resources, Utah State University, Logan, Utah 84321

STATEMENT OF PROGRESS FOR THE PERIOD NOVEMBER 16, 1971 TO NOVEMBER 15, 1972

1. Introduction

One of the main objectives of the jackrabbit study in Curlew Valley has been to describe the observed changes in rabbit density in terms of mortality and natality rates, and to relate changes in these latter two parameters to variation in environmental factors. Thus, not only are we interested in describing the immediate demographic mechanisms of population growth and decline, but also in understanding the intrinsic and extrinsic factors involved in regulation of rabbit numbers. Our knowledge through 1970 as it relates to the above objective has been set forth in two comprehensive documents which are appended to this progress report. One document is a dissertation by L. Charles Stoddart completed in 1972, the other a manuscript which has recently been submitted to the editor of Wildlife Monographs for publication.

The present report describes results obtained during 1972 and discusses the relationship of these results, and in some cases those of 1971, to the pattern of events reported in the above two documents. Methodology, adequately described in the above documents, will not be repeated here.

2. Mortality

As discussed in previous reports and in the appended documents, changes in rabbit density appear to be largely determined by variation in mortality rates during three stages of the rabbits' life history: (1) Population from October census to March census, (2) Adult from March census to October census, (3) Juvenile from birth to October census.

Mortality of the total population from October to March and of the adult population from March to October are correlated with coyote/rabbit ratios

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for the respective time periods (Fig. 1 and 2). It is evident from the regressions in Figure 1 and 2 that summer adult and overwinter population mortality in 1972 fit well with the relationship of these mortality rates to coyote/rabbit ratios observed during the previous years of study. Summer adult and overwinter population mortality rates in 1972 were 45 and 46 percent respectively, somewhat higher than the corresponding rates in 1971 (40 and 30 percent). Evidently this was due to the observed increases, particularly during the March-October period, in coyote/rabbit ratios.

The model in Figure 2 explains only 56 percent of the observed variation in March-October adult mortality. Apparently during the summer months there are other important variables, possible disease or alternate coyote food supplies, which are affecting adult mortality.

Juvenile mortality from birth to October census has been of particular interest. A model (Fig. 3) developed by Stoddart (1972) indicates that juvenile survival is a function of both mean rabbit numbers during the summer months and coyote/rabbit ratio. Juvenile survival rates in 1971 and 1972, however, were considerably below those predicted by the model (values are shown in a later figure). The effect of mean rabbit numbers over summer on juvenile survival can be partitioned out of the model (Fig. 4) by plotting the difference, Δ_s , between observed 10-day juvenile survival rate and survival calculated using only the first two terms ($y = 0.981 - 2.95x_1$, where x_1 is the coyote/rabbit ratio) of the above model, i.e. taking into account only the effect of coyote predation on survival. As shown in Figure 4, the absolute value of Δ_s increases with mean rabbit numbers in a near straight-line relationship through 1970. In 1971 and 1972, however, Δ_s deviates markedly from the trend of previous years, indicating a much lower observed survival of juveniles from birth to fall census than the model would predict.

Two possibilities that explain the observed deviation are: (1) In 1971 and 1972 we were observing some "accumulative" or "carry-over" effect of density on juvenile survival which Christian and Lemunyan (1957) and Chitty (1967) have postulated might result from changes in behavior or genetic composition, (2) We may have been using the wrong variable in describing observed variation in juvenile survival. With regards to this second possibility, Δ_s was plotted against spring rabbit index (Fig. 5) rather than mean rabbit numbers over summer. In this case the 1971 and 1972 values for Δ_s fit the trend established during previous years extremely well, i.e. the observed values for juvenile survival are almost exactly those that would have been predicted using the new independent variable, spring rabbit index. In this case there is no indication of "carry-over." A model (Fig. 6) incorporating this new variable was subsequently made as a second possibility for describing observed variation in juvenile survival. This model accounts for 94 percent of the observed variation in juvenile survival.

Mean rabbit numbers over summer were used in the original model, Figure 3, because of findings by Pontrelli (1966). He observed that juvenile jackrabbits of a few months age were subjected to aggressive behavior from adults. The

Figure 1. Linear regression of instantaneous mortality rate (-log (survival rate)) of total population from October-March on coyote/rabbit ratio over the study area.

Figure 2. Linear regression of instantaneous mortality rate ($-\log(\text{survival rate})$) of adult population from March-October on coyote/rabbit ratio over the study area.

