**Historical Wildlife
Dynamics on Dugway
Proving Ground:
Population and Disease
Trends in Jack Rabbits over
Two Decades**

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August 1986

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the U.S. Army Test and Evaluation Command
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SUMMARY

In an effort to determine whether U.S. Army activities on the Dugway Proving Ground (DPG) have had an impact on resident wildlife, intensive studies have been conducted on the biology and ecology of the black-tailed jack rabbit (Lepus californicus) since 1965. In addition, the incidence of endemic diseases in several species of resident wildlife on the DPG have been studied from the late 1950s through the mid-1970s.

The objectives of this report are to 1) compile and summarize the jack rabbit data and some of the disease information that is presently contained only in annual reports, 2) compare the DPG jack rabbit data to data available on other jack rabbit populations, and 3) analyze the data for unusual or unexplained fluctuations in population densities or in incidence of disease.

POPULATION BIOLOGY AND ECOLOGY OF THE JACK RABBIT

Two complete cycles in jack rabbit density occurred during the 21 years (1965 to 1985) that rabbit populations were monitored. During these population cycles, jack rabbit densities ranged from 5.5 to 190 rabbits/km². Variations in both the amplitude and length of the two population cycles were noted. In general, however, fluctuations observed in the DPG jack rabbit population were similar to those observed in both the area surrounding DPG and in more distant locations.

A number of potential factors were observed that may have biased the estimated population indices obtained during this study. These potential biases included changes in the flushing behavior of jack rabbits relative to time of day, temperature, and rabbit density. Changes in methods used to record data may have also influenced the indices that were derived.

The breeding season for jack rabbits on or near DPG extended from December through July, with peak activities in March. Breeding was synchronized within the population, with peaks of activity at approximate 40-day intervals throughout the breeding season. Litter size for adult females varied with the month the rabbit was collected, stage of fetal development, and rabbit density. Less than 4% of the juvenile females examined during this study bred, and no clear

relationship was detected between the proportion of juveniles breeding and population density. Prenatal loss was highly variable, but appeared to peak during periods of population decline.

The proportion of juveniles in fall collections of rabbits reached a peak 2 years prior to when peak population densities were achieved. No significant changes were noted in jack rabbit population densities before the proportion of juveniles in fall collections exceeded 50%.

The overall sex ratios of collected adult and juvenile jack rabbits did not vary significantly from 50:50 throughout the 21 years of study; however, adult sex ratios were much more variable and appeared to fluctuate with population density. In addition, a decreasing linear trend was noted in the proportion of adult females in the samples collected over a 12- to 13-year period.

The incidence of tularemia (Francisella tularensis) and Q fever (Coxiella burnetii) in rabbits was low throughout the study, but increases were noted in the incidence of these diseases during the declining phases of rabbit populations. In contrast, the incidence of Rocky Mountain spotted fever (Rickettsia rickettsii) was high, and no clear relationship to rabbit density could be detected.

UNUSUAL OR UNEXPLAINABLE FLUCTUATIONS

Both the timing and amplitude of the cyclic fluctuations in DPG jack rabbits appeared to be normal when compared to other jack rabbit populations. The only unusual fluctuations in DPG jack rabbit populations occurred in 1981, when a temporary suppression of rabbit numbers was noted during a normal increasing cyclic phase. The age ratio of collected jack rabbits also appeared to behave in an atypical manner in the 1981 to 1982 period. During this period, changes in the age ratio and population density of jack rabbits coincided with one another; whereas, before 1981, changes in the age ratio of collected rabbits preceded population density by 2 years.

The proportion of adult females in collections of jack rabbits decreased substantially during the first 12 to 13 years of this study. Why this trend occurred is unknown.

Three abnormalities were noted in the incidence of disease. There was a statistically significant elevated level of Q fever in rodents collected from the central portion of DPG, and there was a statistically significant higher incidence of tularemia in coyotes collected from the area surrounding DPG. In both of these cases, the trends in disease incidence were similar for DPG and non-DPG animals, perhaps indicating that the differences were the result of natural causes. In addition, there was an unusually high incidence of Rocky Mountain spotted fever in small rodents on DPG in 1970.

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INTRODUCTION

The United States Army began sponsoring studies in 1953 of the natural resources of the Dugway Proving Ground (DPG), located in Utah. These investigations covered a wide variety of topics but emphasized the biology and ecology of endemic diseases in resident vertebrates and invertebrates on DPG. Intensive studies of the ecology of the black-tailed jack rabbit (Lepus californicus) began in 1965, although fairly extensive collections of jack rabbits for analysis of diseases had taken place prior to this date. Biannual counts of jack rabbits on 119 permanent transects and systematic collections of jack rabbits for analysis of the incidence of disease and reproductive performance began in 1965. The primary objective of the jack rabbit studies were to determine whether U.S. Army activities on DPG have had an impact on this species and, if so, to what extent and what was the associated mechanism.

Ecological field studies on DPG were conducted by the University of Utah (1953 to 1969), EcoDynamics Corporation (1969 to 1973), and the Dugway Proving Ground Environmental and Ecology Branch (1973 to 1985). Data obtained during these investigations were published in annual reports from 1954 to 1973 and in intermittent reports from 1974 to the present. In January 1986, the Pacific Northwest Laboratory (PNL) began compiling, summarizing, and analyzing the existing data on "Population and Disease Trends of Wildlife in Western Utah," (PNL Proposal Number 300A02812). This document serves as the final report for that project. The objectives of this report are to 1) compile and summarize the jack rabbit data that is presently contained only in annual reports, 2) compare data on DPG jack rabbits to data available on other jack rabbit populations, and 3) analyze the data for unusual or unexplained fluctuations in population densities or in incidence of disease.

STUDY AREA

This study was conducted on the Dugway Proving Ground in west-central Utah (Figure 1). However, comparisons were made between jack rabbit population cycles on or near DPG and jack rabbit cycles in the Curlew Valley of northern Utah and on the Idaho National Engineering Laboratory (INEL) of south-central Idaho (Figure 1).^(a)

DUGWAY PROVING GROUND

Dugway Proving Ground is located approximately 100 km southwest of Salt Lake City. The DPG, which is 3,249 km² in size, was established in 1942 for the purpose of testing chemical and biological weapon systems for the U.S. Army

FIGURE 1. Dugway Proving Ground and Surrounding Area

(a) Personal communication from L. C. Stoddart, U.S. Fish and Wildlife Service, Logan, Utah, to L. E. Eberhardt on March 11, 1986.

(Figure 1). Public access to DPG is prohibited. The western half of DPG is dominated by the Great Salt Lake Desert and the eastern half by valley floors and mountain ridges. Elevations on the site range from 1,286 m in the Great Salt Lake Desert to 2,154 m on Granite Peak (Figure 2). The climate is characterized by hot, dry summers and relatively cold winters. Average annual precipitation is 17.6 cm and occurs primarily in winter and early spring (Pinkham et al. 1982). Eight distinctive plant communities occur within DPG; these include pickleweed (*Allenrolfea occidentalis*), vegetated dunes, shadscale (*Atriplex confertifolia*)-gray molly (*Kochia vestita*), shadscale-gray molly-greasewood (*Sarcobatus vermiculatus*), greasewood, shadscale-budsage (*Artemisia spinescens*), juniper (*Juniperus* spp.)-brush, and mixed brush (Vest 1962). Much of the western half of DPG is characterized by barren salt flats.

FIGURE 2. Location of Census Transects for Jack Rabbits on or near the Dugway Proving Ground, Utah

COMPARISON SITES

The climate in both of the comparison sites is similar to that of DPG (Gross et al. 1974, Anderson et al. 1978). Annual precipitation is approximately the same at the INEL (18 to 20 cm) (Anderson et al. 1978) as it is at PG and is slightly higher at Curlew Valley (18 to 36 cm) (Gross et al. 1974).

Eighty percent of the INEL site is dominated by big sagebrush (Artemisia tridentata) (Anderson et al. 1978), while four major vegetation types occur at Curlew Valley, these include Utah juniper (Juniperus osteosperma), big sagebrush, shadscale, and greasewood (Gross et al. 1974).

The climate in both of the comparison areas is similar to that of 1940-1950. At alt. 1970', Anderson et al. (1971) Annual precipitation is approx-
imately the same as the 1940-1950 (Anderson et al. 1971) 82 in 1940
and is slightly higher at Carlew Valley (1940-1950) 80 in 1940.

