8217452

Petryszyn, Yaroslaw

POPULATION DYNAMICS OF NOCTURNAL DESERT RODENTS: A NINE YEAR STUDY

The University of Arizona PH.D. 1982

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106

POPULATION DYNAMICS OF NOCTURNAL DESERT RODENTS: A NINE YEAR STUDY

by

Yar Petryszyn

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN ECOLOGY AND EVOLUTIONARY BIOLOGY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1 9 8 2

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Yar Petryszyn

entitled Population Dynamics of Nocturnal Desert Rodents: A Nine Year Study

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

E Lendell Cockrum	27 October 1981
	Date
Charles T Mason Jr.	4 November 1981
	Date
Alfred H. Ward	1 December 1981
	Date
Robert W. Hoshaw	8 December 1981
	Date
Wm. J. McCauley	15 dec 1981
	Date

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

E Lendell Cockrum	27 October 1981
Dissertation Director	Date

STATEMENT BY AUTHOR

SIGNED: Yar Petryszyn

ACKNOWLEDGMENTS

A major undertaking usually involves the help of numerous people and this dissertation is no exception. It is similar to building a house- the expertise, materials, and labor incorporated determines the quality and endurance of the structure. Hopefully this work will reflect this principle in a positive way.

Foremost thanks to Dr. E. Lendell Cockrum who saw a spark of possibility so many years ago. He had the courtesy and patience to allow that spark to extinguish of its own accord or flare into a resemblance of productivity. Thanks for being allowed to develop and mature at my own rate- the input and help was always there for the asking.

A big thank you to my committee members- Drs. William J. McCauley, Charles T. Mason, Jr., Oscar G. Ward, Robert W. Hoshaw, and Willard Van Asdall for occasionally making me toe the line and giving feedback and advice throughout this endeavor.

This study would never have gotten off the ground if it were not for the tremendous amount of effort on the part of Tom and Pam Vaughan, Ron Olding, Carl Hoagstrom, John Wondolleck, Ed Roth, and Mark Courtney.

The biggest thanks is reserved for the many students of mammalogy class and personal friends who volunteered their time to help in field work. The many miles walked in baiting and checking traps were made much easier by their camaraderie.

TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS--Continued

LIST OF TABLES

ABSTRACT

Demography of nocturnal desert rodents was monitored for nine years. Three dissimilar areas were sampled with three distinct trapping configurations and time regimes. All three areas contained similar rodent species.

Increased plant growth and seed production resulting from variations in rainfall seemed to have the most profound effect on both rodent densities and species composition.

Deviations from the bimodal rainfall pattern occurred in the latter parts of 1972, 1977, and 1978 and early 1973, 1978, and 1979. During these times there was a 2-4 fold increase in rainfall. This pattern produced "desert blooms" in the spring of 1973, 1978, and to some extent 1979. In addition, 1972 and 1978 were years of high rainfall.

The reaction of the rodents to the increased plant production was rapid and dramatic. Heteromyid numbers increased approximately six fold with some species increasing twelve fold within a matter of five months.

The smaller heteromyids, *Perognathus amplus* and *P. penicillatus*, were the first to increase substantially, while the larger rodents reached peak populations in the following year. The resulting population crash that followed the high densities was as dramatic as the increase.

Neotoma albigula populations did not increase substantially after the first rainfall phenomenon but did so dramatically after the second period of aberrant rains. The densities of *N. albigula* remained high long after the heteromyid populations decreased to "normal" levels.

The three areas were found to be dominated by different species while the overall rodent densities in the three areas were very similar within the same time frame.

CHAPTER 1

INTRODUCTION

Few long term studies of population dynamics of desert rodents have been carried out. In North America, Beatley (1969) has done some rodent population studies in the Mohave Desert; Bradley and Mauer, 1973; French, et. al., 1974; Maza, French, and Aschwanden, 1973, in the Nevada Desert; and O'Farrell 1974, in the Chihuahua Desert.

At the eastern edge of the Sonoran Desert, in the ecotone between the desert proper and the adjacent desert grassland, Reynolds (1958, 1960) and Turkowski and Vahle (1977) conducted population studies of desert rodents for a number of years. Unfortunately, their samples were taken only during the month of December.

This study has also been conducted at the eastern edge of the Sonoran Desert, not only in the degraded desert grassland of the Santa Rita Experimental Range (SRER), but on two lower sites of the desert proper. As will be detailed later, the schedule of sampling has been designed to maximize information concerning annual variations in nocturnal rodent populations.

In this portion of the Sonoran Desert of Southern Arizona, nocturnal rodent populations consist of a mixture of graminivorous heteromyid rodents and some dietetically heterogenous cricetid rodents.

Environmental conditions, in this area have resulted in an unusually large assemblage of related rodent species, primarily heteromyids, in a relatively small area.

The problems of coexistence of these related and ecologically similar heteromyids have been investigated by numerous workers (e.g., Rosenzweig and Winakur, 1969; Rosenzweig and Sterner, 1970; Rosenzweig, 1973; Brown and Lieberman, 1973; Christopher, 1973; Smigel and Rosenzweig, 1974; Congdon, 1974; and Shroder and Rosenzweig, 1975). Unfortunately, most investigated population interactions were for only short time periods.

The long term ecological and evolutionary significance of the findings of such studies might well be debatable if, as has been documented in other ecosystems, the various species present undergo varying patterns of multiannual population fluctuations (such as the lemming cycles in the Arctic).

If such multiannual fluctuations do occur in desert rodents, then intraspecific interactions observed in a given year may well reflect only a part of a complex relationship. Short term studies would only provide fugative values for such basic questions as: What is the carrying capacity of the system under extremes of climatic conditions? What strategies-reproductive, spatial, and foraging for example- are utilized by different coexisting species under these extremes? What limiting factors are involved during these periods? How and when is dispersal initiated?

The potentiality and capability of a species to deal with its environment are only arrived at by observing its behavior in the extremes of its environment. Short termed studies involving co-existence, habitat selection, resource allocation, and habitat partitioning are more susceptible to misinterpretation when they are conducted under narrow temporal and spatial regimes.

A random sampling would more often occur during a "normal" period, since extreme drought and extreme rainfall occur infrequently. Thus the survival and reproductive strategies at this time are the status quo. During exceptional rain years, with the desert in bloom from ephemerals, food supply increases dramatically followed by a population explosion in some, if not most, rodent species. During these periods, food supply becomes of lesser concern, whereas factors such as spatial crowding may increase in importance. In this study, nocturnal rodent populations increased, in some instances, from a total of 13 individuals per hectare to 120 individuals per hectare. The ramification of a nine fold increase in numbers has to be considered in any discussion on population dynamics.

Even though one may be fortunate to encompass an extreme fluctuation in an environmental parameter (in this case rainfall), restraint must be used in making broad generalizations when interpreting the data. A case in point is the vastly different details in the dynamics of population change in the two wet periods separated by a four year dry spell in this study. If the study were conducted for six years, the population pattern of change would inaugurate a concept ascertaining this was the way these animals responded to the increase and decrease of precipitation via seed production, cover, etc. Fortunately, this study was continued and a similar rainfall phenomenon occurred, with variations, a second time. The rodent population increased accordingly but with some very noticeable differences. In some cases there was a dramatic difference in rodent response between the two rainfall periods. This only emphasizes the need for a broader temporal base for field studies involving population dynamics.

Two of the studies presented here were originally set up through the aspects of the International Biological Programme (IBP) through the National Science Foundation. I continued the studies long after IBP and the resulting funding went defunct. It is unfortunate that more of the programs initiated by IBP did not survive beyond its life because it is now, some 10 years since inauguration, that a comprehensive image is emerging in this study.

This study is unique in that it encompasses three different habitats in three different areas, utilizing three different census methods. All three areas contain essentially the same nocturnal rodent species. Yet in spite of all the differences, the rodents react with a oneness that is startling. Though in retrospect, this is not surprising since the one singular all-important variable is availability of water.

Throughout the ecosystem one gets the feeling that most of life is poised, waiting for the special events that produce an abundance of moisture. In a short span of time a dazzling propagation of plant life is closely followed by a similar dazzling propagation of animal life.

This display of ecological fireworks is all too soon followed by a sobering return to what really dictates the environment-dryness. But in this brief interim what profound changes are being wrought-the tremendous acceleration of species interaction, magnitudes of genetic matter cast into the environmental sea to be chosen for fitness under more stringent parameters, and the invasion of new territories propelled by sheer numbers of individuals. As this frenzy abates, time and the harsh hand of a desert environment deals selectively with the aftermath. Life then maintains, until the next damp bounty from the heavens.

CHAPTER 2

HISTORY

Originally the site on the Santa Rita Experimental Range was established in 1970 as part of the Desert Biome Study under the aspic of the International Biological Programme (IBP) funded by the National Science Foundation. The overlying principle of IBP was to compare and correlate biological productivity in different biomes around the world.

In the desert biome each study area was to have a control whereas natural populations were monitored, and a manipulated area, or series of manipulated areas, where perturbation could take place.

After two years a decision was made to move the desert biome site to a "more typical" Sonoran Desert setting. Ultimately, the study area was established at the present Silverbell location after the original Silverbell site was disrupted by the drilling of test holes by a mining company.

Both the SRER and the Silverbell sites utilized in this study are from the control areas. An exception is part of the Silverbell site. Of the four sets of parallel lines, two are on an area that was originally perturbated by multiple crossing by four wheel drive vehicles. The effect of this perturbation seemed short lived since very little evidence remained after a few years. This rapid repair of the area may have been due largely to the exceptional rains that occurred in 1972-73.

Also during this time, Dr. E. L. Cockrum of the University of Arizona had students interested in other aspects of population assessment. One proposal had been the testing in a desert environment of the standard minimum method as put forth by Grdzinski, Pucek, and Ryszkowski in 1966. The Red Hill site was established in 1972 for this purpose.

The Santa Rita Experimental Range site, referred to as SRER for the remainder of this paper, was first monitored in July of 1970. It has been sampled continuously, with minor exceptions, on a monthly basis until the present. Most of the data utilized for this study will only include May 1972 to September 1980.

The Silverbell site of this study was originally monitored in June of 1972 and again in October of that same year. The following year it was monitored in May and early September, which was the case for the remainder of the study.

The Red Hill site was first sampled in September of 1972. Since the sample method consisted of snap trap removal, the site is sampled only once a year in early September. In 1974 it was sampled in September then again in October. In all other years sampling was restricted to September only.

Except for the early perturbation on half of the Silverbell site, and the necessary removal once a year at the Red Hill site, disturbance is kept to a minumum. Out of necessity, the rodents need to be handled and toe clipped. Aside from that, no manipulation was attempted. The areas were free from cattle grazing and, for the most part, any vehicle or foot traffic except for time of sampling.

Funding of IBP went defunct in the mid-1970's, as did most of the resulting programs. These three sites were maintained on the initiative of Dr. E. L. Cockrum and myself for the remainder of the study.

Location

Silverbell Site - The site is situated in Section 21, Range 9 East, Township 11 South, Pima County at an elevation of 658 meters. This site is located on a section of fenced Bureau of Land Management land.

Red Hill Site - This site is located in Section 34, Range 9 East, Township 11 South, Pima County at an elevation of 670 meters. A portion of the site encompasses the lower slope of Red Hill (Elevation 722 meters). The southeast corner of the research site is approximately 18.3 meters lower in elevation than the northwest corner. This site is also on BLM land that is fenced and ungrazed.

Santa Rita Experimental Range Site - The site is located in Pima County at the junction of four sections - SE¼ Section 10, SW¼ Section 11, NW¼ Section 14, and the NE¼ Section 15, Range 14 East, Township 18 South at an elevation of 963 meters.

The area is part of the 21522 hectare Santa Rita Experimental Range maintained by the USDA Forest Service for research on semi-desert ecosystems.

Description of Areas

The Silverbell site is located on a bajada dominated by creosote bush flats dissected by shallow washes running in a general west to east direction. The area is rich in cacti of many varieties.

The flats are dominated by creosote bush (*Larrea divaricata*) and triangle-leaf bursage (*Franseria deltoidea*). The little leaf paloverde (*Cercidium microphyllum*), saguaro (*Carnegiea gigantea*), and ironwood (*Olneya tesota*) dominate along the washes, although they occur throughout the area. In addition, the wash areas contain whitethorn acacia (*Acacia constricta*), and catclaw acacia (*A. greggii*). Lowe (1964) refers to the area as the creosotebush-bursage and paloverde-saguaro plant communities.

Bursage, a perennial, constitutes the first layer of ground cover. A bush 0.5 meters high at the crown, it is sparsely distributed with distances of two meters between plants common. Generally there is little ground cover among the bursage, creating a relatively open habitat.

Cacti are common and frequent. Saguaro is distributed throughout the area. Many young saguaros of one meter or less in height are common to the area. The columnar and pad opuntias (*Opuntia spp.*) are well represented as well as the barrel cactus (*Ferocactus sp.*).

Most of the surface soils have formed as alluvium from the Silverbell Mountains. These are primarily granitic and volcanic in origin. The soil is a course sand-gravel with desert pavement apparent in a few areas.

The deeper washes in the area have some weathered rock outcrops. These outcrops are small and scattered. For the most part, the slopes of the washes are gravelly while the bottom of the washes consist of sand.