Figure 3. Multiple regression of percent juvenile survival (calculated as a 10-day survival rate) from birth to October census on the coyote/rabbit ratio and mean rabbit numbers/square mile during the period March-October.

Figure 4. Plot of Δ_s against mean rabbit numbers/square mile during the March-October period where Δ_s = difference between observed 10-day juvenile survival rate and 10-day survival rate calculated with the model: $y = 0.981 - 2.95x_1$ where x_1 = coyote/rabbit ratio (cf. Fig. 3).

Figure 5. Linear regression of Δ_s on spring rabbit index where Δ_s = difference between observed 10-day juvenile survival rate and 10-day survival rate calculated with the model: $y = 0.981 - 2.95x_1$ where x_1 = coyote/rabbit ratio.

$$y = 0.9807 - 2.745x_1 - 0.0006332x_2$$

$$r^2 = 0.94$$

Figure 6. Multiple regression of percent juvenile survival (calculated as a 10-day survival rate) from birth to October census on the coyote/rabbit ratio during the period March-October and March rabbit index.

level of aggression was apparently a function of the immediate rabbit density. Increased aggression resulted in increased juvenile mortality. This same behavior has been observed in other animal species. However, if juvenile survival is, instead, a function of spring rabbit numbers (Fig. 6) possibly an endocrine system response to density (Christian and Davis, 1957) is indicated in which maternal care decreases and postnatal mortality consequently increases.

Also, we do not fully understand the mechanics of coyote involvement in juvenile mortality. It may be that coyotes kill juveniles, particularly very young juveniles, whenever they are encountered. If this is the case, juvenile mortality would be a function of coyote density rather than coyote/rabbit ratio. If coyote density is substituted into the model in Figure 6, a new model (Fig. 7) is obtained which, though not fitting the data as well as the previous model, explains 81 percent of the observed variation in juvenile survival.

Clearly, from the above discussion, at this stage in the jackrabbit studies some controlled experiments might be very fruitful in trying to determine the true functional relationships of environmental factors to rates of rabbit mortality, particularly juvenile mortality.

3. Natality

As discussed in the 1971 report, since 1967 spring densities (Fig. 8) have been going up while the number of fetuses produced per female surviving the breeding season (Table 1, column A) has been continuously going down. Spring rabbit density decreased in 1972 to an index value of 87 from 130 in spring 1971. If the above inverse relationship between fetus production and density were to continue to hold in 1972 one would expect to see some increase over 1971 in the number of fetuses produced per female. In fact, however, the number of fetuses produced per female, 7.5, made the most marked decrease we have yet observed (cf. Table 1).

The number of fetuses produced per female surviving the breeding season has decreased since 1967 for two reasons. One is the observed continuous decrease in mean size of the four annual litters (cf. 1971 progress report). This trend did not continue in 1972, however, and was not responsible for the extremely low number of fetuses produced per female. Litter sizes in 1971 for the first three litters totaled 9.6 compared with 10.6 in 1972.

The second reason for decrease in numbers of fetuses produced per female is the number of litters produced. In general four litters are produced each year. However, the synchronized breeding usually stops in the middle of the fourth conception period (cf. Stoddart, 1972) so that all females produce the first three litters but only half, for example, will produce a fourth litter. This procedure has varied during only three years of the study. In 1967 and 1968 there were five conception periods resulting in all females producing four litters and some a fifth litter in these two years. The fifth litter contributed substantially to the large number of fetus produced per female (Table 1, column 1) in 1967 and 1968. Breeding in 1972 stopped

$$\hat{y} = 0.9661 - 0.03197x_1 - 0.0003074x_2$$

$$r^2 = 0.81$$

Figure 7. Multiple regression of percent juvenile survival (calculated as a 10-day survival rate) from birth to October census on the mean coyote numbers/square mile from March-October and March rabbit index.

Figure 8. Spring and fall jackrabbit population trends in Curlew Valley as determined by the semi-annual censuses.

Table 1. Mean number of fetuses produced per female surviving the breeding season, and mean number of fetuses produced and mean number of juveniles alive at fall census per female alive January 1 from 1963-70.