Eighty percent of the fall rain is dominated by the following:

Clouds (Anderson et al. 1971) while four major vegetation types occur at
Carlew Valley, these include Juniperus arbuscula, Pinus
banksiana, Abies, and grasswood (Griggs et al. 1971).

METHODS

Three major aspects of jack rabbit ecology were monitored during this study; these were population density, reproductive performance, and incidence of disease.

RABBIT NUMBERS

Changes in jack rabbit population densities were monitored on 119 permanent transects that were established in the spring of 1965. These transects, each 1.6 km long, were placed systematically in typical rabbit habitat on DPG and surrounding areas (Figure 2). In March and August of each year, a survey team consisting of a driver and two observers drove over the transects during daylight hours. The March survey provided an index to the number of animals entering the breeding season, and the August survey indicated productivity for a given year. Survey teams did not cover transects during periods of inclement weather. Information that was recorded during transect counts included: date, time, weather conditions, number of jack rabbits observed, individual flushing distances,^(a) and lateral distance of the rabbit from the transect (only during 1969 and from the late summer of 1984 to present).

The mean number of rabbits/transect/season and the density estimators of Hayne (1949) and Gates (1969) were calculated as indices to DPG jack rabbit density. Because there was a high correlation between the density estimators and mean number of rabbits/transect/season ($r^2 = 0.97$ and 0.84 for the Gates and Hayne estimators, respectively) (Figure 3), the simpler index, mean number of rabbits/transect/season, was used for most comparative purposes. Indices to jack rabbit densities on the comparison sites (Curlew Valley and INEL) were obtained with the Fourier Series estimator of program TRANSECT (Burnham et al. 1980) (L. C. Stoddart, pers. commun.). These values were considered as indices to population density because some of the assumptions of the estimation technique may not have been met (L. C. Stoddart, pers. commun.).

(a) Distance between the observer and rabbit when the rabbit first moves in response to the observer's approach.

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To evaluate the impact of historical DPG activities on jack rabbit population levels, comparisons were made between the mean number of rabbits recorded on transects located within the boundaries of DPG (onsite; N = 45) and transects located outside the boundaries of DPG (offsite; N = 74). To test for equality of the two population curves, polynomial regression equations (7th order) were fitted first to the log-transformed on- and offsite curves and then to a combined population curve for both areas (Neter and Wasserman 1974). Other statistical techniques were considered for comparing and analyzing population curves, for example time series, but were not used because of limitations of the data set or the technique. Additional nonquantitative comparisons were made between population curves for jack rabbits on or near DPG and jack rabbit population data for the Curlew Valley of northern Utah and the Idaho National Engineering Laboratory of southern Idaho (Figure 1).

REPRODUCTIVE PERFORMANCE

Rabbits have been shot and collected on a routine basis since 1954 for disease analyses and since 1964 for evaluation of reproductive performance. Attempts were made to collect 500 rabbits each year from a 13,000-km² area that included DPG and surrounding areas. Only a few rabbits were collected during the months of November and December. Male breeding status was assessed by the weight of one testis. Reproductive tracts of females were examined macroscopically for evidence of pregnancy and embryo resorption. The crown rump length of fetuses was measured, and conception dates were estimated by back-dating the age of the fetuses using modified age length curves from Bookhout (1964) (Table 1). Ovaries were sectioned by hand and examined macroscopically for corpora lutea. The presence or absence of lactation was also recorded. The length of the breeding season was estimated by the time period between the earliest and latest conception dates obtained from back-dated fetuses. Estimates of prenatal losses were obtained by calculating the percentage of visibly pregnant females that had resorbed at least one fetus and by comparing corpus luteum counts with fetus counts in pregnant females near term (fetus age >30 days).

TABLE 1. Crown Rump Length for Jack Rabbit Fetuses Based on Modified Age Length Curves from Bookhout (1964)

<u>Length (mm)</u>	<u>Estimated Age (d)</u>
0 - 3.5	5
3.5 - 4.4	10
4.5 - 5.4	11
5.5 - 6.9	12
7.0 - 8.4	13
8.5 - 9.9	14
10.0 - 11.9	15
12.0 - 13.9	16
14.0 - 16.9	17
17.0 - 19.4	18
19.5 - 22.0	19
23 - 25	20
26 - 28	21
29 - 31	22
32 - 35	23
36 - 38	24
39 - 42	25
43 - 46	26
47 - 51	27
52 - 56	28
57 - 61	29
62 - 66	30
67 - 71	31
72 - 76	32
77 - 82	33
83 - 86	34
87 - 92	35
93 - 96	36
97 - 102	37
103 - 108	38
109 - 112	39
113 - 117	40
118 - 122	41
123 - 128	42
129+	43

The age of collected rabbits was estimated using eye lens weight (Larson and Taber 1980). One eyeball was obtained and fixed in 10% formalin at the time of death. The lens was later separated from the eyeball, dried for 15 days at 90°C, and weighed. The lens weights of eyes from laboratory reared jack rabbits of known age were used to estimate ages of the collected wild

rabbits (Table 2). The percentage of young rabbits in the fall and winter collections was calculated based on eye lens weight.

DISEASE ANALYSES

Blood and tissue samples were obtained from collected jack rabbits and analyzed for the presence of pathogens. Samples of sera were examined for the presence of antibodies to various pathogens by using the methods of tube agglutination, slide agglutination, complement fixation, hemagglutination, or other tests (Ecology and Epizootology Research Staff 1966). Tissue samples were homogenized, pooled, and injected into laboratory animals for the isolation and identification of pathogens (Ecology and Epizootology Research Staff 1966). Because of inconsistencies in the manner the results of pathogen analyses were

TABLE 2. Relationship Between Eye Lens Weight and Age of Jack Rabbits^(a)

<u>Lens Weight (mg)</u>	<u>Estimated Age (mo)</u>
60-85	1-2
86-110	2-3
111-135	3-4
136-160	4-5
161-185	5-7
186-210	7-10
211-235	10-13
236-260	13-18
261-285	18-27
286-310	27-42
311+	42+

(a) Ages <13 months are based on laboratory-reared jack rabbits. Ages >13 months are based on Teimeier and Plenert (1964).

reported in annual reports, the unavailability of the original data forms, and to keep the data as compatible as possible from year-to-year for trend analyses, only the serological evidence of pathogen presence is presented in this report.

DATA ANALYSES

The DPG jack rabbit data presented in this report were obtained from three sources: 1) annual reports by the University of Utah, EcoDynamics, and the Environmental and Ecology Branch of DPG, 2) computer tapes containing the results of the jack rabbit transect censuses and analyses of reproductive tracts, and 3) raw data. When possible, forms containing raw data were examined to resolve any inconsistencies noted between the recorded data on the computer tapes and that reported in annual reports. The raw data for reproductive performance for most years was apparently destroyed; however, the raw data for 1974 through 1975 were available for examination, and the information they contained agreed with that on the computer tapes. Nearly all analyses were performed on the data contained in the computer tapes. SAS® System computer software (SAS Institute, Inc. 1985) was used for statistical and graphical analyses.

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RESULTS AND DISCUSSION

During the period 1965 to 1984, 8,878 jack rabbits were collected and analyzed for reproductive patterns and diseases (Table 3) (data on reproductive performance for 1964 was obtained but not recorded on computer tapes). Comparatively few rabbits were collected during periods of population lows and in November and December of all years. Fifty-one percent (4,520) of the rabbits

TABLE 3. Total Number of Jack Rabbits Collected on or near Dugway Proving Ground by Month and Year

Year	Month												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
1965	11	73	25	19	28	10	37	25	101	0	0	0	329
1966	67	49	25	50	73	53	38	10	17	41	0	0	423
1967	44	16	44	8	48	56	38	45	38	13	0	0	350
1968	36	25	46	38	69	69	41	47	55	32	0	0	458
1969	58	64	54	26	58	44	62	52	84	15	0	0	517
1970	58	52	54	46	66	74	40	53	53	60	0	0	556
1971	80	45	80	68	99	54	59	67	75	59	0	0	686
1972	48	109	68	78	68	101	56	45	45	32	0	0	650
1973	23	3	15	51	38	0	41	10	27	0	49	0	257
1974	17	14	5	32	56	5	25	11	17	8	27	0	217
1975	13	2	0	22	30	0	13	8	5	6	24	0	123
1976	8	0	0	0	9	0	1	5	33	1	15	0	72
1977	9	19	9	5	22	0	20	0	2	0	0	0	86
1978	15	12	5	28	12	15	0	0	47	175	0	0	309
1979	0	116	28	120	344	92	378	0	242	0	0	0	1320
1980	28	100	49	77	145	91	34	0	120	0	0	0	644
1981	22	97	0	136	85	75	0	0	92	14	0	0	521
1982	0	64	69	86	130	146	134	0	129	0	0	0	758
1983	0	139	0	96	82	81	95	0	66	19	0	0	578
1984	0	0	15	0	2	0	4	0	0	0	0	3	24
TOTAL	537	1014	576	986	1462	968	1116	378	1248	475	115	3	8878

collected were from DPG; the remaining rabbits were obtained in areas immediately surrounding DPG (Appendix 1). An additional 2,904 lagomorphs were collected on or near Dugway from 1959 to 1964 for disease analyses only.