The Red Hill site is partly situated on the lower slope of Red Hill, a low singular hill 5.5 kilometers to the east of the main chain of the Silverbell Mountains. Due to the steeper slope and exposure of bedrock in the northwestern quarter of the grid, brittlebush (*Encelia farinosa*) and ocotillo (*Fouquieria splendens*) are much more common then at the Silverbell site. The lower portions of the site are a series of small creosote flats bisected by shallow washes. A large arroyo transects the southern edge of the site.

The dominant plants are similar to those of the Silverbell site with the addition of false mesquite (*Calliandra eriophyllum*), white thorn acacia (*Acacia constricta*), and jatropha (*Jatropha cardiophylla*) common along the washes.

Bursage is the predominant "ground cover" as it was on the Silverbell site. Paloverde, opuntias, barrel cactus, and saguaro are well represented. The immediate area does not contain quite the abundance of ironwood found on the Silverbell site.

The soil consists of gravel much more than at the Silverbell site. In the northwest corner of the site, bedrock is exposed as it is along many of the shallow washes. The western edge contains gravelly soils which grade into a coarse sand towards the east.

The Santa Rita Experimental Range site is an ecotone between elements of the lower Sonoran Desert of lower elevations and desert grassland elements of higher elevations. Ground cover of perennials is much more prevalent than in either the Silverbell or Red Hill sites. The area is dominated by burroweed (_Haplopappus tenuisectus_), snakeweed (_Gutierrezia sarothrae_), and to a lesser extent desert zinnia (_Zinnia pumila_). Stands of perennial grasses are distributed throughout the area. The major grasses are grama (_Bouteloua rothrockii_), three awm (_Aristida barbata_), cottontop (_Trichachne californica_), bluestem (_Andropogon barbinodis_), and tanglehead (_Heteropogon contortus_). Also common in this first layer of vegetation is Mormon tea (_Ephedra trifurca_) and ratany (_Krameria grayi_).

The intermediate layer of plants consist primarily of several cacti species and desert hackberry (_Celtis pallida_). The common cacti are the cholla (_Opuntia versicolor_) and (_O. fulgida_), and prickly pear (_O. engelmannii_).

The uppermost layer is dominated by paloverde (_Cercidium floridum_) and mesquite (_Prosopis juliflora_). Along the washes, catclaw acacia (_Acacia greggii_) occurs frequently.

Density of plants is much greater than at the other two sites. Many more perennials constitute the base layer. Even though there are relatively greater numbers of plants, a considerable amount of open ground occurs among the vegetation.

The soils in the area are predominately sand intermixed with gravel in some areas. Washes are narrow and shallow. A few of the deeper washes are sufficiently deep to expose a coarse gravel. No bedrock is apparent in the area.

CHAPTER 3

CLIMATE

General

Southern Arizona's climate is mild, sunny and relatively dry. Monthly temperatures at lower elevations are fairly consistent from year to year. The mean monthly minimum during the winter months is generally half of that during July and August (Figure 1).

Rainfall is relatively sparse and seasonal. An increase in elevation is normally reflected by an increase in rainfall. Annual precipitation varies around the state from less than 70 mm. at Yuma in the southwestern corner of the state to over 500 mm. at higher elevations.

Number and duration of freeze spells are influenced by elevation and proximity to high mountain ranges. Extremely windy days are uncommon, occur sporadically and last for only a couple of days.

Temperature

Mean monthly temperatures remain fairly constant from year to year (Turnage and Mallery, 1941). Although winters are relatively mild at lower elevations, local temperatures are greatly influenced by proximity to high mountain ranges, major river drainages, wind patterns, and elevation.

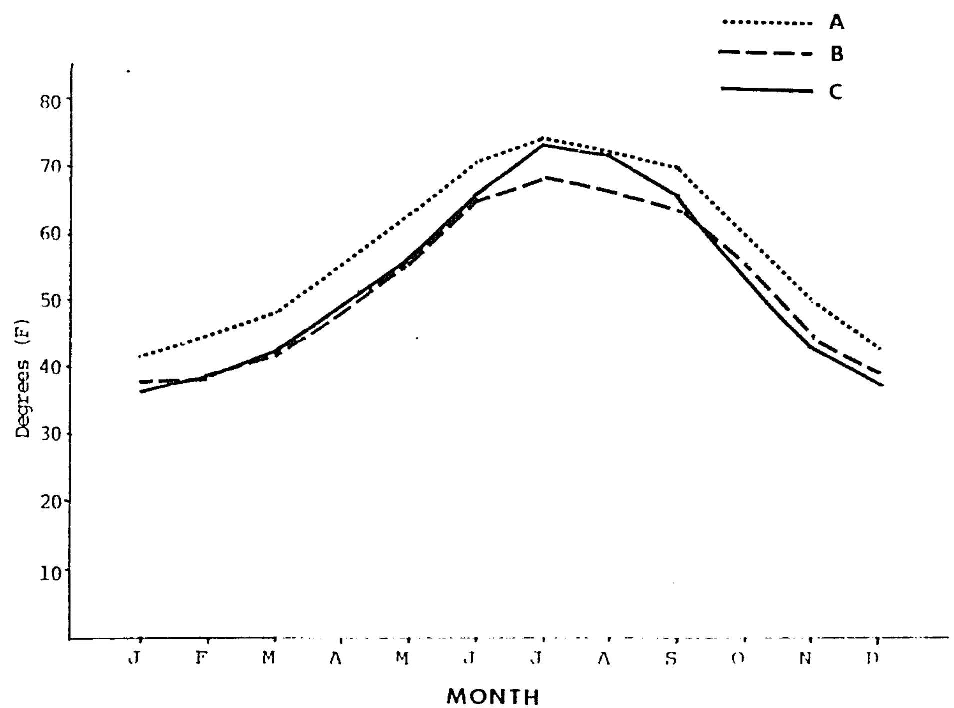

Figure 1. Monthly Mean Daily Minimum Temperature on Three Sites: A. Silverbell Mine; B. Santa Rita Experimental Range; C. University of Arizona.

Comparison of the research areas to the Tucson Basin shows that the mean monthly minimum temperature at the SRER at an elevation of 1494 m. is very similar to that of the Tucson Basin, even though the basin is 700 meters lower in elevation (Figure 1). This may be attributed to cold air drainage from the high Santa Rita Mountains (elevation above 2700 meters) down the Santa Cruz River drainage as well as from the equally as tall Santa Catalina Mountains to the north. At times the mean monthly minimum in the Tucson Basin is lower than that of the SRER.

The mean monthly minimum at Silverbell mine at an elevation of 838 meters is, in all cases, higher than either the Tucson Basin or SRER. Even though it is higher in elevation than the Tucson Basin, the Silverbell mine is surrounded by relatively low mountains that do not provide the cold air as do the Santa Rita and Santa Catalina Mountains. This overall higher mean monthly minimum at the Silverbell area is reflected in the profusion of iron wood (*Olneya tesota*).

Evaporation

Evaporation patterns, being primarily a function of temperature and relative humidity, remain consistent from year to year in southern Arizona. As would be expected, the mid-summer months have the highest evaporation rates and the mid-winter months the lowest (Figure 2). This can be directly attributed to the high summer temperatures.

The mean annual evaporation for the Tucson Basin from 1970 to 1979 was 297.6 cm. Deviation from the annual mean was minimal, averaging 2.58% with a range of -8.7 to +4.7 percent.

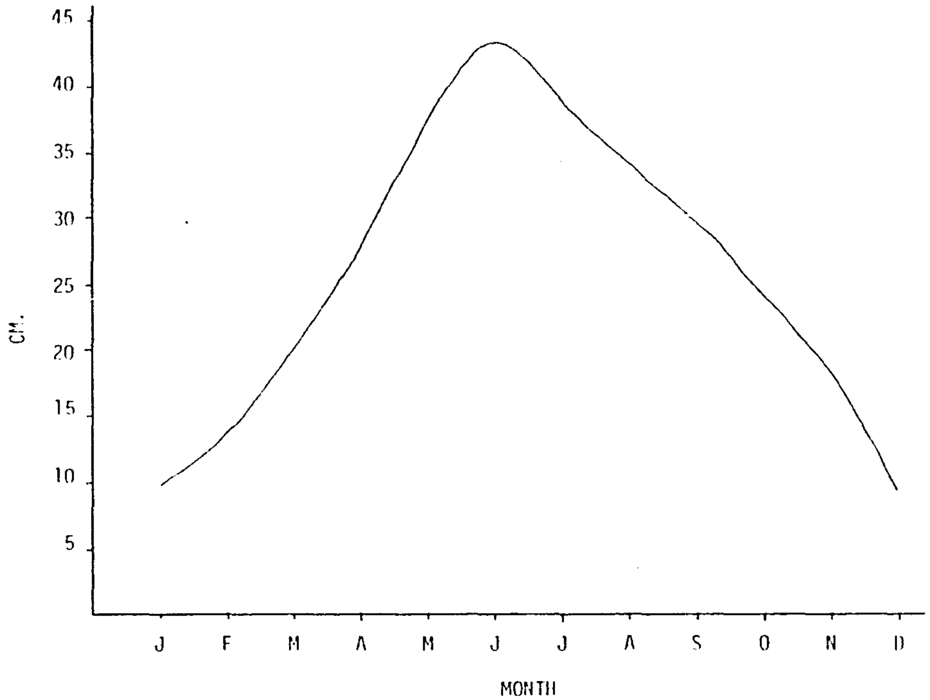

Figure 2. Mean Evaporation at the University of Arizona, 1970-1981.

The highest rate of evaporation was in June with 429.8 cm. per month. Although July and August are normally hotter, the slightly reduced evaporation rate for these months is due to the high relative humidity resulting from summer monsoons. June has very little rainfall with high air temperatures creating low relative humidity.

The stability of evaporation rates would suggest that changes in evaporation would not provide the impetus for great changes in rodent numbers via plant response.

Rainfall

The rainfall in southern Arizona follows a bimodal pattern with the majority of rain falling in mid-summer and another, lesser peak, in mid-winter (Figure 3).

Summer rains generally arise from the Gulf of Mexico and move into the state from the southeast (Turnage and Mallery, 1941). These often times are sudden, violent, and local in character. A large amount of rain may be deposited in a very brief period of time, creating rapid runoff of great quantities. Due to the turbulence produced by cooler air moving across hot desert valleys and up slopes of isolated mountain ranges, summer rainfall generally increases with an increase in elevation (Figure 4).

The milder winter rains originate off the west coast of North America and moves easterly. These rains are generally light, wide ranging, and may last for several days. This type of rain creates very little runoff, thus the moisture is more readily incorporated into the soil.

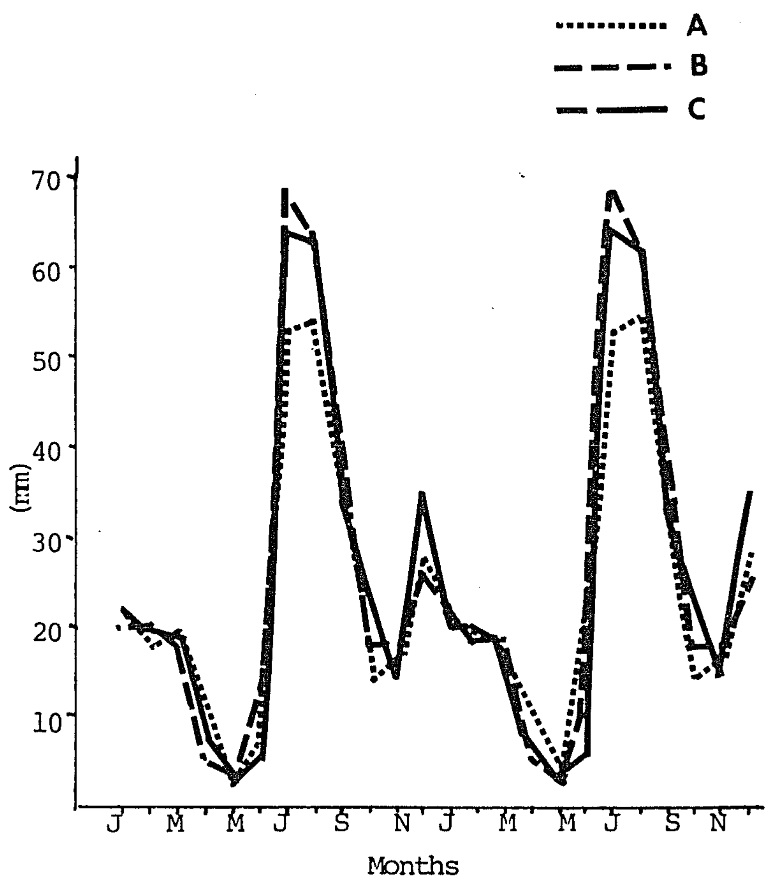

Figure 3. Mean Monthly Rainfall at Three Sites, 1940-1980: A. Tucson Basin; B. Santa Rita Experimental Range; C. Silverbell Mine.