Year	(A)	(B)	(C)
	Fetuses/Female	Fetuses/Jan. 1 Female	Observed Juv. in Fall/ Jan. 1 Female
1963	13.5	5.4	4.1
1964	15.3	6.1	1.9
1965	13.1	6.3	2.1
1966	12.2	5.8	1.9
1967	18.9	7.3	2.4
1968	18.6	11.2	6.9
1969	14.1	9.9	3.9
1970	13.1	8.7	2.8
1971	11.3	8.0	1.2
1972	7.5	4.7	0.6

during the third conception period; only 33 percent of the females produced three litters. This was the first year of the study that all females did not produce at least three litters.

Even though spring density declined markedly in 1972, the breeding season may have ended early, thus continuing the trend of decreasing production per surviving female, because of an "accumulative" density effect as discussed above. Or, it may have ended early in response to weather. Curlew Valley had the lowest rain fall in 1972 ever recorded, and as a result plant phenology was advanced by about a month as compared with 1971. These factors may have brought on the early cessation of breeding. This points out again the need for controlled experimentation

to facilitate our development of true functional relationships.

The mean number of fetuses produced per female alive January 1 (Table 1, column B) is determined from the litter sizes and from adult mortality rates from January 1 to parturition of each litter. The reduction in the number of fetuses/female, column A, to fetuses/January 1 female, column B, results from adult mortality during the breeding season. The value in 1972 for the number of fetuses/January 1 female, 4.7, is the lowest recorded for the study. It is not extremely low compared with the first five years of the study, however, because of relatively low coyote/rabbit ratios in 1972 (Fig. 1 and 2) which resulted in relatively low adult mortality rates during the 1972 breeding season.

The number of fetuses/January 1 female, column B, is reduced through juvenile mortality to the number of juveniles at time of fall census/female alive January 1, column C. In 1972, there were only 0.6 juveniles in fall per female alive January 1. Again, this is the lowest value measured for the study and is 50 percent below the 1971 value. The number of juveniles in fall 1972 per January 1 female is much lower relative to other years than the number of fetuses/January 1 female because of the high juvenile mortality from birth to fall in 1972 (88 percent) which was apparently a population response to the relatively high 1972 spring density (Fig. 8).

4. Summary of density change

The fall 1971 density index of 161 was reduced to the observed 1972 spring density index of 87 through a 1971-72 winter mortality rate (Fig. 1) of 46 percent (mean during the years of study is 53 percent). This is the second highest spring density observed, but is a reduction of 33 percent from the spring 1971 level of 130. Because of the low reproductive rate in spring 1972 (Table 1, column A) and because of the very high juvenile mortality rate (88 percent compared with a mean of 63 percent) the rabbit population actually decreased from spring to fall for the first time during the study (Fig. 8). Oversummer adult mortality, 67 percent, was somewhat above the observed mean, 58 percent. The overall result was a fall 1972 density index of 64, a reduction of 60 percent from fall 1971.

As mentioned, density change has mainly been a function of variation in mortality rates. Even though natality rates have varied and thus affected density for that year, they have had little effect on the general population trend. There is no constant relationship between the number of fetuses produced per female (column A) and the number of juveniles observed in fall per January 1 female (column C). Using the most extreme case for an example, in 1972 if the number of fetuses produced per female had been an average value of 14, the fall density index would have been about 100, resulting in a density decrease of 40 percent. This is markedly different from the observed decrease of 60 percent but yet the trend in density change is the same.

5. Prediction for 1973

The rabbit population will likely continue to decrease, though perhaps not as rapidly as in 1972. Because of an increase of almost 100 percent in coyote numbers from fall 1971 to fall 1972 and because of a decrease in rabbit numbers in fall 1972, the coyote/rabbit ratio will likely increase by a factor of 4-5 for the October 1972-March 1973 period. This will result in a relatively high overwinter population mortality of about 60 percent, leaving a spring density index of about 25. Since the coyote population is responding to rabbit numbers (Clark, 1972) as well as to its own density, it is difficult with our present information to predict what the coyote numbers will be during summer 1973. Our best estimate is that the coyote population will remain about the same as in summer 1972, perhaps slightly lower. This means the summer coyote/rabbit ratio will increase about 2-3 times.

Even though a good bit of the population density pressure may be removed from juvenile survival (Fig. 6) the increase in coyote/rabbit ratio will hold the juvenile mortality rate relatively high, 60-65 percent. Assuming that the number of fetuses/female is able to increase to a near-mean level, the population will likely increase for spring to fall by a factor of about 2 or slightly less. This would produce a fall 1973 density index of about 45, a decrease of 30 percent from fall 1972.

6. References

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