RABBIT NUMBERS

Population Dynamics

Two complete cycles in jack rabbit densities occurred during the 21 years the transects were censused (Figure 4 and Appendix 2). The time required for a complete population cycle (low to low) was 8 years during the first cycle and 10 years during the second. It took approximately 5 years to go from a population low to a population high during the increasing phase of both cycles; whereas, population declines were much more abrupt, requiring only about 3 years. Greater than 90% of this decline in population levels was accomplished in a 2-year period during both cycles. Peak, late-summer, population

FIGURE 4. Spring and Late Summer Indices to Jack Rabbit Densities on or near the Dugway Proving Ground from 1965-85

levels were maintained over a 3-year period during the second cycle, in contrast to the first cycle, where peak numbers existed for only 1 year.

Based on the Hayne's (1949) estimator, densities of jack rabbits ranged from a minimum of 5.5 rabbits/km² in the late summer of 1985 to a maximum of 190 rabbits/km² in the late summer of 1971 (Figure 3). This range in densities was similar to that observed in other studies on this species (Teimeier 1965; Gross et al. 1974; Smith and Nydegger 1985). The amplitude variation from population low to high and high to low ranged from 1:11 to 1:30, which also compares to amplitude variation observed in other studies (Gross et al. 1974; Keith 1963). During the first and second cycles peak density indices for late summer were considerably different, with peak population levels in the second cycle being approximately 65% of those achieved during the first cycle. However, peak spring population levels for the two cycles did not differ nearly as much (Figure 4). Jack rabbit density indices during the population lows recorded in this study (1967, 1975, and 1985) were approximately the same (Figure 4). Late summer population levels were higher than spring densities in all years except in the decreasing phase, when mortality during the spring and early summer must have exceeded production.

Comparison to Other Populations

Comparing the populations of jack rabbits on DPG and in the Curlew Valley of northern Utah (L. C. Stoddart, pers. commun.) for 1965 to 1985 revealed some differences in the characteristics of their population cycles (Figure 5). The density of jack rabbits in the vicinity of DPG was considerably higher during their first population cycle than the second; whereas, at Curlew Valley, jack rabbits reached their highest densities during their second cycle. In addition, based on correlation analyses (Table 4), there was approximately a 1-year lag between peak population densities for the two areas during the first cycle. No discernible lag occurred during the second cycle (Table 4).

Polynomial regression curves that were fitted to the population data indicated significant ($F = 6.4$; $df = 8,26$; $P = 0.001$) differences between the population cycles of jack rabbits on DPG (onsite population) and jack rabbit cycles in the area immediately surrounding DPG (offsite population) (Figure 6). Differences were noted in both the amplitude and phase lag of these cyclic

FIGURE 5. Comparison of Fluctuations in Numbers of Jack Rabbits on the Dugway Proving Ground, Curlew Valley, and the Idaho National Engineering Laboratory (INEL) (1 = Spring Populations, 2 = Late Summer Populations)

TABLE 4. Measurement of Lag Time (Correlation Coefficient, r) Between Population Cycles for Contrasted Populations of Jack Rabbits

	Onsite Versus Offsite No. of Years Lagged ^(a)			DPG Versus Curlew Valley No. of Years Lagged ^(b)		
	0	1	2	0	1	2
Both Cycles (Spring)	0.68	0.65	0.40	0.53	0.51	0.15
Both Cycles (Late Summer)	0.72	0.75	0.42	0.56	0.46	0.14
1st Cycle (Spring)	0.92	0.76	0.28	0.72	0.97	0.71
1st Cycle (Late Summer)	0.92	0.89	0.40	0.90	0.91	0.69
2nd Cycle (Spring)	0.78	0.86	0.65	0.74	0.46	-0.25
2nd Cycle (Late Summer)	0.75	0.87	0.63	0.84	0.59	0.06

(a) Offsite population lagged.

(b) Curlew Valley population lagged.

FIGURE 6. Comparison of Fluctuations in Numbers of Jack Rabbits on Census Transects Located on the Dugway Proving Ground (Onsite) and Transects in the Area Surrounding the Dugway Proving Ground (Offsite) (1 = Spring Populations, 2 = Late Summer Populations)

fluctuations. The amplitude of cycles for the onsite population was greater and more variable than the amplitude for the offsite population. Offsite jack rabbits reached approximately the same maximum population levels during both cycles; however, onsite population levels were considerably lower during the second cycle compared to the first (Figure 6). Based on correlation analyses (Table 4), both the on- and offsite populations appeared to reach peak densities at approximately the same time in the first cycle, but there was at least a 1-year lag between the times the two populations reached peak numbers during the second cycle.

The general appearance of the on- and offsite population curves (Figure 6) after the mid-1970s suggests that some event, either natural or unnatural, may have occurred on DPG that resulted in a reduction in the overall amplitude and a delay in reaching peak numbers for onsite jack rabbits during their second population cycle. However, natural irregularity in amplitudes of successive cycles was also noted in the Curlew Valley population (Figure 5) located

approximately 175 km northeast of DPG (Figure 1) and has been observed in other cyclic, mammalian species as well (Bulmer 1974).

Both the on- and offsite populations demonstrated additional irregularities in their population cycles during the 1980-81 period (Figure 6). During this period, the offsite population, which at the time was declining from the peak densities attained in the late summer of 1979, increased in the late summer of 1981 and then resumed its decline. Similar changes were also observed during a declining phase for jack rabbits on the Idaho National Engineering Laboratory (INEL) in southern Idaho (L. C. Stoddart, pers. commun.) (Figure 5). In contrast, the onsite jack rabbit population for late summer of 1981 was apparently suppressed during its increase to the cyclic population high reached in the late summer of 1982. This irregularity was not observed during the first population cycle for either the on- and offsite population, nor was it observed in the recorded jack rabbit cycles at Curlew Valley or INEL.

Potential Biases

A number of potential biases were observed in the data obtained during this study. These biases probably influenced the indices that were derived for jack rabbit density. These biases involved changes in rabbit behavior relative to time of day, temperature, and rabbit density. In addition, changes in the methods of recording data may have biased density estimates.

The time of day during which censuses were conducted clearly influenced the number of rabbits observed and the flushing distances of these rabbits (Figure 7). Based on recorded observation times for 12,311 rabbits, the mean number of rabbits observed per transect was greater during the mid-morning and early-evening hours than during mid-day (Figure 7). This probably reflects the nocturnal and crepuscular activity patterns that are characteristic of jack rabbits (Lechleitner 1958). During this study, jack rabbits were counted during daylight hours, with most censuses conducted between 0900 and 1500 (Figure 8). The sightability of jack rabbits varied considerably during this time period (Figure 7) and probably resulted in biased indices of jack rabbit density.

FIGURE 7. Influence of the Time of Day on the Number and Flushing Distance of Jack Rabbits Observed on Transects

The distance at which jack rabbits were flushed also varied in a crepuscular manner, with peaks in mid-morning and evening and lows during mid-day (Figure 7). Time-related changes in flushing behavior also probably biased the density estimators, especially those that directly incorporated flushing distance into their calculations (Gates 1969; Hayne 1949; see Figure 3).