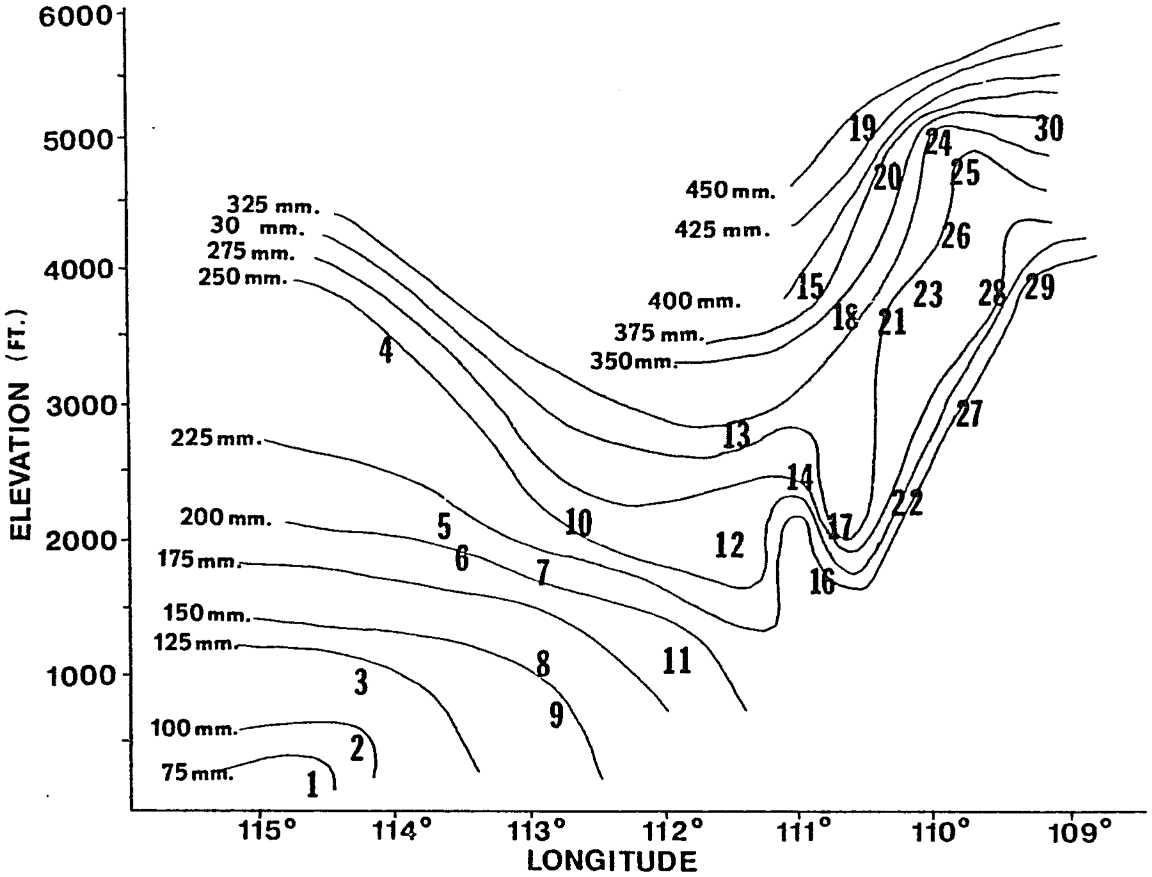

Figure 4. Mean Annual Rainfall in Relation to Elevation and Longitude in Southern Arizona. 1. Yuma 2. Parker 3. Quartzsite 4. Kingman 5. Wikieup 6. Salome 7. Ajo 8. Tonopah 9. Gila Bend 10. Wickenburg 11. Phoenix 12. Apache Junction 13. Mormom Flat 14. Tucson 15. Nogales 16. Casa Grande 17. Winkelman 18. San Manuel 19. Canelo 20. Fort Huachuca 21. Benson 22. San Carlos 23. Tombstone 24. Fort Grant 25. Pearce 26. Wilcox 27. Safford 28. Douglas 29. San Simon 30. Portal.

Winter rains are not normally influenced by changes in elevation. These are large fronts that may cover the entire state. For the Tucson area, 50% to 60% of the annual rainfall occurs during summer monsoons. The greatest amount of rain falls in the months of July and August with over 50 mm. falling in each month. May and June are the driest months of the year with less than 10 mm. of precipitation for each of these months.

Figures 5 and 6 show that the bimodal rain pattern applies to most areas of southern Arizona. The effect of summer rains diminishes from east to west, also in a decrease of elevation. The winter rainfall remains fairly constant in most areas throughout the southern half of the state.

Although there is some variation and differences in magnitude of seasonal rains, the similarities make it feasible to conclude that rain pattern is consistent for most of southern Arizona south of the Mogollon Rim and east of the Colorado River Basin.

Rainfall - Tucson Basin

In the course of attempting to realize the effect of short term climatic changes on desert nocturnal rodent populations, the question arose as to the magnitude and area affected by any particular set of rains. Especially since much of the rain falls in the summer months and these storms are generally violent and local in nature.

As discussed earlier, the long term rainfall patterns are very similar for most areas of southern Arizona, but these are mean

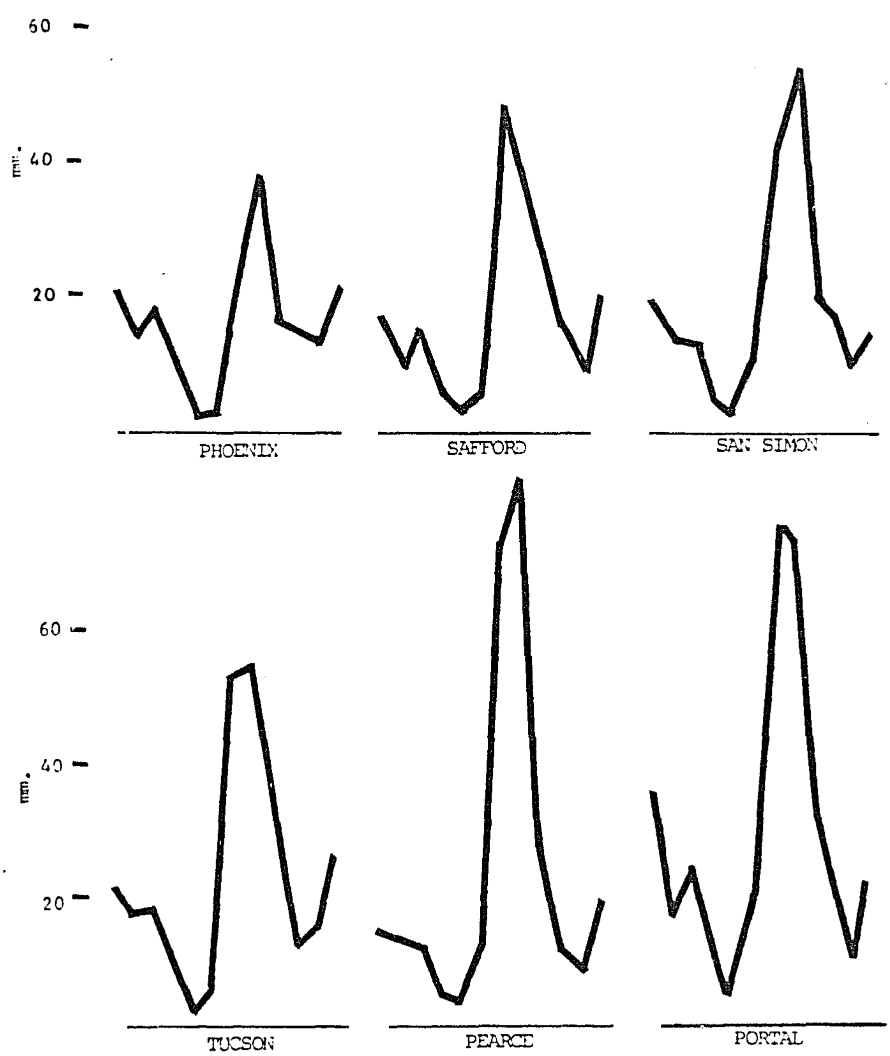

Figure 5. Mean Monthly Rainfall from January through December on Six Sites in Southern Arizona.

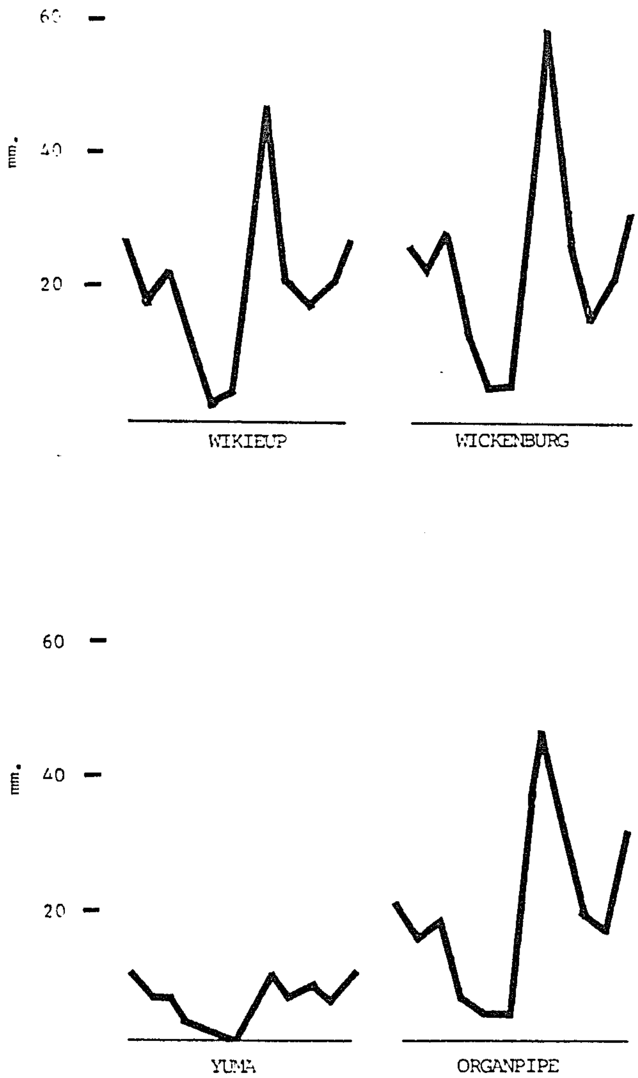

Figure 6. Mean Monthly Rainfall from January through December on Four Sites in Southwestern Arizona.

values over a period of 40 years or more and may not reflect the immediate conditions.

To adequately compare distant areas in a set time frame, the question of whether certain rainfall patterns are repeated in separate areas during the same period of time, had to be answered.

In most cases no weather data is available for an immediate research area. This was partially the case in this study. Originally, weather data gathering facilities were present on the Silverbell and SRER sites. Also a National Weather Bureau station was operating from the Silverbell site.

The station at Silverbell mine was closed in 1974 and the stations at the Silverbell and SRER sites went defunct in mid-1976. There is a functioning station maintained by the Forest Service approximately two kilometers south of the SRER site. It has been operational since 1923.

As a basis for comparison, the rainfall in the Tucson Basin will be utilized throughout this study. The Tucson Basin rainfall as used here, is an average based on the records of three collecting stations: Tucson International Airport, University of Arizona campus, and the University of Arizona farm at Campbell Avenue.

A comparison of the Silverbell area rainfall to the Tucson basin rainfall indicates that rainfall follows very similar monthly patterns as well as monthly amounts (Figure 7). Likewise, a comparison of Tucson basin to the SRER shows the same pattern (Figure 8). Here, for the most part, the only difference is in amplitude due to the

