MASTER

TECHNICAL PROGRESS REPORT - COO-1329-16

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

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STATEMENT OF PROGRESS FOR THE PERIOD NOVEMBER 16, 1970 TO NOVEMBER 15, 1971

1. Introduction

The major 1971 objective of this project has been to continue measuring demographic parameters of the Curlew Valley jackrabbit population, and the environmental correlates of changes in those parameters. The species undergoes pronounced population fluctuations in the region, and these fluctuations are apparently of an oscillatory nature with a reported periodicity of somewhere around 7 years, although in 9 years of study this population has not yet completed a phase. The techniques used to measure population density in March and October to measure reproductive rates and population age composition, and to estimate seasonal mortality rates during several stages of the life history have been described in numerous earlier reports, and will not be repeated here.

Completion of 1971 field operations closes a year in which the population entered the breeding season with the highest spring density so far measured (Fig. 1): Higher than the lowest recorded density by a factor of roughly 19. The result of this unusual condition was a new pattern of events not previously witnessed, and the addition of a new tile to the population mosaic which each years' research has progressively filled in. That mosaic will soon be filled in to where the full range of population responses over the oscillatory phase of the population will be evident. Knowledge of that full range is needed in order to provide variables required for a complete predictive model of which we now have a preliminary version (see supplements to this report).

2. The Pattern Evident Through 1970.

The pattern evident by the end of 1970, and reported in the last, annual progress report, in two papers presented at the 1971 meetings of the Southwestern and Rocky Mountain section of A.A.A.S., and in the preliminary model developed in concert with I.B.P./Desert Biome modelers, was as follows:

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Figure 1. Spring and fall jackrabbit population trends in Curlew Valley as shown by the semi-annual censuses.

(a) Reproductive rate per female surviving the breeding season had not varied materially between years. Females were attempting about four, well synchronized litters each year. The size of these had varied little between years, and it appeared that nearly all females were conceiving at each littering period.

Reproductive output per 100 females alive at the beginning of each breeding season did vary between years, largely because of marked warm-season mortality of adult females which varied substantially between the different years of observation. In some years, less than half of the females survived the breeding season and produced the full four litters; while in other years, most survived.

(b) Mortality (1) of the entire population over winter, (2) of the adults between spring and fall, and (3) of young between birth and fall tended to follow similar annual trends, being heavy in the early and mid 1960's, and declining in the late 1960's. A possible exception to this was what might have been a rising postnatal mortality rate of young in 1970, and possibly to some degree in 1969.

(c) The population declined from fall, 1962 when the first census was taken to a low point in 1967, and the increased during the three following years. The high, 1970 fall density was approximately nine times the 1967 fall value.

(d) The population change appeared to be largely determined by the variations in mortality rates which in turn appeared largely to be a function of coyote predation. Coyote populations varied with rabbit numbers, and the intensity of predation, and of mortality at the post-natal, winter, and summer adult periods appeared to be largely associated with the ratio of rabbits to coyotes.

3. Events of 1971

With the extremely high breeding density of 1971, several events occurred which, of themselves were quantitatively different from previous years. But, in retrospect, these were events which extended sequences which probably began some years earlier. These events were as follows:

(a) The size of the first litter was about normal, but the second, third, and fourth dropped down below previous years (Fig. 2). The total number of young born per female surviving the breeding season dropped 13.1, the mean for the years of observation being 16.5 and the highest total (1967) 21.4 (Fig. 3).

(b) Summer adult mortality continued below the long-term average (50 percent compared with 56), as did the overwinter loss (30 percent compared with 53). However, the postnatal juvenile mortality rose to its highest level: 85 percent compared with a mean of 61. The percentage of young in the fall population dropped to 60, compared with values ranging from 86 to 93 during the 1960's.

(c) The fall population declined about 13 percent from the 1971 level (Fig. 1), evidently because of the reduced reproductive effort and the very high juvenile summer mortality.

Figure 2. Yearly variation in mean litter sizes in Curlew Valley jackrabbits. Litter sizes tend to vary inversely with density.

Figure 3. Yearly variation in total young produced per female surviving the breeding season. The total is the sum of the mean size of each litter, shown in Fig. 2, for that year. The reproductive rate tends to vary inversely with density.