Ambient temperature had an obvious influence on both the number of rabbits observed (Figure 9) and their mean flushing distance (Figure 10). The mean number of rabbits observed/transect increased in a linear fashion with respect to temperature ($r^2 = 0.28$, $F = 22.1$, $P = 0.0001$) up to a maximum at approximately 26°C and decreased sharply thereafter (Figure 9). Mean flushing distance (Figure 10) showed a similar trend with respect to temperature, except that the maximum mean flushing distance occurred at approximately 16°C . The pattern observed in the flushing distance data probably reflected the energetic costs to jack rabbits of flushing. That is, at higher temperatures, the energy

FIGURE 8. Frequency Distribution for Census Times of Jack Rabbit Transects on or near the Dugway Proving Ground from 1965-85

FIGURE 9. Comparison of Ambient Temperature and the Mean Number of Jack Rabbits Observed (N = 6,353)

FIGURE 10. Comparison of Ambient Temperature and the Flushing Distance of Jack Rabbits (N = 6,353)

required to dissipate the heat created by flushing and leaving an area of shade may be comparatively high and result in a tendency for the rabbit not to flush. At low temperatures heat may be lost as a result of flushing, thus resulting in increased energy demands on the rabbit and a hesitancy to flush. The relationship between mean flushing distance and temperature could be described with a third-order regression equation ($F = 10.26$, $P = 0.001$, $r^2 = 0.28$) (Figure 10). No matter what the cause, the fact that the number of rabbits observed and their flushing distances varied with temperature probably biased the density indices; this may be particularly true when comparing the spring and late-summer estimates.

Changes in flushing distances of jack rabbits were also noted with respect to rabbit density (Figure 11). As the density of rabbits increased, their flushing distances also tended to increase. This relationship was different between spring and late summer (Figure 11); however, during both seasons a significantly increasing linear trend was noted (spring: $F = 16.01$, $P = 0.008$,

FIGURE 11. Comparison of Jack Rabbit Density and Mean Flushing Distance During Spring and Late Summer Censuses

$r^2 = 0.44$; late summer: $F = 12.92$, $P = 0.002$, $r^2 = 0.40$). Differences in flushing distances between spring and late summer might have been partially related to differences in ambient temperatures. However, in contrast to observations made by Gross et al. (1974), the factors resulting in differences in seasonal flushing distances were apparently at least partially dependent on density because the slopes of the regression equations (Figure 11) were significantly different ($P < 0.01$). Again, these differences in flushing behavior between seasons probably biased the density indices to some degree.

In addition to biases resulting from changes in rabbit behavior, density indices were also probably biased to some degree by changes in methods of recording the flushing distances of rabbits. From 1965 to 1973, flushing distances were recorded at 5-yard intervals up to 80 yards at which point the distances were grouped into a single category (80 + yards). From 1975 to 1985,

flushing distances were recorded at 5-yard intervals up 30 yards and then at 10-yard intervals up to 90 yards. These differences may have been responsible for the substantial increase in mean sighting distance after 1975 (Figure 12). In addition, these changes in recording methods may account for some of the larger differences noted between the density indices (Hayne's and Gates' versus the mean number of rabbits/transect) during the second population cycle relative to the first (Figure 3).

REPRODUCTIVE PERFORMANCE

Information was obtained on the timing of reproductive activities, natality of adult and juvenile females, prenatal mortality, and age and sex ratios from 8,878 jack rabbits collected on or near the Dugway Proving Ground from 1965 to 1984 (Table 3).

FIGURE 12. Changes in the Mean Flushing Distance of Jack Rabbits Relative to the Year of Census

Timing

Based on the weights of adult male testes and the percentage of pregnant adult females (unweighted mean) (Figure 13), peak breeding activities occurred in March. Although jack rabbits were not collected during December, the shape of the testes weight curve and the fact that 28% (unweighted mean) of the adult females collected in January were visibly pregnant indicated that breeding activities must have begun during this period. The estimated earliest breeding date for jack rabbits from DPG area, based on back-dated fetuses, was December 24. Breeding activities ceased in July, and the latest recorded conception date based on back-dated fetuses was July 28.

Plots of weights of eye lenses from 5,719 jack rabbits revealed a clear separation between adults and juveniles, as well as some unusual breeding dates (Figure 14). One individual, collected in early November (Julian date = 310), had a lens weight of 42 mg, indicating an estimated age of less than 30 days (Figure 14 and Table 2). This individual must have been conceived in early

FIGURE 13. Seasonal Timing of Breeding Activities of Adult Jack Rabbits Collected on or Near the Dugway Proving Ground--Based on Testes Weights and Percentage of Pregnant Females

September and born in mid October. Two other individuals collected in early February (approximate Julian date = 40) had lens weights of approximately 90 mg (Figure 14). These individuals were approximately 2 months old (Table 2), indicating a conception date of late October or early November and a birth date of early December. It is unknown whether these unusual conception dates (September through November) were real or a result of recording errors.

In many years, breeding activity appeared to be synchronized, with peaks in breeding occurring at systematic intervals of approximately 40 days throughout the breeding season (Figure 15). Rabbits collected in 1971 demonstrated the clearest example of synchronized breeding (Figure 15), and data collected during most years demonstrated a number of distinct periods of breeding. However, small sample sizes and inconsistent sampling efforts (Table 5) probably masked breeding peaks in many years. Also, the large area sampled in conjunction with spatial variability in breeding times may have masked trends in some years. The lack of recognizable breeding periods in some years restricted the

FIGURE 14. Eye Lens Weights for 5,719 Jack Rabbits Collected over a 21-Year Period on or near the Dugway Proving Ground

FOR ALL YEARS COMBINED

FOR 1971 ONLY

FIGURE 15. Breeding Synchrony in Adult Female Jack Rabbits on or near the Dugway Proving Ground--Based on Back-Dated Fetuses

TABLE 5. Percentage of Adult Females in Monthly Collections of Jack Rabbits on or near the Dugway Proving Ground from 1965 to 1984

Year	Month										
	1	2	3	4	5	6	7	8	9	10	11
1965 ^(a)	100(11) ^(b)	100(73)	100(25)	100(19)	100(27)	100(10)	72(18)	50(20)	44(43)	-- ^(c)	--
1966	57(67)	51(16)	56(25)	56(48)	63(16)	63(16)	63(8)	75(4)	44(9)	42(26)	--
1967	57(44)	63(16)	41(44)	33(6)	51(39)	72(32)	45(20)	45(20)	53(15)	50(6)	--
1968	44(36)	52(25)	74(46)	53(36)	66(56)	52(21)	44(9)	30(10)	60(10)	83(6)	--
1969	48(58)	44(64)	46(54)	77(26)	51(41)	78(27)	75(24)	60(15)	39(18)	0(4)	--
1970	55(58)	42(52)	39(54)	58(45)	50(42)	48(42)	63(16)	56(9)	39(18)	42(31)	--
1971	50(80)	64(45)	45(80)	39(67)	51(93)	68(25)	50(16)	53(32)	41(22)	49(41)	--
1972	50(48)	68(109)	32(68)	55(77)	44(41)	62(45)	42(33)	64(25)	55(29)	38(24)	--
1973	78(23)	100(3)	40(15)	45(47)	53(36)	--	32(25)	67(6)	73(11)	--	42(36)
1974	65(17)	57(14)	40(5)	48(29)	49(43)	67(3)	46(13)	29(7)	33(15)	17(6)	53(17)
1975	31(13)	100(2)	--	--	43(14)	--	0(7)	50(2)	0(2)	75(4)	63(8)
1976	50(8)	--	--	--	33(9)	--	0(1)	50(2)	37(11)	--	75(4)
1977	56(9)	21(19)	22(9)	60(5)	29(21)	--	63(8)	--	--	--	--
1978	40(15)	42(12)	40(5)	32(22)	0(3)	--	--	--	75(4)	41(54)	--
1979	--	62(116)	50(28)	37(118)	49(254)	71(34)	49(176)	--	40(80)	--	--
1980	57(28)	59(100)	49(49)	32(77)	48(142)	60(87)	65(23)	--	44(43)	--	--
1981	27(22)	55(97)	--	38(136)	63(84)	44(70)	--	--	58(48)	20(5)	--
1982	--	55(64)	38(69)	46(85)	52(122)	46(63)	78(41)	--	52(27)	--	--
1983	--	45(139)	--	41(94)	49(73)	72(60)	57(54)	--	25(40)	43(7)	--
1984	--	53(15)	--	--	--	0(1)	0(3)	--	--	--	--
TOTAL(b)	537	1014	576	937	1189	536	495	152	445	214	65
Unweighted mean ^{(a)(d)}	51	52	44	47	49	61	55	51	46	42	48
Weighted mean ^(a)	52	55(e)	45(e)	44(e)	51	59(e)	53	53	45(e)	43(e)	49

(a) Data from 1965 not used in calculating means because males were not recorded for at least the first 6 months (based on annual reports).