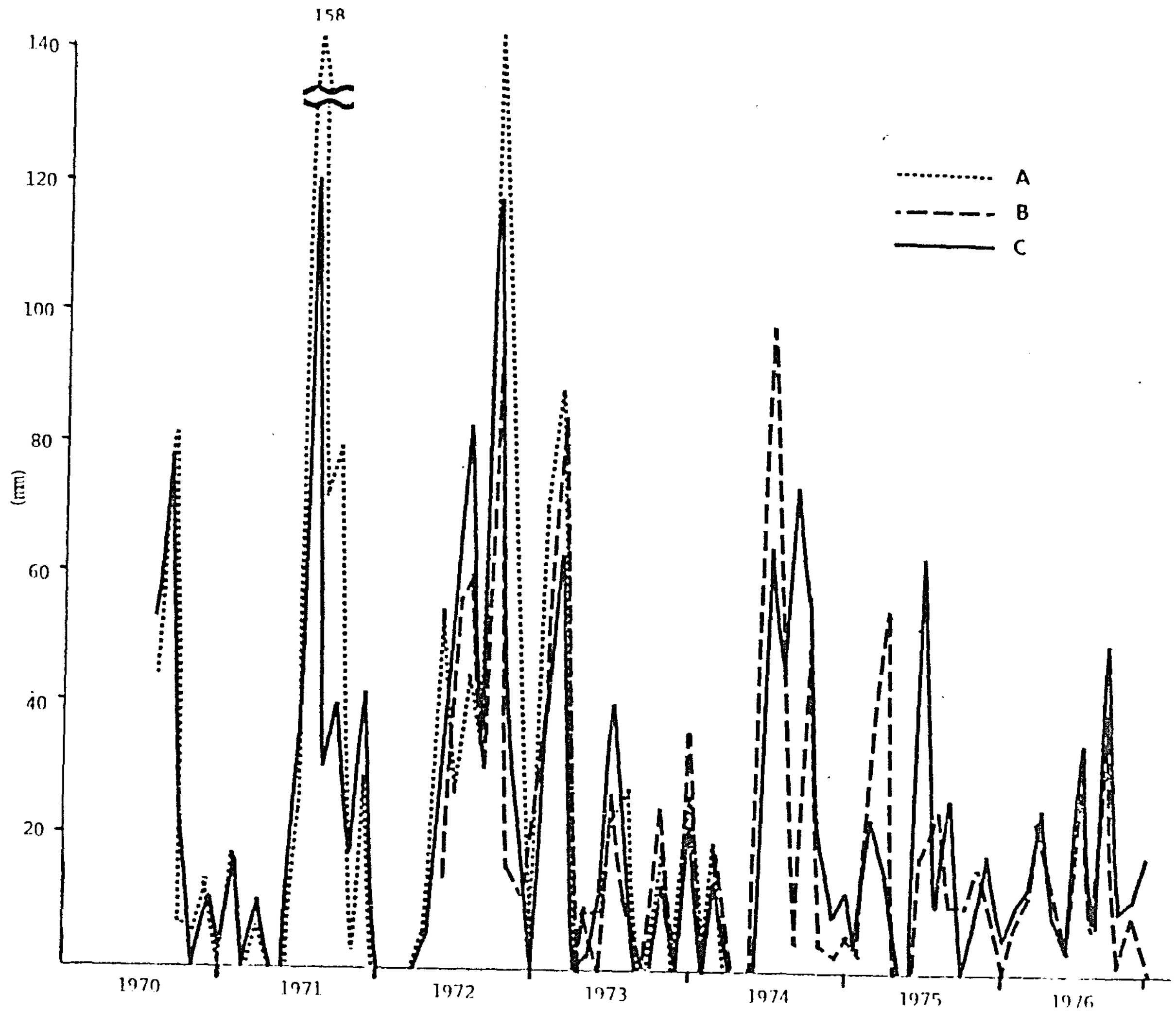

Figure 7. Monthly Rainfall on Three Sites from 1970-1976: A. Silverbell Mine; B. Silverbell Research Site; C. Tucson Basin.

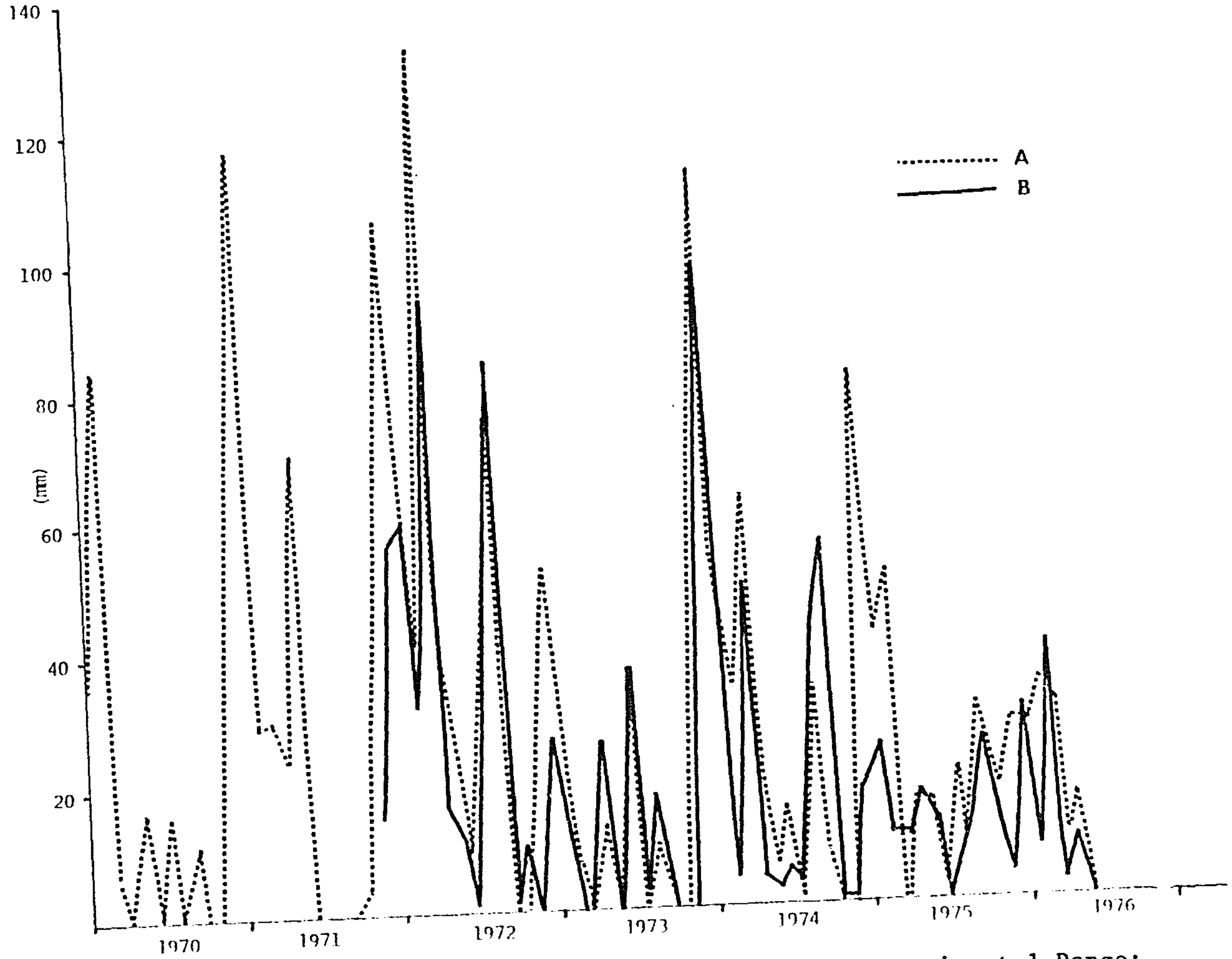

Figure 8. Monthly Rainfall on Two Sites from 1970-1976: A. Santa Rita Experimental Range; B. Tucson Basin.

higher elevation of the SRER site. The Silverbell and the SRER sites are approximately 110 kilometers apart with the Tucson basin situated near the midpoint.

Viewed with these similarities in mind, it would be reasonable to assume that any deviations in rainfall pattern, either time of occurrence or amount, will manifest itself over a fairly wide area. Presumably in any area that had similar patterns of rainfall.

A model of cause and effect is much more pertinent if it can predict phenomena outside the narrow temporal and spatial regimes in which it was concieved.

Rainfall Phenomena

Comparing the monthly rainfall data during the study period to long term mean monthly rainfall data revealed that three major digressions occurred (Figure 9). These digressions consisted of extremely high rainfall in late fall-early winter (September, October, and November) followed by extremely high rainfall in late winter-early spring (January, February, and March). This pattern is sufficiently rare that it has occurred only seven times in the last 41 years. Three of those times were during this study. The others occurred in 1940-41, 1954-55, 1957-58, and 1962-63.

During this study the spring immediately following these rainfall phenomena produced a spectacular flower bloom that literally carpeted the desert floor. These floral displays were widespread and prolonged, lasting up to two months. Springs of other years did not produce this colorful array of floral brilliance.

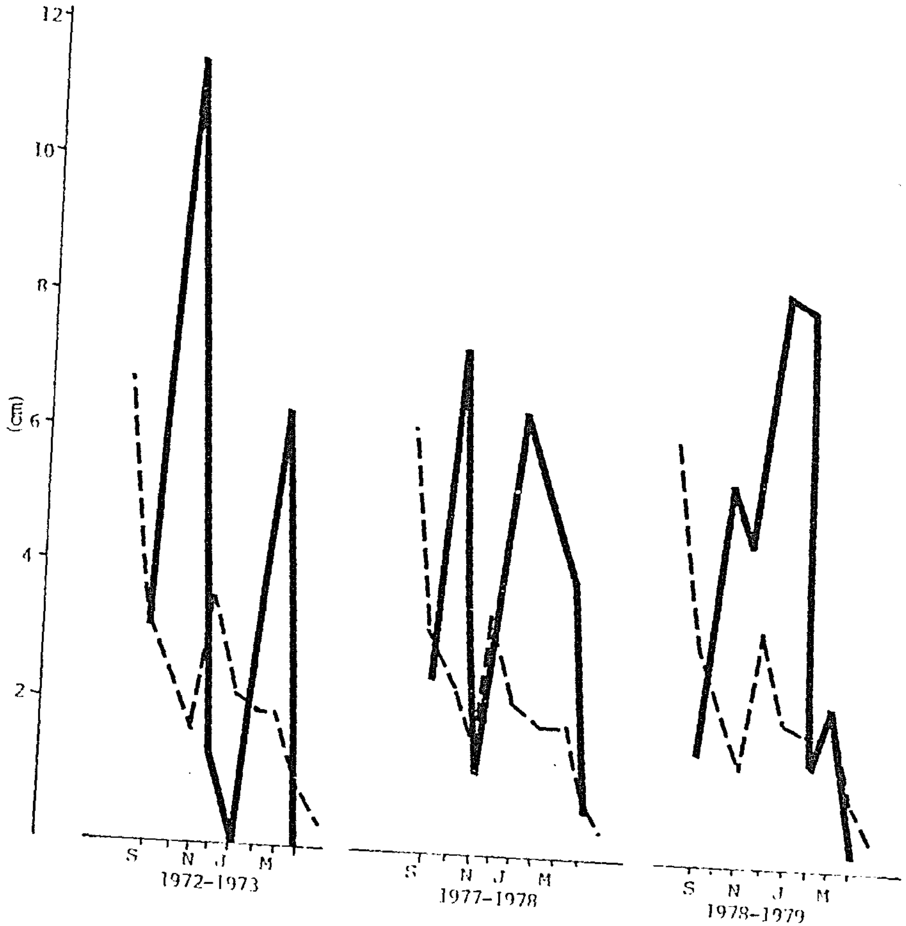

Figure 9. Monthly Rainfall during Three Periods. (Dashed line is mean).

Although there have been years where there was abnormal high rainfall in one of those periods but not both concurrently (see Figures 8 and 10, note late 1974 and early 1977), none have produced the floral displays common to 1973, 1978, and to a slightly lesser extent, 1979.

It could be argued that these desert blooms were not the product of the rainfall pattern so much, as a function of the total annual rainfall in the previous year, since abnormal heavy rainfall did occur in 1972 and 1978 (Figure 11). If only the 1972-73 period was considered, a strong argument could ensue, but with the addition of the 1978 bloom the cause would have to be re-evaluated.

In 1972-73, the bloom occurred <u>after</u> the high annual rainfall and also <u>after</u> the heavy late fall-early spring rains. The bloom in 1978 occurred <u>before</u> the high annual rainfall and <u>after</u> the high late fall-early spring rains. If, in fact, the early spring blooms were produced by high annual rainfall, it would be that of the previous year. In this case, 1977 was a very normal rainfall year.

So it seems that the rare and spectacular desert blooms in early spring are triggered by heavy late fall-early winter rains followed by heavy late winter-early spring rains. It must be noted that the desert blooms are dominated by ephemerals. Annuals such as many of the crucifers, poppies, and mallows are very prominent during these times.

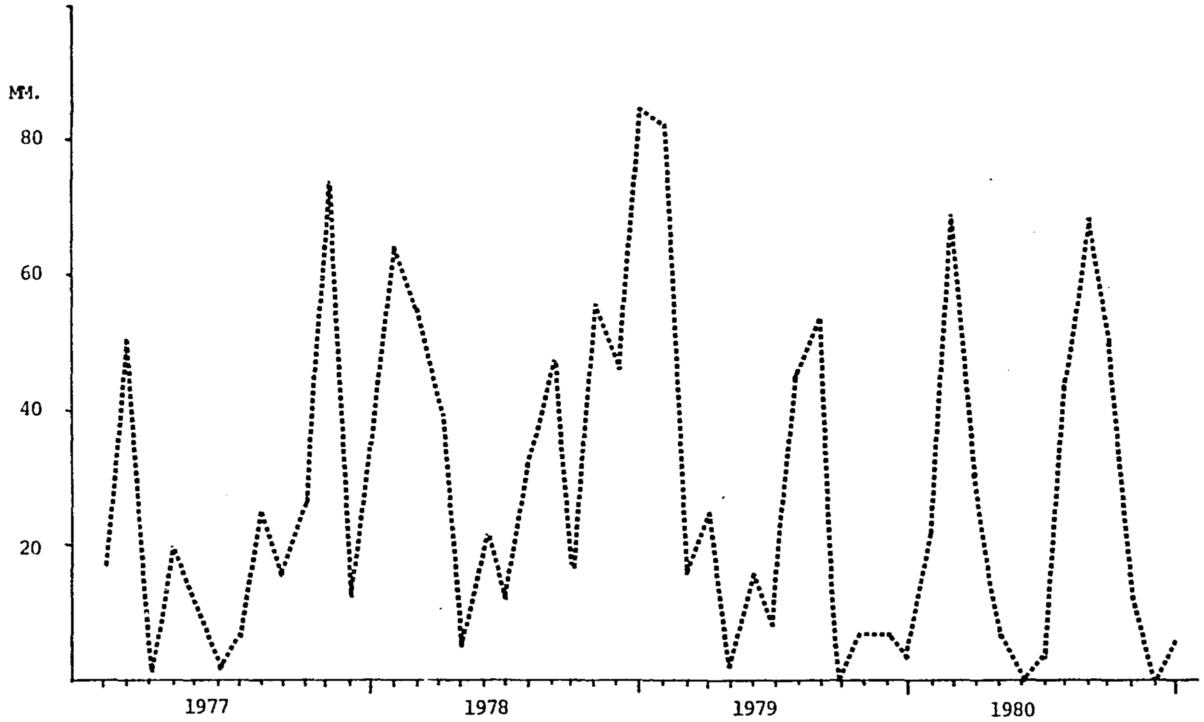

Figure 10. Monthly Rainfall in the Tucson Basin (1977-1980).