(d) Preliminary evidence on the coyote population trend indicates no population increase, a suspicion perhaps borne out by the continued low summer adult and overwinter mortality levels. Hence, the increased juvenile mortality would not seem to have been related to coyote changes, and some relationship to population density may be surmised.

4. The General Pattern as Seen at the End of 1971

In a study such as this one the sequential changes in an annually varying population, hypotheses will inevitably be developed as time passes. And as new stages in the population pattern develop, these hypotheses will gradually change until they become increasingly realistic. Like so much of science, the process is the increasingly accurate description of reality. The 1971 events appear to give some indication of the events that will characterize the initial stages of population decline, events which were guessed at in earlier reports.

(a) The decline in reproductive rate is doubtless a density response. It is now fairly clear that the reproductive effort is an inverse function of density (Fig. 2 and 3), at least in the second and third litter, and possibly the fourth. During the two low years 1967 and 1968, there was even an attempt at a fifth litter by a limited fraction of the females (Fig. 2). Discernment of this relationship required the 1971 extremes in order to really see the trend. In past reports we have emphasized the relative constancy of the reproductive rate. While the variation has not been great, it is now evident that it does vary and that variation can be provided for in a model.

(b) The pattern does not seem to have changed from that described in earlier reports in the case of summer adult and winter mortality patterns. These losses may still be largely a function of coyote predation, and because of the lag in coyote population response, these losses appear to be inversely density dependent (Fig. 4).

The postnatal juvenile loss pattern is more complex, being a function, perhaps, of both coyote predation and whatever the density pressures are. Consequently, in the early and middle 1960's, when the rabbit population was low and coyote numbers high but declining, the postnatal loss rates were relatively high. They declined in the late 1960's as the coyote population declined, and hence to this point, the postnatal loss patterns have been similar in trend to the summer adult and winter losses (Fig. 5). But with increases in the population, postnatal loss rates have risen sharply and, for the present, appear to be positively density dependent.

5. Additional Observations Needed

Based on the accumulated findings to date, we could now hazard predictions for the pattern of the next few years. Although the fall, 1971 population declined some 13 percent below the corresponding 1970 value, it is still quite high in comparison with previous years. It follows that the spring 1972 population will also probably be the second highest for the years of study. We can predict on the basis of overwinter mortality for the past 4 years: That mortality has averaged 41 percent, and hence we might expect that the spring, 1972 index value will be about

Figure 4. Yearly variation in adult mortality rates between March and October, and in overwinter mortality rates (October to March) of the entire population. The rates tend to vary inversely with density and apparently are primarily the result of coyote predation.

Figure 5. Yearly variation in the postnatal mortality rate (from birth to October) of young rabbits. At low rabbit density, the mortality appears to be importantly the result of coyote predation. At high rabbit densities, when the rabbit/coyote ratio is high and coyote predation low, the mortality appears to result from population pressures of yet unidentified nature.

60 percent of the fall index, or $.60 \times 161 =$ about 97. With a breeding population of this level, the reproductive effort will probably be below average again as it has been the last 2 years.

Since the coyote population apparently did not increase markedly in 1971, the overwinter jackrabbit mortality rate may, as suggested above, not differ too greatly from the mean of the past 4 years. However, with the rabbit population remaining high, coyote numbers could perhaps be expected to increase in 1972 as they have increased in most years with high rabbit populations. Accordingly, we should see some decrease in the rabbit/coyote ratio in 1972, and perhaps some coyote-induced increase in postnatal and summer-adult mortality. In addition, the high population pressures are likely to result in continued high postnatal loss, and consequently this parameter will probably be as high as or higher than, the 1971 value.

The result of all of this will probably be another year of decline, perhaps more marked than in 1971. The pattern predicted for 1972 could perhaps continue for another year beyond 1972; but by 1974 the population may well have declined to the point where we first observed it in 1962 or 1963. At this point, the population will have declined to where the reproductive rate will be released from the density pressures of the early 1970's. But rabbit/coyote ratio will now be down to the point where mortality, mostly predation, will be high enough to offset the enhanced reproductive level. The oscillatory phase will have been completed.