(b) The number in parentheses is the number of rabbits collected per month.

(c) Dash (--) indicates no data was collected.

(d) For months in which ≥ 10 rabbits collected.

(e) Significantly different from a 50:50 ratio at the 5% level.

analysis of female reproductive data to monthly periods rather than the more meaningful biological time frame, breeding (conception) periods, used by Gross et al. (1974).

The length of the breeding season varied considerably between years, ranging from 108 days in 1978 to 210 days in 1969 (Figure 16). The small sample sizes of visibly pregnant adult females obtained during some years, for example 1975-78, probably contributed to the observed variability. The average length of the breeding season for the 17 years in which more than 10 visibly pregnant adult females were collected was 156 ± 7 (1 SE) days. The median length of the breeding season was 155 days. Despite the variability in the data, some trends in the length of the breeding season relative to population levels were apparent (Figure 16). The two longest breeding seasons both occurred during the increasing cyclic phase (1969 and 1977), approximately 3 years before the rabbits reached peak population densities. Some of the shortest breeding seasons,

FIGURE 16. Comparison of Length of Breeding Season for Females and a Spring Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Located on or near the Dugway Proving Ground from 1965-83

1972 and 1973, occurred during the decreasing phase in rabbit numbers. The extremely short breeding season in 1978, which occurred during an increasing phase in rabbit numbers, may have resulted from the relatively small sample size ($N = 20$).

Natality

Mean ovulation rates, based on counts of corpora lutea for adult females, increased from a low of 1.6 ± 0.1 (1 SE) in January to a high of 5.2 ± 0.1 (1 SE) in April (Figure 17). These rates are similar to those presented by Gross et al. (1974) and Lechleitner (1959).

Mean litter size for adult females varied with the month collected and age of the fetus. Regression of the litter size (dependent variable) on the age of the fetus and month the fetus was collected (independent variables) revealed that approximately 30% of the variability in litter size could be explained by these variables ($F = 349.7$, $P = 0.0001$, $r^2 = 0.30$, $df = 1667$). Because month collected has little biological meaning relative to a rabbit with a 40- to 43-day gestation period, the proportion of the variability explained above

FIGURE 17. Ovulation Rates for Adult Female Jack Rabbits Collected on or near the Dugway Proving Ground

would probably have increased had a more realistic time factor been used in place of month collected, for example, the conception period used by Gross et al. (1974). The intercept for this regression equation (litter size = $1.59 - 0.02$ (fetus age) + 0.72 (month collected)), that is when month = January and fetus age = 0, was 1.59, which is identical to the number of ova produced by adult females in January. This similarity indicates that the regression equation may have some biological reality.

The mean litter size for adult females (fetuses of all ages included) was low early in the breeding season (1.4 ± 0.1), reached a peak in April (5.2 ± 0.1), and decreased during the rest of the season (Figure 18). This seasonal trend in litter size was similar to that observed elsewhere (Lechleitner 1959; French et al. 1965; Gross et al. 1974). The unweighted mean litter size for adult females near term during the peak breeding months (April-June) of all years was 4.41. Annual trends in litter size relative to population density were also noted (Figure 19). Mean litter sizes for adult females reached their maximum values 2 to 3 years prior to peak population densities and then decreased to comparatively low values during peak populations

FIGURE 18. Monthly Mean Litter Sizes for Adult Female Jack Rabbits Collected on or near the Dugway Proving Ground

(Figure 19). Some of the variability in mean litter size in Figure 19 may have resulted from the relatively small sample sizes. The small sample sizes were a result of restricting this analysis to those litters from adult females near term that were collected during peak breeding months (April-June) because litter size varied with month the animal was collected and stage of fetal development.

Breeding By Juvenile Females

During this study, 1,317 juvenile females were examined for reproductive status; of these, 50 (3.8%) had corpora lutea present and 22 (1.7%) had visible embryos present. The annual percentage of juvenile females showing evidence of pregnancy (corpora lutea) ranged from 0 to 17.3 (unweighted mean = 4.8%) (Figure 20). No evidence of juvenile pregnancy was detected in 6 of the 18 years when more than 10 juvenile females were examined. No clear evidence of a relationship between juvenile pregnancy rates and population density could be detected (Figure 20). Pregnant juveniles were present in rabbit collections

FIGURE 19. Annual Mean Litter Size of Adult Female Jack Rabbits Collected Near Term and During Peak Breeding Months (April-June) on or near the Dugway Proving Ground from 1965-83--Relative to a Spring Population Density Index (Mean Number of Rabbits/Transect)

FIGURE 20. Comparison of the Percentage of Juvenile Females Showing Evidence of Pregnancy (Corpora Lutea) and a Spring Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Located on or near the Dugway Proving Ground from 1965-83

during population highs, lows, and during both the increasing and decreasing cyclic phases. There was a slight indication that fewer juvenile pregnancies occurred during periods of population highs (Figure 20).

Prenatal Mortality

Based on the difference between the number of fetuses and corpora lutea present in collected rabbits, the percentage of adult, near-term (fetuses >30 days old) females losing at least one fetus was highly variable, ranging from 4.5 to 47.6% per year (Figure 21). The average prenatal loss for all years (unweighted) was 22.4% and the median was 22.6%. The average percentage of an individual litter lost prior to parturition ranged from 0.6 to 24.6% per year ($\bar{x}$ = 9.3) (Figure 21). The annual fluctuations in the percentage of an individual litter lost and the percentage of adult females losing at least one fetus per litter prior to birth were nearly identical (Figure 21).

FIGURE 21. Comparison of the Annual Percentage of Adult Female Jack Rabbits Near Term Losing at Least One Fetus and the Mean Annual Percentage of an Individual Litter Lost Prior to Birth

Prenatal loss, as measured by the percentage of adult females losing at least one fetus, appeared to peak during the periods of population decline (1965, 1973, and 1983) and drop during population highs (1970-1972 and 1980-1983) (Figure 22). In general, the monthly mean percentage (all years combined) of adult females losing at least one fetus per litter tended to increase during the course of the breeding season (Figure 23).

The percentage of visibly pregnant adult females resorbing young ranged from 0 to 20.6% and averaged 7.1% (unweighted mean for years in which >10 visibly pregnant adult females were examined). Resorption rates tended to increase during population declines, at least in 1965 and 1983 (Figure 24). The low resorption rates observed during the 1973 to 1975 population decline (Figure 24) may be a reflection of the small sample sizes. Another possible non-biological explanation for the absence of recorded resorption from 1973 to 1976

FIGURE 22. Comparison of the Percentage of Adult Females Losing at Least One Fetus and a Spring Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Located on or near the Dugway Proving Ground

FIGURE 23. Monthly Mean Percentage (All Years Combined) of Adult Female Jack Rabbits Losing at Least One Fetus

FIGURE 24. Comparison of Resorption Rates of Fetuses by Adult Females and a Spring Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Located on or near the Dugway Proving Ground from 1965-83

may be that data on resorption were not recorded during this time because of major changes in project personnel. The raw data forms, however, were not available to confirm this.

Resorption of entire litters was apparently not a frequent event, at least after the first week of pregnancy (embryos are not visible until 1 week after implantation) (Gross et al. 1974), since only three adult females out of 1,682 examined showed evidence of resorption of their entire litter. All three of these litters were from 1982 and ranged in size from 1 to 5 individuals.

Age and Sex Ratios

Juvenile jack rabbits first appeared in the monthly collections in April (Table 6 and Figure 14). Subsequently, the proportion of juveniles in the collections rose rapidly, reached a peak in September, and declined in October and November. The drop in the percentage of juveniles in monthly collections in October and November may have been related to increased mortality in

TABLE 6. Percentage of Juveniles in Jack Rabbits Collected on or near the Dugway Proving Ground (Data Presented by Year and Month.)