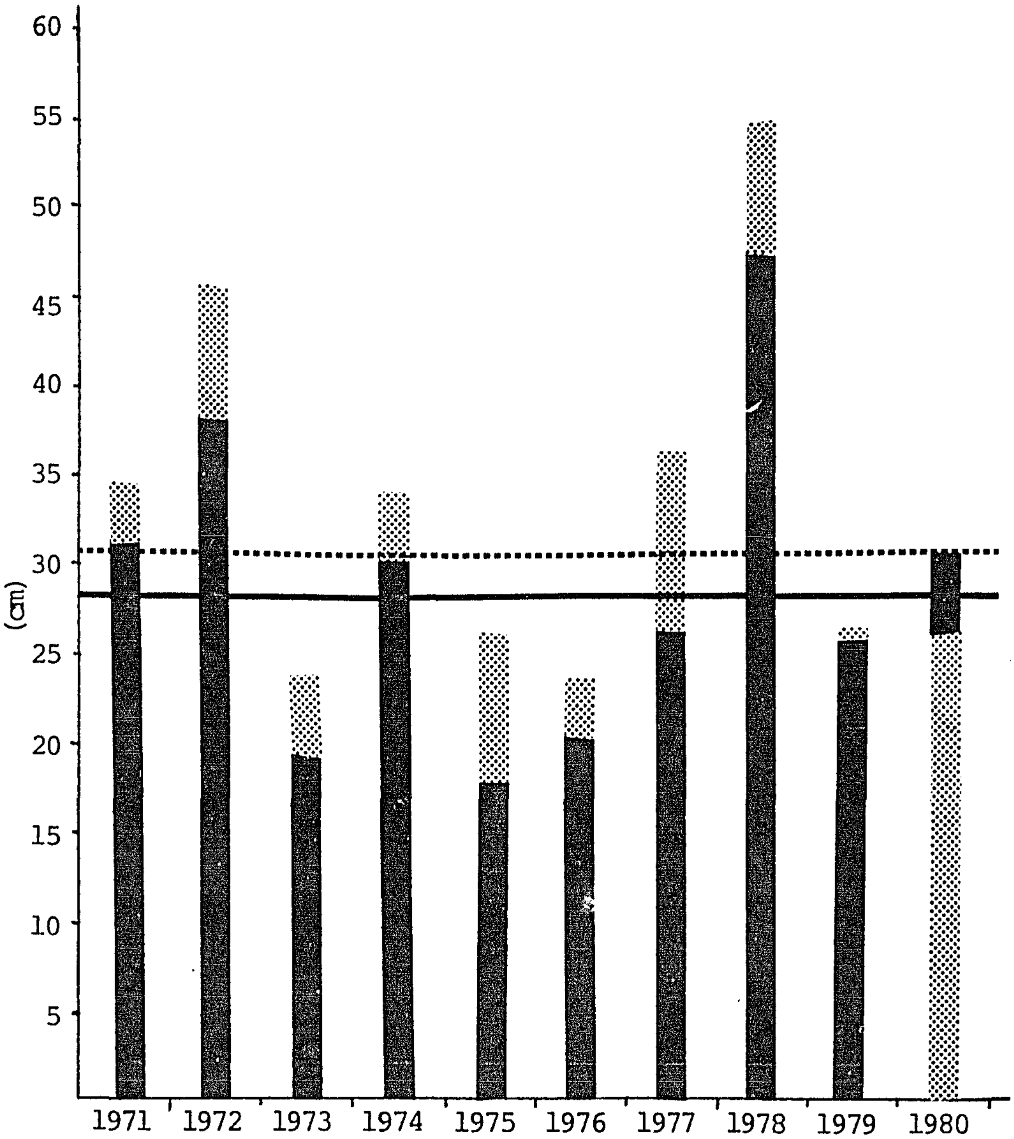

Figure 11. Annual Rainfall on Two Sites.

Solid Bar = Tucson Basin; Shaded Bar = SRER; Solid Line = Mean Annual Rainfall for Tucson Basin; Dotted Line = Mean Annual Rainfall for SRER.

Rainfall - Study Period

During the study period the Tucson Basin mean annual rainfall was 285 mm. This was slightly higher than the 40-year mean of 281 mm per year. This was also true of the SRER where the study period mean annual rainfall was 331 mm compared to the 59 year mean of 294 mm of rainfall per year. Only during 1980 did rainfall in the Tucson basin surpass that of the SRER.

The Tucson basin rainall in 1972 and 1978 considerably exceeded the mean annual rainfall (Figure 11). This also occurred at the SRER. Four of the nine years had above average rainfall in the study areas. The years of 1973, 1975, and 1976 were exceedingly dry with 192 mm, 178 mm, and 200 mm of total rainfall in the Tucson basin and 240 mm, 262 mm, and 233 mm at the SRER. These values are reflected at the Silverbell site.

An analysis of long term weather patterns shows that approximately 22% of the years will be "dry" (2/3 of mean or less) while 10% of the years will be "wet" (1/3 greater than the mean or more) at the Tucson basin. This is interpreted as less than 200 mm and greater than 380 mm of rainfall per year. It becomes apparent that exceedingly wet years are very uncommon. In the Tucson basin those years surpassing 360 mm of annual rainfall were 1940, 1941, 1973, and 1978 (in the last 41 years). The 1978 rainfall of 477 mm was the highest recorded for the 41 year period.

At the SRER a similar situation occurred. Twenty percent of the years have an annual rainfall of less then 200 mm which is approximately 2/3 of the mean. "Wet" years occurred more frequently than at the lower elevation of the Tucson basin, with 15% of the years having over 400 mm of rainfall (approximately 1/3 greater than the mean). Those years surpassing 400 mm were 1954, 1964, 1965, 1967, 1972, and 1978. The rainfall of 552 mm in 1978 was the highest for the 41 year period at the SRER.

The extremes of rainfall were greatest at the SRER with a range of 130 mm to 552 mm, whereas the Tucson basin had a range of 148 mm to 477 mm during the same time period.

CHAPTER 4

PLANT RESPONSE

The effect on vegetation by deviations in rainfall patterns was profound. As mentioned earlier, the spring of 1973, 1978, and to a lesser extent, 1979, produced a tremendous bloom of desert wildflowers. These, for the most part, were ephemerals that germinate, grow, flower, and produce seed all in a very short period of time. By the time hot weather of early summer arrives the parent plant is dead. The seeds are the only reminder of the prolific vegetative matter and colorful bloom that existed only a short period earlier.

The most conspicuous of these plants are the poppy, *Eschscholtzia mexicana*; lupines, *Lupinus sparsiflorus* and *L. concinnus*; owl clover, *Orthocarpus purpurascens*; globe mallow, *Sphaeralcea coulteri*, and the many members of the mustard family, Cruciferae. The more common include bladder pod, *Lesquerella gordoni*; spectacle-pod, *Dithyrea californica*; pepper grass, *Lepidium* sp.; and fringe-pod, *Thysanocarpus amplectens*.

These periodic spring blooms are more apparent in the lower desert. Here, there may be less competition from perennials. Considering the greater amount of bare soil exposed in the lower elevations than at the SRER where perennials cover much of the soil, it is highly probable that this is the case.

I have noted that bloom and seed production of perennials such as bursage, *F. deltoidea*, creosote bush, *L. divaricata*, and mesquite, *P. juliflora* are not so dependent on exceptional high autumn and early spring rains. This is also true of many of the cacti. In these cases, adequate rains are sufficient to produce flowers and fruit. The water storage facilities of many of the perennials (tap root, succulent tissues, new growth, and expansion of size) make them more in tune with the overall rainfall of the previous year. Beatley (1974) working in the Mojave desert, found that seed production of shrubs was not as sensitive to timing of rains as were the annuals. Only two species in Orions and Solbrig's (1977) sample of perennials, showed an adaptation to winter rain patterns of southern Arizona. Turkowski and Vahle (1977) also found that habitat conditions at the SRER, which is dominated by perennials, respond to annual precipitation of the previous year.

The dormancy of winter would, for the most part, eliminate a sensitivity to winter rains. This coupled with a later season of seed production for many of the perennials, allows leeway in plant production via plant growth and fruiting.

The bulk of the annuals, on the other hand, do not have leeway in timing of growth and seed production. With them it is a case of all-or-none. Conditions have to be right, for there are no false starts. Once germination begins there is no turning back or another chance for those seeds next year. With the perennials, seeds may be produced almost any year in some quantity to be dispersed into the environment. If conditions are not satisfactory there is always the presence of the parent stock to reseed the following year. The annuals do not have this back up system.

At the Silverbell and Red Hill sites the perennial ground cover plants are sparse and lacking in diversity, composed primarily of _F. deltoidea_. Much open ground between plants is apparent in most years. In contrast, the ground level plants at the SRER are numerous and varied. Relatively little ground is exposed. Perennials such as _Gutierrezia_, _Haplopappus_, _Zinnia_, and five species of perennial grasses, make up the first layer of plant cover.

This comparative richness of perennial flora produces a habitat that has closer packing of plants, thus reducing the openness of the environment. This in turn, reduces the area available for annuals to establish themselves during prime moisture conditions in addition to the increased competition for moisture from the already established numerous perennials.

It then appears that seed resources as concerning Heteromyid rodents is dominated by seed production of the annuals at the Silverbell and Red Hill sites, wherein at the SRER site the perennials contribute much more to the Heteromyid rodent seed resources. Future investigations to determine what seeds are specifically utilized in each of the environments should be attempted.

CHAPTER 5

RODENT COMPOSITION

The species composition of nocturnal rodent populations is very similar for all three study areas (Table 1). The heteromyids contribute the bulk of the species found and total numbers involved. *Dipodomys merriami* is the only kangaroo rat trapped on the three sites. Of the perognatheans, *Perognathus amplus*, *P. penicillatus*, and *P. baileyi* are commonly found on all three sites. *Perognathus intermedius* occurs on the Red Hill site and to a lesser degree on the Silverbell site. It does not occur on the SRER site. On rare occasions *P. flavus* is trapped on the SRER site.

Of the criciteds, *Neotoma albigula* comprises most of the individuals trapped. It is found commonly on all three sites. *Onychomys torridus* is regularly taken at the SRER site but infrequently at the other two sites. *Peromyscus* of several species are intermittently found on all sites, especially the SRER site. They are never common on any of the sites. *Sigmodon arizonae* is trapped in limited numbers following desert blooms on all three sites. During these same periods the murid, *Mus musculus* also make an appearance but in very small numbers except for one exception.

This report will be concerned primarily with the more common heteromyid rodents and the pack rat, *N. albigula*. These species comprise at least 99% of the total numbers and biomass of nocturnal rodents in

Table 1. Nocturnal Rodent Species Present on Three Sites.

Species	SRER	Silverbell	Red Hill
Perognathus flavus	X		
Perognathus amplus	X	X	X
Perognathus baileyi	X	X	X
Dipodomys merriami	X	X	X
Dipodomys spectabilis	X		
Onchomys torridus	X	X	X
Neotoma albigula	X	X	X
Peromyscus maniculatus	X		
Peromyscus leucopus	X		
Peromyscus eremicus	X	X	X
Sigmodon arizonae	X	X	X
Mus musculus		X	X
Reithrodontomys megalotis	X		
Reithrodontomys fulvescens	X		
Reithrodontomys montanus	X		

these areas during the study period. Mention will be made of the other species when appropriate.

The diurnal rodent species consist of *Ammospermophilis harrisi* and *Spermophilis tereticaudus*. These species were not monitored in this study, although on occasion they were found in the traps. Their influence on the predominant heteromyid rodents should be minimal since they have different activity and dietary regimes. They may be competing somewhat with *N. albigula* since their diets, in all probability, overlap. This is an area that needs further exploration.

Mention should be made of the lagomorphs since they do occur commonly in all three areas. Both *Sylvilagus auduboni* and *Lepus californicus* occur on all areas. *Lepus alleni* is found in reduced numbers at the SRER site only. These animals should have a minimal influence on the nocturnal rodent populations due to differing dietary and activity patterns.

CHAPTER 6

METHODS

Sample Areas and Techniques

In monitoring the native nocturnal rodent populations on the study sites, three different sample configurations and methods were utilized.

At the Silverbell site a series of parallel trap lines were placed in a large U shape. These four sets of parallel lines utilized 256 live traps. Each set of parallel lines consisted of two lines, set 15 m apart. Each line contained 16 trap stations with stations set at 15 m intervals. Two traps per station were utilized on all lines. The sets of parallel lines were approximately 1700 m apart.