Several unknowns remain which need to be ferreted out in order to make our understanding sufficiently precise to permit the development of an accurately predicting model. The first is the cause or causes of the high, density-related postnatal mortality. Several possibilities suggest themselves: (1) Abandonment by the females at early ages when the young still need suckling, and/or (2) insufficiency of milk production by the females. Density-induced declines in maternal care, such as these, have been reported in rodents (Christian, 1956; Southwick, 1955).

(3) A third possible source of increased juvenile mortality could be an increase in predation pressure by predators other than coyotes. While they are small, young jackrabbits are undoubtedly vulnerable to numerous predator species, especially some raptors. Increase in their numbers in response to higher rabbit densities could result in heavier predatory pressure.

Platt (1971) conducted a survey of raptor populations and summer food habits in 1969 when the rabbit population was just beginning to increase. Although rabbits were staple items of diet for only two species--golden eagle and ferruginus hawk--they were taken in limited numbers by great-horned owl, Swainson's hawk, and red-tailed hawk. In addition, we have flushed harriers, one of the most numerous hawks in Curlew Valley, from fresh kills of young rabbits. Collectively, these species could exert material predation pressure on vulnerable, young rabbits if raptor numbers increased markedly. It would be desirable in 1972 to repeat Platt's survey to determine whether any marked raptor increase has taken place.

Another unknown which may appear in the population is what Wagner et al (1965:135) termed "population momentum." As many animal populations fluctuate under the impetus of density pressures, they tend to gain momentum during the decline and increase phases. Consequently, the reduced reproductive rate and/or higher mortality rate of the decline period may persist for a year or two after the population declines beyond its long-term mean. Conversely, a population may retain high reproductive rates and/or low mortality rates for a year or two after it has increased beyond its mean density.

There is some slight suggestion of this in Fig. 2 and 3. The reproductive rates in 1969 and 1970 were as high as, or higher than, the rates of the early and middle 1960's despite the fact that the densities of these two years were substantially higher. This suggests that the advantages which accrued to the population by 1967 and 1968 remained despite the higher population pressures of 1969 and 1970.

If the momentum phenomenon is real, it should follow that the low fecundity and juvenile survival rates setting in 1971 will persist for some years after substantial decline has taken place. Two schools of thought exist to explain this phenomenon: One is the Chitty (1952, 1957) school which postulates genetic oscillations in the population. The other is the nongenetic transmission, via the prenatal environment, of physiological and demographic traits (cf. Christian and Lemunyan, 1957; Wagner, 1965:135). Whatever the explanation, if the phenomenon is present in the Curlew Valley jackrabbit population, it will need to be identified so that it can be provided for in a predictive model.

6. Conclusion

The goal of our Curlew Valley jackrabbit studies is an understanding of the population ecology of this species in the Curlew Valley ecosystem, and a description thereof. The description to which we aspire is a simulation model of the species' population changes. Such a model is a quantitative description which collectively expresses the interactions between the numerous environmental variables affecting the species and many stages of its life-history. It enables one to assess the relative importance of different factors operating at different times. And it permits one to predict the effects on the population of manipulating one or more of the factors operating, or of intruding a new factor (e.g., artificial control) into the system.

In order to develop such a model, it is necessary to derive the functional relationship between each factor operative on the population, and the particular life-history stage upon which that factor operates. The variables are measured each year, and the form of the function becomes evident when enough observation points (years) are available to delineate it.

In a "cyclic" or oscillatory species like the jackrabbit, the full range of values for the different variables is not observed until the species has undergone a complete oscillatory phase. It is therefore important that this study continue for 2 to 3 more years in order that

the full range can be measured and the project brought to fruition in the form of a finished model. A preliminary model has been developed on the basis of data available through 1970. The major value of that model is to develop its structure, and to lend precision of thought to considering the measurements being made, ensuring that no variables are being overlooked. The final version will undoubtedly have much the same structure but, based on measurement through the full oscillatory phase, will have more refined delineation of the functions, and therefore more precise predictive capability.

The value of this study not only rests in the complete understanding of this species which is virtually at hand. Its value, additionally, rests in fact that the jackrabbit is the major, wild vertebrate herbivore in the Curlew Valley ecosystem. The system is now being studied as a major project of the U.S./I.B.P. Desert Biome. In consequence, the project is contributing a major part of the total research effort underway in the valley. Hence, this project will not only contribute understanding of the species' population ecology per se, but in addition is contributing to an understanding of species' role in total ecosystem.

7. References

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