Year	Month										
	1	2	3	4	5	6	7	8	9	10	11
1965	0(11) ^(a)	0(73)	0(25)	0(19)	0(28)	0(10)	51(37)	20(25)	57(101)	-- ^(b)	--
1966	0(67)	0(49)	0(25)	4(50)	33(73)	70(53)	79(38)	60(10)	47(17)	37(41)	--
1967	0(44)	0(16)	0(44)	25(8)	19(48)	43(56)	44(36)	56(45)	61(38)	54(13)	--
1968	0(36)	0(25)	0(46)	3(37)	19(69)	70(69)	78(41)	79(47)	82(55)	81(32)	--
1969	0(58)	0(64)	0(54)	0(26)	29(58)	39(44)	61(62)	72(52)	79(84)	73(15)	--
1970	0(58)	0(52)	0(54)	2(46)	36(66)	43(74)	60(40)	83(53)	66(53)	47(59)	--
1971	0(80)	0(45)	0(80)	1(68)	6(99)	54(54)	73(59)	52(67)	70(74)	31(59)	--
1972	0(48)	0(109)	0(68)	1(78)	40(68)	55(99)	38(52)	40(42)	36(45)	25(32)	--
1973	0(23)	0(3)	0(15)	8(51)	5(38)	--	39(41)	33(9)	58(26)	--	22(46)
1974	0(17)	0(14)	0(5)	0(29)	22(55)	40(5)	48(25)	36(11)	12(17)	25(8)	29(24)
1975	0(13)	0(2)	--	22(18)	46(13)	--	46(13)	75(8)	60(5)	33(6)	67(24)
1976	0(8)	--	--	--	0(9)	--	0(1)	60(5)	67(33)	100(1)	73(15)
1977	0(9)	0(19)	0(9)	0(5)	5(22)	--	60(20)	--	100(2)	--	--
1978	0(15)	0(12)	0(5)	21(28)	75(12)	100(13)	--	--	91(47)	67(165)	--
1979	--	0(116)	0(28)	2(120)	26(342)	63(92)	53(378)	--	67(242)	--	--
1980	0(28)	0(100)	0(49)	0(77)	1(144)	4(91)	32(34)	--	64(120)	--	--
1981	0(22)	0(97)	--	0(136)	0(85)	7(75)	--	--	48(92)	64(14)	--
1982	--	0(64)	0(69)	1(86)	6(130)	57(146)	69(134)	--	79(129)	--	--
1983	--	0(139)	--	2(96)	11(82)	26(81)	43(95)	--	39(66)	63(19)	--
1984	--	0(15)	--	--	--	50(2)	25(4)	--	--	--	--
Weighted mean	0	0	0	2.4	17.6	44.4	55.5	59.4	64.3	53.9	40.4
Unweighted mean ^(c)	0	0	0	3.0	19.7	45.1	54.6	55.2	60.2	54.2	47.8

(a) Total number of rabbits examined.

(b) Dash (--) indicates that no data was collected.

(c) For months in which >10 rabbits collected.

juveniles or changes in the relative vulnerability of juveniles to collection (Gross et al. 1974). Based on eye lens weights of collected rabbits (Figure 14 and Table 2), most juvenile jack rabbits did not appear susceptible to the collection methods until they were approximately 2 to 3 months old.

The percentage of juvenile rabbits in annual collections after August ranged from 25.0 in 1974 to 80.6 in 1968 and averaged (unweighted) 57.0. The cyclic fluctuations in the ratio of juveniles to adults in the population was remarkably similar to cyclic fluctuations in density, although the two curves were out of phase (Figure 25). In general, there appeared to be a 2-year time lag between when changes in the fall age ratio were reflected by changes in population density. However, based on past fluctuations, the age ratio data of rabbits collected in fall 1982 (Figure 25) was unexpected. The anomaly of the 1982 age ratio is demonstrated in a plot of the late summer population index and fall age ratio (advanced 2 years) (Figure 26). In 1982, the population density appeared to respond immediately to the change in age ratios

FIGURE 25. Comparison of the Late Summer Age Ratios (Juveniles/Adult) and a Late Summer Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Collected on or near the Dugway Proving Ground from 1965-83

FIGURE 26. Relationship Between the Late Summer Population Index (Mean Number of Rabbits/Transect) and the Late Summer Age Ratio (Juveniles/Adults) of 2 Years Earlier--1982 Not Included in the Regression

(Figure 25), why this occurred is unknown. If the 1982 data was eliminated, a significant linear relationship ($F = 29.5$, $r^2 = 0.66$, $P = 0.0001$) existed between the fall age ratio and the population index 2 years later (Figure 26).

Late summer jack rabbit populations did not appear to increase significantly over spring populations when the percentage of juveniles was less than or equal to 50% of the fall collections (Figure 27). However, substantial increases in population densities were noted when the percent of juveniles in fall collections was greater than 50%.

Adult ($N = 5,915$) and juvenile ($N = 2,553$) sex ratios for collected animals were not significantly different than 50:50 ($\chi^2 = 0.09$ and 0.00 , respectively; $P < 0.001$) for all months and years combined (1965 data was excluded in analyses because of large discrepancies between the sex ratio data reported in the annual report and that recorded on the computer tape). However, some significant differences were noted in the monthly sex ratios for adult jack rabbits (Table 5). A disproportionately high number of females were collected in February and June, and fewer females than expected were collected in March,

FIGURE 27. Relationship Between the Ratio of Late Summer to Spring Population Densities and the Percentage of Juveniles in Late Summer Collections of Jack Rabbits on or near the Dugway Proving Ground

April, September, and October (Table 5). The biological explanation for this monthly variation in adult sex ratios could not be determined, and such changes may have been due to chance. In fact, the lower than expected ratio of females in March and April was opposite that noted by Gross et al. (1974).

Some substantial changes in sex ratios, particularly for adults, were noted on a yearly basis (Figure 28). Sex ratios of collected juvenile jack rabbits fluctuated from year to year, but generally remained around 1.0 (Figure 28). No discernible pattern was detected in the fluctuations of juvenile sex ratios relative to adult sex ratios or population levels. Adult sex ratios, however, showed substantial changes from year to year in what appeared to be a nonrandom pattern (Figure 28). Fluctuations in sex ratios of collected adults coincided with population densities (Figure 28). In general, when

FIGURE 28. Comparison of the Sex Ratios of Juveniles and Adults (Females/Males) and a Spring Population Density Index (Mean Number of Rabbits/Transect)

population densities were high, the relative number of adult females to adult males was high. An apparent exception to this pattern occurred in 1968. The coincidence between the two curves in Figure 28 may be a reflection of real changes in the sex ratios of the population or may be, at least partially, caused by changes in the vulnerability of adult females with changes in population density. Based on changes in monthly sex ratios of collected jack rabbits, Gross et al. (1974) speculated that adult females may have been more vulnerable to hunting when they had young. If the presence of young was responsible for increased vulnerability of adult females to hunting, then adult female vulnerability should have been highest during the increasing phase of the population cycle when the breeding season was the longest (Figure 16) and the proportion of juveniles in the population was highest (Figure 25). This may explain the high proportion of adult females observed in 1968, although similar high proportions of adult females were not observed during the second population cycle (Figure 28). It is possible that stress associated with

producing young combined with social stresses at high population densities may have contributed to the vulnerability of adult females during these time periods.

One other trend noted in adult sex ratios was a downward, almost linear, drop in the ratio of females to males from 1966 to 1977 (Figure 28). This decreasing trend would be further emphasized if the recorded sex ratio for 1965 (5.3:1) was added to Figure 28. However, information presented in annual reports (University of Utah 1965) indicate that the 1965 estimate, which was obtained from the computer tape, may have been incorrect. No explanation for this decreasing trend in the proportion of females could be found.

DISEASE DYNAMICS

The preceding sections of this report summarize the population dynamics of jack rabbits on or near DPG, including: the numerical fluctuations in density, reproductive performance, prenatal mortality, age ratios, and sex ratios. This section summarizes the available information on the dynamics of several endemic diseases in jack rabbits and other vertebrate species on DPG.