Traps consisted of sheet metal boxes with screen tops. The dimensions of 10 cm x 10 cm x 26 cm made them acceptable for capturing the smallest rodents to the large pack rats. The simple drop treadle design worked efficiently enough to be tripped easily by the small rodents as well as the large.

The lines were run in May and early September. May was chosen because it would sample the populations before an influx of young from the summer breeding season. Early September sampling would normally monitor the population after breeding and before many of the smaller rodents became inactive above ground due to colder temperatures of the winter months.

During a sample period, traps were baited in late afternoon with dry rolled oats. The traps were checked between 10:00 pm and 12:00 midnight, animals removed and the traps rebaited. Traps were again checked at sunrise, rodents removed and traps closed until rebaiting the following afternoon. This procedure was repeated for three days in May and again for three days in early September.

Animals captured were identified, marked by toe clipping if not previously marked, weighed, sexed, and released. Information such as breeding condition, ectoparasites, and other notable observations were recorded. The same type of information was also recorded at the SRER.

The SRER site consisted of a 14 x 14 grid of 196 trap stations placed ten m apart. The same type of trap utilized at Silverbell was used here. Each station contained one trap.

The site was normally monitored for three days every month utilizing the same format as at the Silverbell site- bait, check and rebait, and check again in the morning. From October through March, traps were checked before midnight, rodents removed and traps closed until the following afternoon due to the low night temperatures. This prevented any problems with cold stress from remaining in the metal traps throughout the night.

The Red Hill site consisted of 256 trap stations set on a 16 x 16 grid. The stations were spaced at 15 m intervals. Each station contained two snap kill traps, either museum specials or large rat traps, or a combination of the two.

The area was prebaited for at least two nights previous to actual trapping. The traps were then baited in late afternoon with a mixture of rolled oats, peanut butter, and water. Traps were then checked at sunrise the next morning. Rodents were removed to be processed later. Sampling was continued for at least seven nights.

Since this was a removal form of sampling, the site was trapped in early September only, hopefully to catch the population at its peak density.

This sampling technique is the "Standard Minimum Method" as developed by Grdzinski, et al. (1966). Olding and Cockrum (1977) discussed the results of testing this method at the Red Hill site and on their own site on the Santa Rita Experimental Range. Chudoba and Huminski (1980) described a modified version of the standard minimum method to estimate rodent densities.

Estimation of Densities

Densities of rodents were determined by utilizing a sample area demarked by the actual area within the boundaries of the grid, or parallel lines, plus the radius of estimated home range for each of the rodents (Table 2). Thus, there is a sample area for each species in each of the study sites.

Estimated densities were determined by incorporating regression line analysis on daily captures. Use of regression lines is inherent in the "Standard Minimum Method." If only actual number captured is utilized in estimating densities on live trapping sites, an underestimation is generally the result. Although the incidence of untrapped

Table 2. Home Range Values and Computed Sample Area (Hectares) for Each Species.

Species	r-value (meters) Home Range	SAMPLE AREA SRER	Silver-bell	Red Hill
Perognathus amplus	16.6	2.64	4.88	6.64
Perognathus penicillatus	14.8	2.53	4.48	6.46
Perognathus intermedius	14.4	-	4.44	6.42
Perognathus baileyi	16.7	2.65	4.92	6.65
Dipodomys merriami	20.3	2.88	5.76	7.02
Neotoma albigula	15.3	2.56	4.60	6.51

animals declines (Figure 12) as sampling progresses from night to night, it cannot be assumed that all animals resident in the sample area are captured in only three nights of effort.

It was found that, in general, the parallel lines underestimated the density to a far greater degree than the grid. This would be expected since a live trap grid saturates an area, whereas parallel lines only bisect an area, thus having a greater ratio of "border" to internal area.

Figure 12 indicates that an additional night of sampling would insure capture of most of the individuals present. During peak population years, additional nights of trapping or additional traps per station would be needed to assure a larger percentage of the population to be captured.

Home Range

One possible shortcoming of this study is the utilization of a single home range value for each species throughout the study. It may well be that the home ranges remain fairly constant through time in this area but this assumption, as used in this paper, will have to be viewed with some skepticism.

Maza et al. (1973) did find a shift occurring in size of home ranges from year to year among a group of heteromyid rodents. They also found an inverse relationship between population density and size of home range. However, Maza et al. (1980) did find that the center of activity for *Perognathus formosus* seldom varied more than 7.5 m

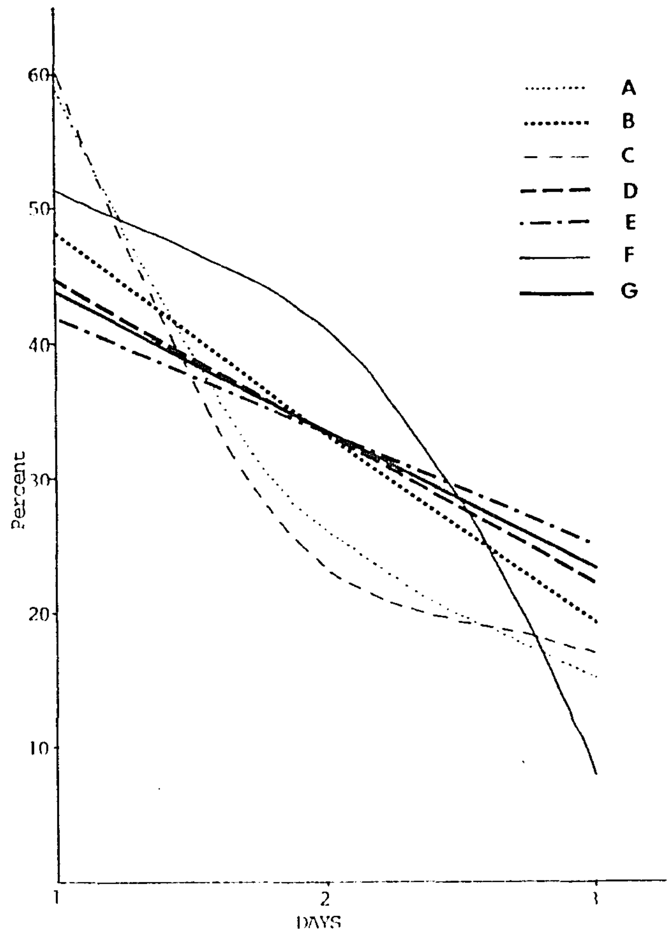

Figure 12. Rate of Capture of New Individuals for Seven Species at the Silverbell Site: A. *Perognathus intermedius*; B. Average for all species; C. *Dipodomys merriami*; D. *Perognathus penicillatus*; E. *Perognathus amplus*; F. *Neotoma albigula*; G. *Perognathus baileyi*.

over a years time. It would be expected that similar principles applied to the heteromyids of this study.

Home range values used here were primarily arrived at by limited sampling on a live trap grid on the Santa Rita Experimental Range. Additional information gleened from the literature was also incorporated to arrive at an "average home range." As long as this use of home range values is consistent and comparison made among the sites within the study, it should reflect general trends and relative densities for those animals dealt in this study.

O'Farrell, Kaufman, and Lundahl (1977) described the use of assessment lines with parallel lines. O'Farrell and Austin (1978) compared different trapping configurations with this assessment line technique for density estimates. It would seem that utilization of assessment lines with parallel lines would alleviate the problem of changing home ranges.

The supposition that home ranges may change dramatically over time needs to be explored in greater depth. It may well prove not to be the case for this study regardless how great the fluctuation of environmental parameters. Future analysis of the ten years of data on the SRER site should shed some light on this subject.

May-September Sampling

Although a study utilizing a monthly trapping regime would be more accurate and give greater insight into population dynamics, a bimodal yearly sample in this particular area should give adequate results. Due to the curtailment of above ground activity by some of the smaller nocturnal rodents, sampling through the winter months does not give an accurate indication of species diversity and population size.

Monthly trapping at the SRER indicated that *Perognathus amplus* and *P. penicillatus* emerge in late March after being inactive above ground through most of the winter (Figure 13). Males precede the females by a week or two and may have scrotal enlargement at that time. Females are frequently pregnant by mid-April, with young appearing above ground by mid-May in many cases. Hoffmeister (1964) also noted a high incidence of males in spring populations of smaller *Perognathus* species.

Other investigators have found that smaller *Perognathus* species become inactive in winter while *Dipodomys* remains active (French, Maza and Aschwander, 1966; Kenegy, 1973; Reichman and Van deGaaff, 1973, and O'Farrell, 1974).

An early May sampling would be indicative of the population survivalship through the winter. The population is sampled shortly after the individuals emerge from winter surface inactivity and prior to an influx of newborn young.

The monthly data at the SRER site show population numbers generally reach a peak in late August and early September (Figure 13). Overall rodent numbers then rapidly decline to a low in January.

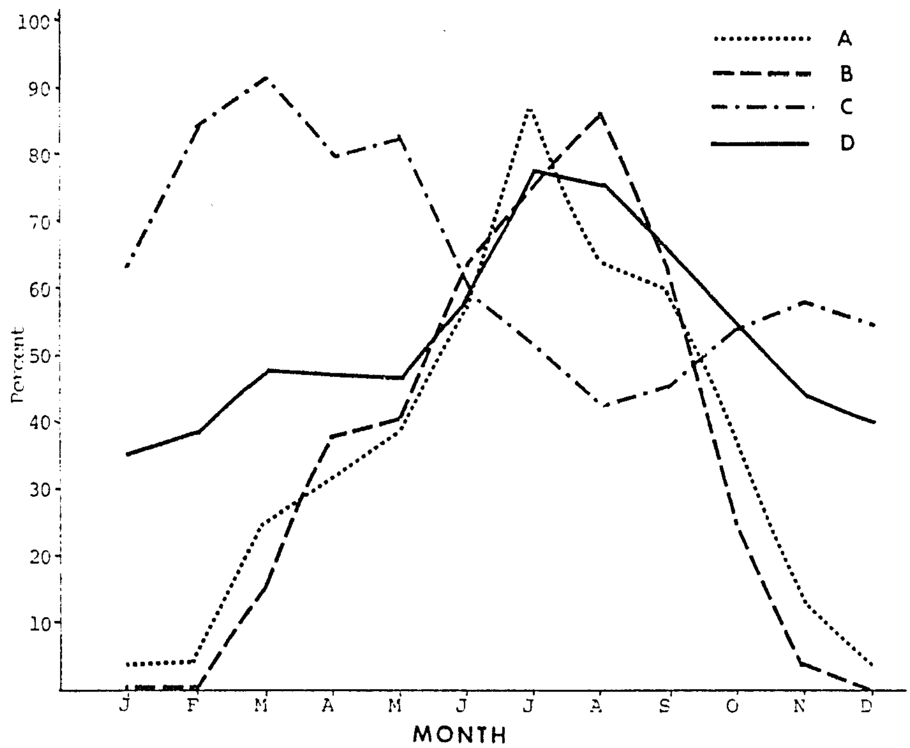

Figure 13. Annual Activity Pattern for Four Species of Heteromyids: A. Perognathus penicillatus; B. Perognathus amplus; C. Dipodomys merriami; D. Perognathus baileyi.

The early September sampling should be reflective of breeding success during the warmer months of the year. Although _P. amplus_ and _P. penicillatus_ follow a high summer-low winter annual cycle above ground, other heteromyid activity above ground is not so well defined. Both _P. baileyi_ and _D. merriami_ are found above ground to varying degrees throughout the year.

The cricetid, _Neotoma albigula_ seems to peak in summer and slowly decline in winter. It is active throughout the winter. The winter decline in numbers may be more to predation of young than to abatement of activity.

The desert _N. albigula_ constructs an above ground den of sticks, cactus segments, and debris. This affords protection from predators and the elements. Until a juvenile pack rat builds its own nest or occupies an abandoned one, it is very susceptible to predation, once it leaves its mother's den. I have noticed on many occasions the difference in behavior in a released juvenile and an adult. The adult generally makes a rush to its den while a juvenile, on many occasions, will run to the nearest object and huddles at its base, very much exposed.

Even though certain nocturnal species may not peak during August-early September, the rodent population, as a whole, does. Consideration must also be given to the fact that this type of sampling regime (May and September) reduces greatly the influence of human presence- bait, trails, handling, soil compaction, etc.- while at the same time acquiring a great amount of data.

Three Day Trapping Periods

In the course of sampling a population, several considerations arise- 1. method, 2. practicality, 3. time, and 4. inherent effect on the population. These factors determine the sample area size, method of capture, frequency of sampling, and duration of study. The optimum situation would be a minimal imput of effort for the maximum return of data. Restricted funding and manpower often necessitate this approach.

May and early September sampling fits into this consideration. A variety of population parameters are arrived at with minimal expenditure of effort. In addition a twice daily, three-day trapping period would maximize return for input. This scheme is utilized at both SRER and Silverbell in this study.

A night and early morning run would increase the intensity of a three-day sampling period. It also should provide insight into the nocturnal activity patterns of individuals and species in general. A three day trapping period, with dual checks per night, seems to adequately capture most individuals in the area. Figure 12 shows that the rate of new captures declines rapidly from the first night to the third. Of all the individuals captured for the three-night period, approximately 20% are captured on the last night.

This rate is fairly constant for the *Perognathus* species. *Dipodomys merriami* and *Neotoma albigula* have a high rate of capture on the first two nights, but greatly reduced on the third night. A fourth night of trapping would probably give a more accurate indication of total numbers present. If the rate of new captures were consistent through time, it would indicate that approximately 10% of the total catch would occur on the fourth night. After this period of time, the effort would be redundant.

Toe clipping does not seem to deter the animals. I have noted, many times, individuals clipped in the evening were again captured by early morning.

CHAPTER 7

RODENT RESPONSE

General

The heteromyid response to extensive desert blooms was rapid and wide ranging (Figure 14, Appendix A, B, and C). Increase in the small heteromyid such as *Perognathus amplus* and *P. penicillatus* was, in some cases, 12 fold within a period of four months. This becomes even more extraordinary when one considers the fact that they are inactive above ground until early spring.

The larger heteromyid species reached peak population numbers at a later date then the smaller ones. This may be due, in part, to a slower breeding strategy.

All three research sites showed tremendous heteromyid biomass increases (Figure 15). The maximum biomass attained was very similar among the sites and between the two peak periods of 1974 and 1979. Although the composition and circumstances of the rainfall and desert bloom were different for the two "wet" periods, the peak heteromyid biomass and numbers were essentially the same even though their relative species composition was different.

This leads me to believe that the carrying capacity of the system was closely approached. Whether this is due to resource limitations or to a density dependent mechanism will be explored later in this report.

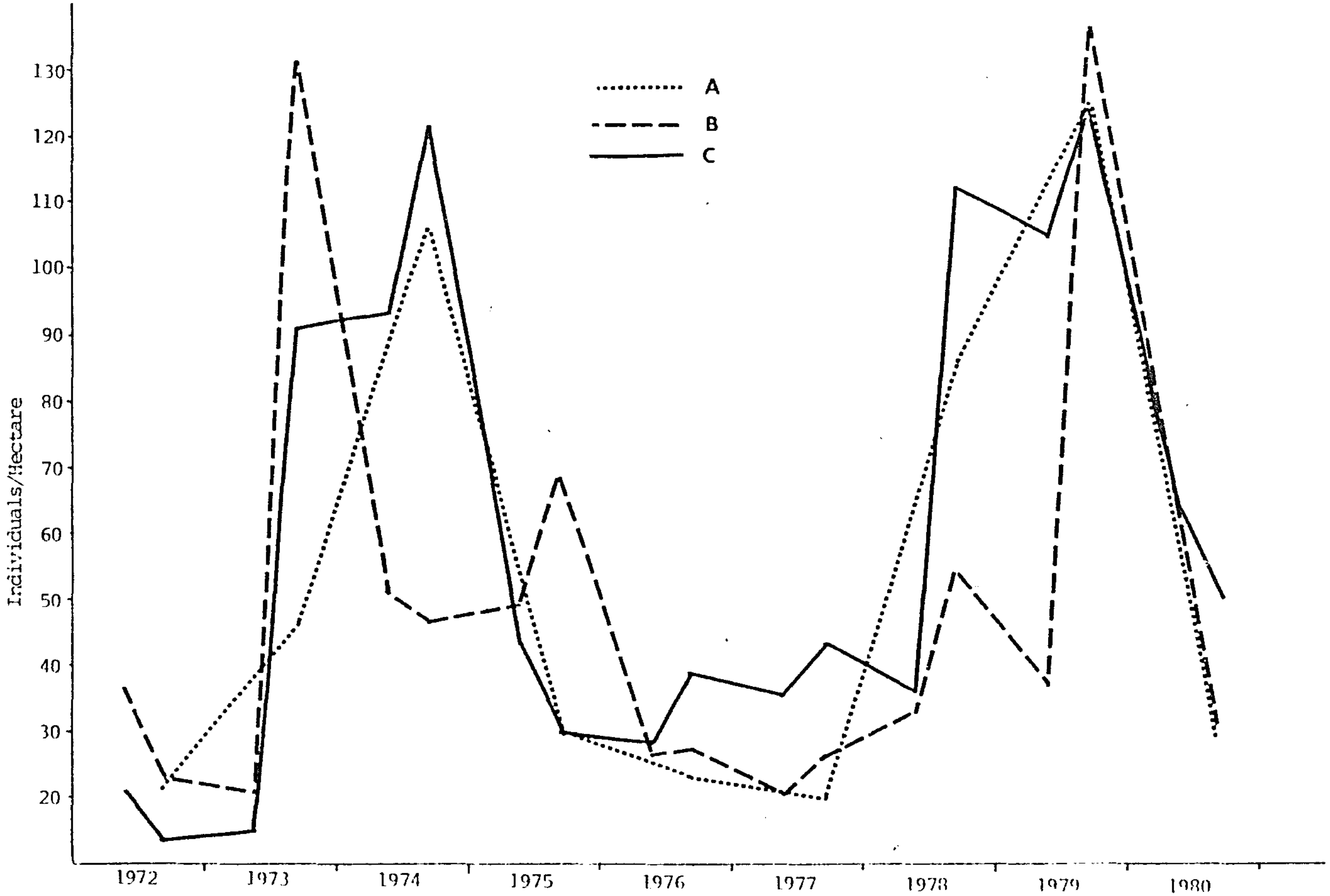

Figure 14. Heteromyid Numbers on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

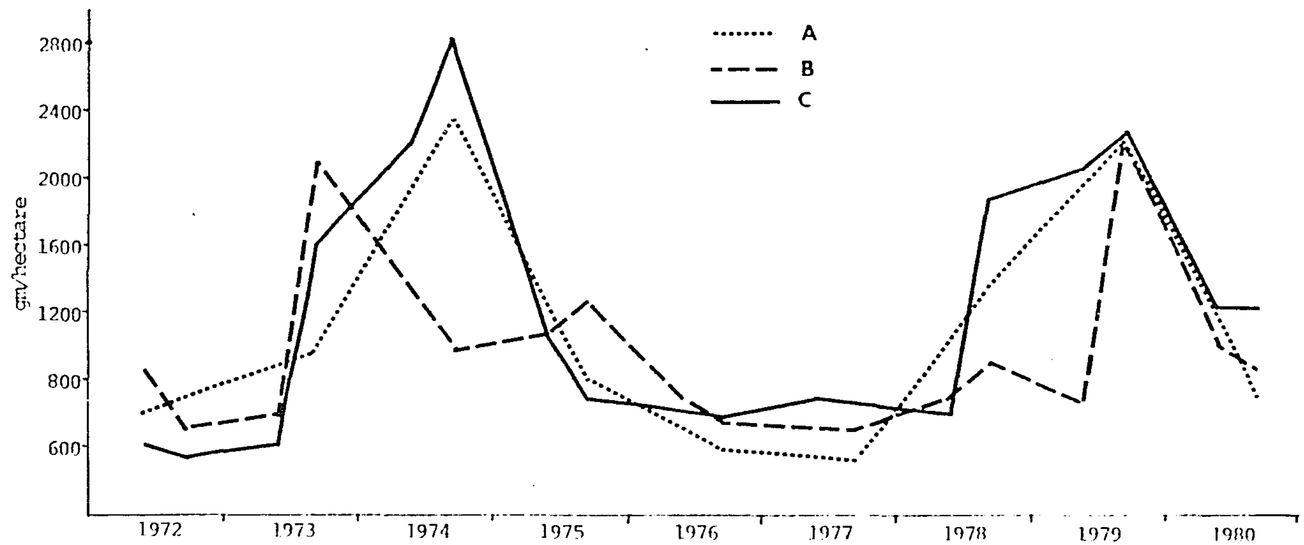

Figure 15. Heteromyid Biomass on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

The pack rat, _N. albigula_, increased slightly in all areas after the first desert bloom. It was not until after the sequence of events during the second wet period did _N. albigula_ increase dramatically in numbers (Figure 16, Appendix D).

Other cricetids also increased in numbers after the wet periods. _Sigmodon arizonae_, _Onychomys torridus_, and _Peromyscus_ all increased in numbers at Silverbell and Red Hill. The SRER site also saw an appearance of _S. arizonae_ where normally none occur in any number. _Onychomys torridus_ and _Peromyscus_, although present in all years at SRER, did increase in numbers following the wet periods.

Perognathus amplus

The base population of 105 g/hectare in spring of 1973 increased four-fold to 425 g/hectare by September of that same year (Figure 17). A steady decrease ensued the following year until by fall, the population biomass had dropped to 110 g/hectare. In the fall of 1975, only 12 g/hectare of _P. amplus_ biomass was recorded. The population increased from that point to maintain a base biomass of approximately 200 g/hectare through late 1976, 1977, and early 1978.

The summer of 1978 saw the same rapid increase in biomass that occurred in 1973. Although only 632 g/hectare was recorded in early September of 1978, I believe the 795 g/hectare recorded in May 1979 is more indicative of the level _P. amplus_ production reached after summer breeding of 1978. It may be that production of young may have continued into late September or possibly the animals went underground for the

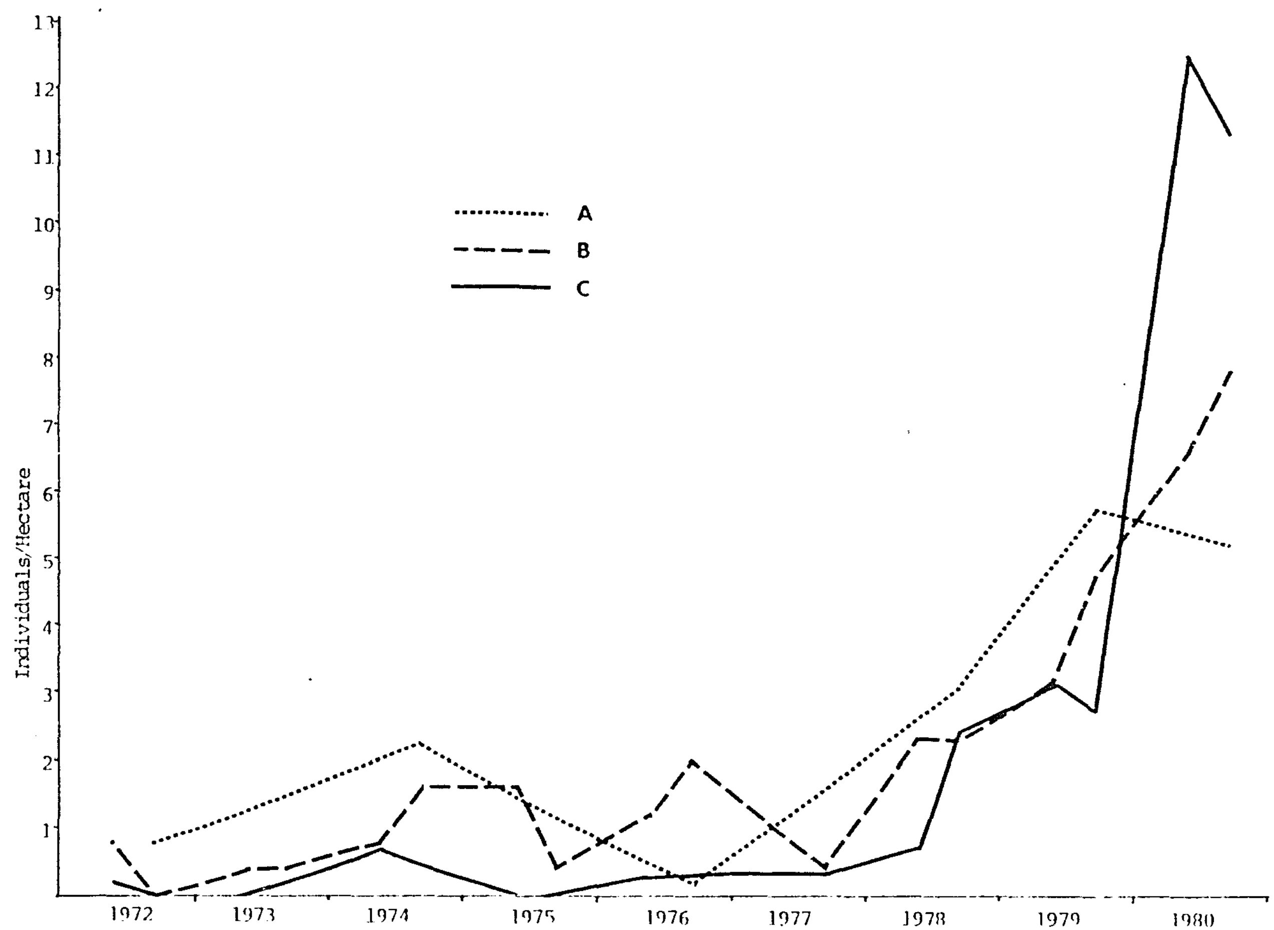

Figure 16. Neotoma albigula Numbers on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