Disease Incidence Rates in Lagomorphs

Incidence of tularemia (Francisella tularensis), Rocky Mountain spotted fever (RMSF) (Rickettsia rickettsii), and Q fever (Coxiella burnetii) in lagomorphs (includes a minor number of desert cottontails, Sylvilagus audubonii) collected on or near DPG were compared with late summer population levels of jack rabbits (Figures 29, 30, and 31, respectively). Incidence rates of tularemia in lagomorphs, as determined by sera antibodies, were low throughout the period examined (Figure 29) despite relatively large sample sizes (Table 7). No clear relationship was evident between the incidence of tularemia and population levels of jack rabbits; peaks in the incidence of tularemia were noted during all phases of the jack rabbit population cycle. This may have been a result of the extremely lethal nature of this disease in jack rabbits and cottontails (Reilly 1970; Stark 1979) and the relatively low probability of collecting a rabbit with this disease. The comparatively high rates of tularemia after 1970 may be at least partially the result of changes in diagnostic techniques (Stark 1979).

FIGURE 29. Comparison of the Incidence of Tularemia in Lagomorphs and a Late Summer Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Collected on or near the Dugway Proving Ground from 1959-73

FIGURE 30. Comparison of the Incidence of Rocky Mountain Spotted Fever in Lagomorphs and a Late Summer Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Collected on or near the Dugway Proving Ground from 1964-73

FIGURE 31. Comparison Between the Incidence of Q Fever in Lagomorphs and a Late Summer Population Density Index (Mean Number of Rabbits/Transect) for Jack Rabbits Collected on or near the Dugway Proving Ground from 1964-73

The incidence of RMSF was high, exceeding 20% of the lagomorphs examined each year (Figure 30). The organism responsible for the high serological reactor rate to the RMSF antigen was never isolated (EcoDynamics 1973). As a result, it was suspected that this organism was not the classical virulent strain of RMSF, but a closely related one (EcoDynamics 1973). The incidence of RMSF appeared to increase during periods of rapid change in lagomorph populations, that is, during the increasing or decreasing phases of the population cycle (Figure 30). The reasons for this apparent relationship, if any, are unknown.

The incidence of Q fever was elevated during the declining phases of jack rabbit population cycles and practically nonexistent during other portions of the population cycle (Figure 31). The elevated levels of Q fever during the decline in jack rabbit numbers may have been related to high levels of stress in the animals at this time (Bell 1970).

TABLE 7. Number of Animals Examined on or near the Dugway Proving Ground for Antibodies to Tularemia, Rocky Mountain Spotted Fever (RMSF), and Q Fever

Year	Wildlife Species Examined		
	No. Lagomorphs	No. Carnivores	No. Small Rodents
1959	438		
1960	419		
1961	556		
1962	511		
1963	547		
1964	433	19	2545
1965	415	30	2654
1966	402	70	2581
1967	338	53	2612
1968	399	34	2900
1969	637	42	3283
1970	692	66	3123
1971	763	52	2977
1972	453	133	2430
1973	266	27	948
1974	241	13	1533
1975	140	15	1017
1976	63	9	456
1977	109	52	306
1978	195	37	165
1979	404	18	
1980	624	32	
1981	524	21	
1982	758	33	
1983	110	37	
1984	24	28	
Mean $\pm$ 1SD	402 $\pm$ 211	39 $\pm$ 27	1969 $\pm$ 1108

Interspecific Comparisons in Disease Incidence

Several interesting relationships were noted in the fluctuations of pathogens in lagomorphs relative to disease fluctuations in other species of wildlife on DPG. Fluctuations of tularemia in lagomorphs and carnivores (primarily coyotes, Canis latrans and kit foxes, Vulpes macrotis) showed similar cyclic characteristics, although the cycles of tularemia in carnivores appeared to have occurred slightly later than those in lagomorphs (Figure 32) and may have reflected the actual population cycles in the carnivores themselves. Incidence of tularemia in small rodents appeared to follow a pattern similar to that in lagomorphs (Figure 32). The cyclic characteristics of RMSF and Q fever were almost identical in rodents and lagomorphs (Figures 33 and 34).

UNUSUAL OR UNEXPLAINABLE FLUCTUATIONS

One of the objectives of this report was to analyze DPG jack rabbit data for unusual or unexplained fluctuations in population densities or in incidence

FIGURE 32. Interspecific Comparisons in the Incidence of Tularemia in Wildlife Collected on or near the Dugway Proving Ground

FIGURE 33. Interspecific Comparisons in the Incidence of Rocky Mountain Spotted Fever in Wildlife Collected on or near the Dugway Proving Ground

FIGURE 34. Interspecific Comparisons in the Incidence of Q Fever in Wildlife Collected on or near the Dugway Proving Ground

of disease. No attempt was made to correlate any unexplainable fluctuations found in our analyses to historic chemical and biological warfare activities on DPG because this information was not available to the authors.

Jack Rabbit Populations

Both the timing and amplitude of the cyclic fluctuations in DPG jack rabbit populations appeared to be normal when compared to other jack rabbit populations (Figure 5). Only one unusual population change was observed in DPG jack rabbits that was not seen in other populations. This was the temporary suppression of jack rabbit numbers in late summer 1981 when jack rabbits on DPG were in their normal increasing cyclic phase (see section on Comparison to Other Populations and Figures 5 and 6). Whether this fluctuation was the result of natural or unnatural causes is unknown. It should be noted, however, that natural variability in jack rabbit numbers was very high and this fact combined with sampling variability could easily mask any but the most dramatic impacts on rabbit numbers.

The age ratio (juvenile/adults) of collected DPG jack rabbits also fluctuated in an atypical manner in 1981-1982 (see section on Sex and Age Ratios and Figures 25 and 26). Changes in population density before 1981 were preceded by changes in the age ratio of collected rabbits; but, in 1982, the changes in age ratio and population density coincided with one another.

The sex ratio of collected adult jack rabbits (females/males) appeared to decrease in a nonrandom, linear fashion from 1965 through 1977 (Figure 28). This decrease occurred in the absence of any substantial changes in the sex ratio of collected juveniles, and also occurred during all stages of a population cycle. The sex ratio did appear to fluctuate with changes in density, at least to a minor degree, during this time period. Similar fluctuations in sex ratios with density were noted by Gross et al. (1974) for jack rabbits in northern Utah. However, despite the apparent relationship between density and adult sex ratios, an overall, decreasing linear trend did appear to persist. Why such a trend should occur is unknown. No apparent changes were made in collection techniques during this time period that might gradually favor the collection of males over females.

Disease Incidence

In general, similar rates of disease (tularemia, RMSF, plague, and Q-fever) were noted between animals collected from the central portion of DPG (the area most likely influenced by past chemical and biological releases on DPG) and animals collected in the region surrounding DPG (Tables 8, 9, and 10; Figures 35, 36, and 37). In only two cases was a statistically significant difference ($\alpha = 0.05$ level) noted in overall disease levels between the two areas (Tables 8, 9, and 10). Carnivores in the area surrounding DPG had a significantly ($\chi^2 = 11.37$, $P < 0.001$) higher incidence of tularemia than did carnivores collected on DPG, and rodents collected on DPG demonstrated a significantly higher level ($\chi^2 = 10.7$, $P < 0.001$) of Q-fever than did rodents collected from areas surrounding DPG. However, in both of these cases, the trends over time in disease incidence were similar for DPG and non-DPG animals (Figures 35 and 36), perhaps indicating that these differences were a result of

TABLE 8. Serological Incidence of Diseases in Small Rodents Collected from the Central Portion of the Dugway Proving Ground and from Areas Surrounding the Dugway Proving Ground

	Tularemia		RMSF		Q-Fever		Plague	
	DPG(a)	SURR(b)	DPG(a)	SURR(b)	DPG(a)	SURR(b)	DPG(a)	SURR(b)
No. showing serological evidence	3	19	89	189	33	45	1	11
No. showing no evidence	9,419	26,771	6,653	18,174	7,043	20,606	7,431	20,390
Percent incidence	0.03	0.07	1.32	1.03	0.46	0.22	0.01	0.05
Probability level(c)	0.280		0.060		0.001		0.266	
Period of years covered	1959-73		1964-73		1964-73		1963-72	

(a) Central portion of the Dugway Proving Ground.

(b) Area surrounding the Dugway Proving Ground.

(c) Based on a 2x2 contingency table adjusted for continuity.

TABLE 9. Serological Incidence of Diseases in Lagomorphs Collected from the Central Portion of the Dugway Proving Ground and from Areas Surrounding the Dugway Proving Ground

	Tularemia		RMSF		Q-Fever		Plague	
	DPG(a)	SURR(b)	DPG(a)	SURR(b)	DPG(a)	SURR(b)	DPG(a)	SURR(b)
No. showing serological evidence	0	22	345	1047	6	42	1	1
No. showing no evidence	1546	5701	730	2412	1141	3609	1182	3895
Percent incidence	0.00	0.38	32.09	30.27	0.52	1.15	0.08	0.03
Probability level ^(c)	----		0.274		0.091		0.954	
Period of years covered	1959-73		1964-72		1964-73		1963-72	

(a) Central portion of the Dugway Proving Ground.

(b) Area surrounding the Dugway Proving Ground.

(c) Based on a 2x2 contingency table adjusted for continuity.

natural causes. Small rodents from the central portion of the DPG demonstrated an unusually high incidence of RMSF in 1970 (Figure 37). This peak did, however, coincide with the apparent normal fluctuation of this disease in small rodents and lagomorphs both on DPG and in surrounding areas (Figure 37).

TABLE 10. Serological Incidence of Diseases in Carnivores Collected from the Central Portion of the Dugway Proving Ground and from Areas Surrounding the Dugway Proving Ground

	Tularemia		Plague	
	DPG(a)	SURR(b)	DPG(a)	SURR(b)
No. showing serological evidence	41	79	6	9
No. showing no evidence	216	198	110	112
Percent incidence	16.95	28.52	5.17	7.44
Probability level(c)	0.001		0.653	
Period of years covered	1963-73		1965-72	

(a) Central portion of the Dugway Proving Ground.

(b) Area surrounding the Dugway Proving Ground.

(c) Based on a 2x2 contingency table adjusted for continuity.

SMALL RODENTS

LAGOMORPHS

FIGURE 35. Incidence of Q Fever in Wildlife Collected on the Central Portion of the Dugway Proving Ground (Test Area) and in Areas Surrounding the Dugway Proving Ground (Control Area)

FIGURE 36. Incidence of Tularemia in Wildlife Collected on the Central Portion of the Dugway Proving Ground (Test Area) and in Areas Surrounding the Dugway Proving Ground (Control Area)

LAGOMORPHS

SMALL RODENTS

FIGURE 37. Incidence of Rocky Mountain Spotted Fever in Wildlife Collected on the Central Portion of the Dugway Proving Ground (Test Area) and in Areas Surrounding the Dugway Proving Ground (Control Area)

Figure 1. Number of Rocky Mountain Spotted Fever in Wildlife collected in the Control Portion of the Jacob River (Control Area) and the Test Portion of the Jacob River (Test Area).

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APPENDIX A

NUMBER AND LOCATION OF JACK RABBITS COLLECTED ON OR NEAR THE DUGWAY
PROVING GROUND

TABLE A.1. Number of Jack Rabbits Collected on or near the Dugway Proving Ground

Area Collected	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	Total
Camelback Mt	21	52	37	60	50	35	163	233	25	21	23	2	15	17	140	1	--(a)	--	--	--	895
Government Creek	9	16	10	24	30	21	28	63	33	39	7	1	--	1	--	--	--	--	--	--	282
South Cedar Mt	9	35	45	15	41	39	44	35	28	25	18	11	7	17	514	347	311	438	427	15	2421
Little Davis Mt	7	16	9	15	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	47
Wig Mt	8	13	16	30	22	55	30	23	--	--	--	--	5	8	--	--	--	--	--	--	210
Big Davis Mt	9	9	16	31	38	31	30	11	--	--	--	--	--	--	--	--	--	--	--	--	175
Condie	5	11	9	11	44	19	21	21	19	11	14	6	15	17	--	--	--	--	--	--	223
Erickson Pass	9	9	14	16	20	16	27	16	--	--	--	--	--	--	--	--	--	--	--	--	127
Lakeside	85	20	20	12	8	23	8	8	--	--	--	--	--	--	--	--	--	--	--	--	184
Iosepa	4	14	16	16	12	17	20	6	12	15	10	9	5	5	--	--	--	--	--	--	161
Rush Valley	12	18	19	16	8	23	40	4	--	--	--	--	--	47	--	296	210	320	151	9	1173
Benmore	12	26	8	6	10	10	8	16	--	--	--	--	--	--	666	--	--	--	--	--	762
West Wendover	4	22	16	8	13	17	18	8	--	--	--	--	--	102	--	--	--	--	--	--	208
North Wendover	11	16	8	2	10	17	16	8	--	--	--	--	--	--	--	--	--	--	--	--	88
South Wendover	4	22	4	5	10	11	14	8	12	11	7	6	1	--	--	--	--	--	--	--	115
East Wendover	11	14	4	7	6	16	11	3	--	--	--	--	--	--	--	--	--	--	--	--	72
Gold Hill	8	9	4	16	31	20	24	16	14	26	9	15	5	--	--	--	--	--	--	--	197
Deep Creek	10	8	8	12	16	16	16	8	--	--	--	--	--	--	--	--	--	--	--	--	94
Callo	8	9	15	16	26	25	24	22	17	10	10	--	7	--	--	--	--	--	--	--	189
Fish Spring	12	8	8	15	14	24	21	16	22	10	10	1	7	37	--	--	--	--	--	--	205
Trout Creek	22	29	25	33	25	23	24	16	--	--	--	--	--	--	--	--	--	--	--	--	197
Dugway Mt	9	13	8	38	8	24	24	16	21	13	5	5	2	--	--	--	--	--	--	--	186
Granite Mt	8	4	5	156	14	21	25	27	29	14	2	--	1	--	--	--	--	--	--	--	165
Test Grid	13	2	6	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	22
Dugway Valley	10	14	12	29	61	53	50	66	25	22	8	16	16	58	--	--	--	--	--	--	440
Old River	9	12	8	9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	38
Total	329	421	350	458	517	556	686	650	257	217	123	72	86	309	1320	644	521	758	578	24	8876

(a) Dash (--) indicates no jack rabbits were collected.

FIGURE A.1. Sampling Locations for Jack Rabbits Collected on or near the Dugway Proving Ground

APPENDIX B

POPULATION ESTIMATES FOR JACK RABBITS COUNTED ON TRANSECTS
LOCATED ON OR NEAR THE DUGWAY PROVING GROUND

TABLE B.1. Population Estimates for Jack Rabbits Counted on Transects Located on or near the Dugway Proving Ground

Year	Month	Population Estimate		
		Mean Number Rabbits/Transect	Hayne (Rabbits/km ²)	Gates (Rabbits/km ²)
1965	3	1.53	--(a)	51.5
1965	8	1.63	58.6	54.4
1966	3	0.97	38.6	32.1
1966	8	1.33	50.1	40.8
1967	3	0.29	17.3	10.8
1967	8	1.08	65.4	49.6
1968	3	0.67	20.1	21.7
1968	8	1.72	89.5	65.1
1969	3	1.57	51.0	37.9
1969	8	4.17	114.7	104.9
1970	3	2.92	87.5	71.8
1970	8	6.70	174.5	176.4
1971	3	3.62	90.5	86.6
1971	8	7.99	190.5	184.4
1972	3	5.41	112.7	115.1
1972	8	7.45	145.5	155.6
1973	3	3.10	67.4	77.6
1973	8	2.59	--	--
1974	3	0.73	--	--
1974	8	0.69	--	--
1975	3	0.24	8.0	9.7
1975	8	0.51	12.6	16.2
1976	3	0.26	11.8	10.2
1976	8	0.94	32.3	25.1
1977	3	0.46	10.4	11.6
1977	8	1.62	33.2	35.4
1978	3	0.99	19.1	20.6
1978	8	3.57	105.0	91.5
1979	3	3.15	49.9	53.8
1979	8	5.12	95.7	100.7
1980	3	4.41	81.2	88.3
1980	8	5.19	107.1	121.4
1981	3	3.61	47.5	46.5
1981	8	4.87	89.0	84.2
1982	3	4.21	51.7	53.2
1982	8	5.15	92.9	85.5
1983	3	2.93	44.3	41.6
1983	8	2.49	60.1	57.1
1984	3	0.62	15.4	14.5
1984	8	0.38	17.2	17.9
1985	3	0.25	9.0	10.6
1985	8	0.27	5.5	8.5

(a) Dash (--) indicates missing data.

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