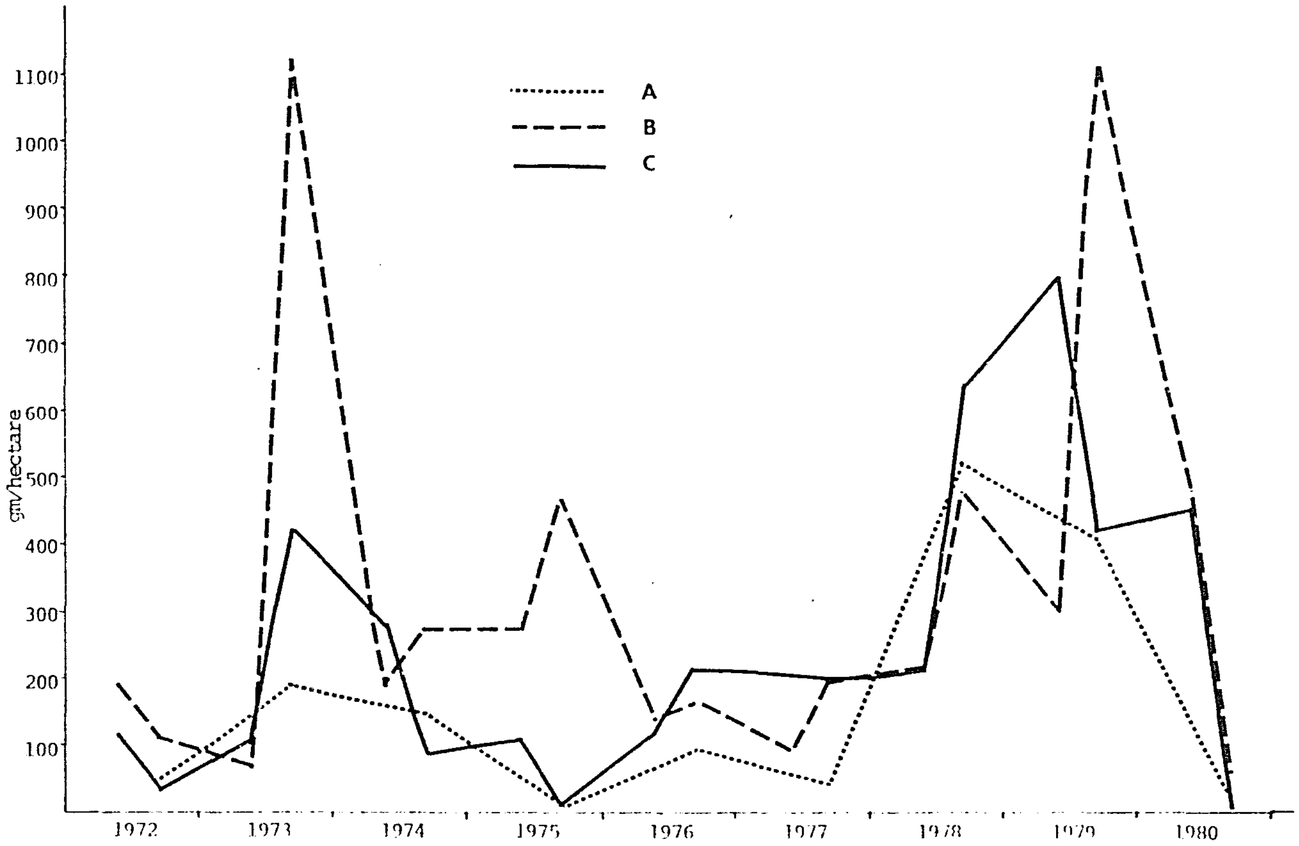

Figure 17. Perognathus amplus Biomass on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

winter earlier that year. Nevertheless, all the individuals of early spring, 1979 most probably came from the previous year.

A rapid decline occurred from spring of 1979 throughout the summer. The population maintained through the winter of 1979-80 with approximately the same biomass present in May of 1980 as was the previous fall. The population continued to decline throughout the summer of 1980.

The response of *P. amplus* at Red Hill essentially followed the same pattern as at Silverbell. This is not surprising due to the similarity of habitat.

From a base of 48 g/hectare in September of 1972, a peak of 187 g/hectare was reached by early September, 1973. A steady decline ensued until the population reached a low in late summer of 1975 as did the population at Silverbell. A biomass of between 50 g and 100 g/hectare was maintained until 1978 when the population rapidly increased to reach a biomass peak of 519 g/hectare. The population steadily decreased from that point, until it reached an all time low of only 3 g/hectare.

The immediate response at SRER in 1973 was the same as in the other two sites but in this case a much greater increase in biomass occurred- from a base of 72 g/hectare to 1120 g/hectare. A 15-fold increase in a matter of four months! The decrease that followed in the next year was just as phenomenal with the population dropping to 189 g/hectare by May of 1974.

The biomass stabilized at between 250 and 300 g/hectare until late summer of 1975 where again there was an increase in biomass. This time it only increased to approximately a third of the 1973 peak. The decline that occurred the following spring was rapid. A base of approximately 150 g/hectare was then maintained for several seasons.

After the rain phenomenon of 1977-78, the population followed essentially the same pattern as in 1973. A rapid increase was followed by a rapid decline. A biomass peak of 1109 g/hectare was reached, which was virtually the same as that of 1973.

It must be noted, though, that there was a drastic difference from the 1973 increase. Whereas, the 1973 increase occurred at the same time as the Silverbell and Red Hill _P. amplus_ populations, during the second phenomenon the SRER population flourished a year later than did the populations of the two other sites.

Perognathus penicillatus

The _P. penicillatus_ population at the Silverbell site showed a rapid increase similar to the _P. amplus_ population (Figure 18). From a base biomass of 40 g/hectare in May 1973, the population swelled to 739 g/hectare by September of that same year. Whereas, _P. amplus_ then rapidly decreased, _P. penicillatus_ continued to increase throughout the following year, reaching a peak of 1187 g/hectare in early September of 1974.

By May of 1975 the population was down to 256 g/hectare and continued to decrease to a low of 157 g/hectare by September of that year. The population remained at this low level throughout 1976 and 1977.

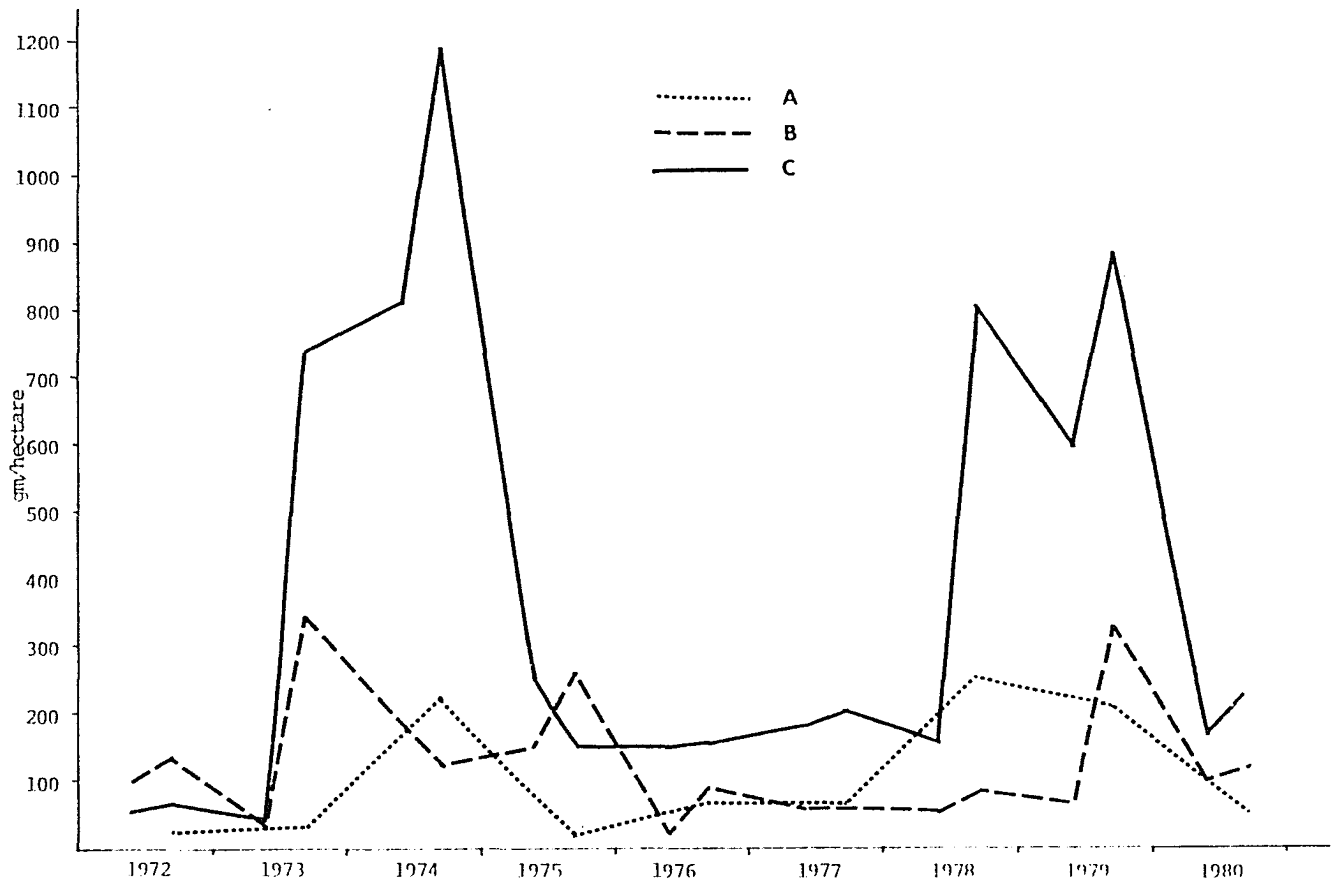

Figure 18. Perognathus penicillatus Biomass on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

In 1978 a pattern very similar to 1973 occurred. The *P. penicillatus* population at this time rapidly increased to 803 g/hectare by early September. After a slight decrease in spring of 1979, the population increased to a peak of 880 g/hectare in late summer. By May 1980 the population was down to pre-phenomenon levels with 175 g/hectare. Very little production occurred in 1980 with the population increasing to 227 g/hectare by early September.

At Red Hill the pattern of fluctuation in the population of *P. penicillatus* was very similar to that of Silverbell but in decreased numbers. Peaks of 222 and 252 g/hectare were reached in September 1974 and 1978, respectively. The base biomass for the other years was generally around 50 g/hectare.

At the SRER site the *P. penicillatus* population increased rapidly in 1973 from 33 g/hectare in May to a peak of 342 g/hectare by early September. A just as rapid decrease followed in 1974.

During the second rain phenomenon, the *P. penicillatus* showed the same strategy as did the *P. amplus* with the increase occurring in 1979 and not in 1978 as at the other two sites. In 1979, the *P. penicillatus* increased from 66 g/hectare in May to 326 g/hectare in September. A rapid decrease occurred the following year.

Perognathus intermedius

Of the three sites, *P. intermedius* is found only on Red Hill and Silverbell. Only on the Red Hill site does this species occur in any great numbers; comprising, on occasion, up to 17.6% of the heteromyid biomass. At the Silverbell site it never reached levels over 4% of the heteromyid biomass, with much of the time less than 1%.

In general, *P. intermedius* population fluctuations followed the same pattern as did the *P. penicillatus* populations of Silverbell and Red Hill. This is not surprising since it most closely resembles *P. penicillatus*.

At Silverbell, peaks were attained in 1974 with 19 g/hectare and again in 1979 with 49 g/hectare. The population at Red Hill also showed this doubling of biomass peaks from one rain period to the other. in 1974, the Red Hill *P. intermedius* biomass reached a peak of 120 g/hectare, while in 1979, 215 g/hectare was reached. In both instances a rapid decrease followed.

Perognathus baileyi

Following the lead of the other *Perognathus* species, *P. baileyi* also responded dramatically to the rainfall phenomena. The summer of 1973 saw an increase from 57 g/hectare in May to 182 g/hectare by September on the Silverbell site. In the following year, even a greater increase occurred, reaching a peak of 940 g/hectare by early September. As with the other rodents, there was a rapid decline in 1975.

Perognathus baileyi followed the same format in 1978 with a nominal increase of 79 g/hectare in spring to 206 g/hectare by late summer, virtually identical rates of increase to that of 1973. In 1979, the biomass increased to a peak of 666 g/hectare by early September. There was a great drop in biomass through the winter and early spring with only 277 g/hectare recorded in May, 1980, but by next

September the population had regained much of the loss with 616 g/ hectare registered (Figure 19).

At the Red Hill site the increases and decreases were even more pronounced. There was an initial two-fold increase from September of 1972 to September of 1973. Through 1974 there occurred a tremendous increase in P. baileyi biomass, reaching 1640 g/hectare in September of that year. This is over six times the pre-rainfall phenomenon population.

In 1975 the biomass fell to 379 g/hectare, very close to the 1972 level. By September of 1977, the P. baileyi biomass at Red Hill reached an all time low of 59 g/hectare.

Again, as with the other Perognathus, another population explosion occurred in 1978 which continued into 1979, reaching a peak in that year of 1247 g/hectare. The population biomass declined to 432 g/hectare by September of 1980. It is interesting to note that the 1979 peak was substantially lower than that of 1974.

At the SRER site, P. baileyi had peaks in 1973, 1975, and 1979 with biomasses of 328, 315, and 541 g/hectare, respectively. This is the same pattern as seen for the other species of Perognathus at the SRER.

The P. baileyi pattern is quite different at the SRER compared to the other sites- primarily, the timing of the first peak. At the SRER, the peak occurred in 1973 whereas in the others, it occurred in 1974. The second population explosion saw peak biomasses of P. baileyi occurring in 1979 in all three areas.

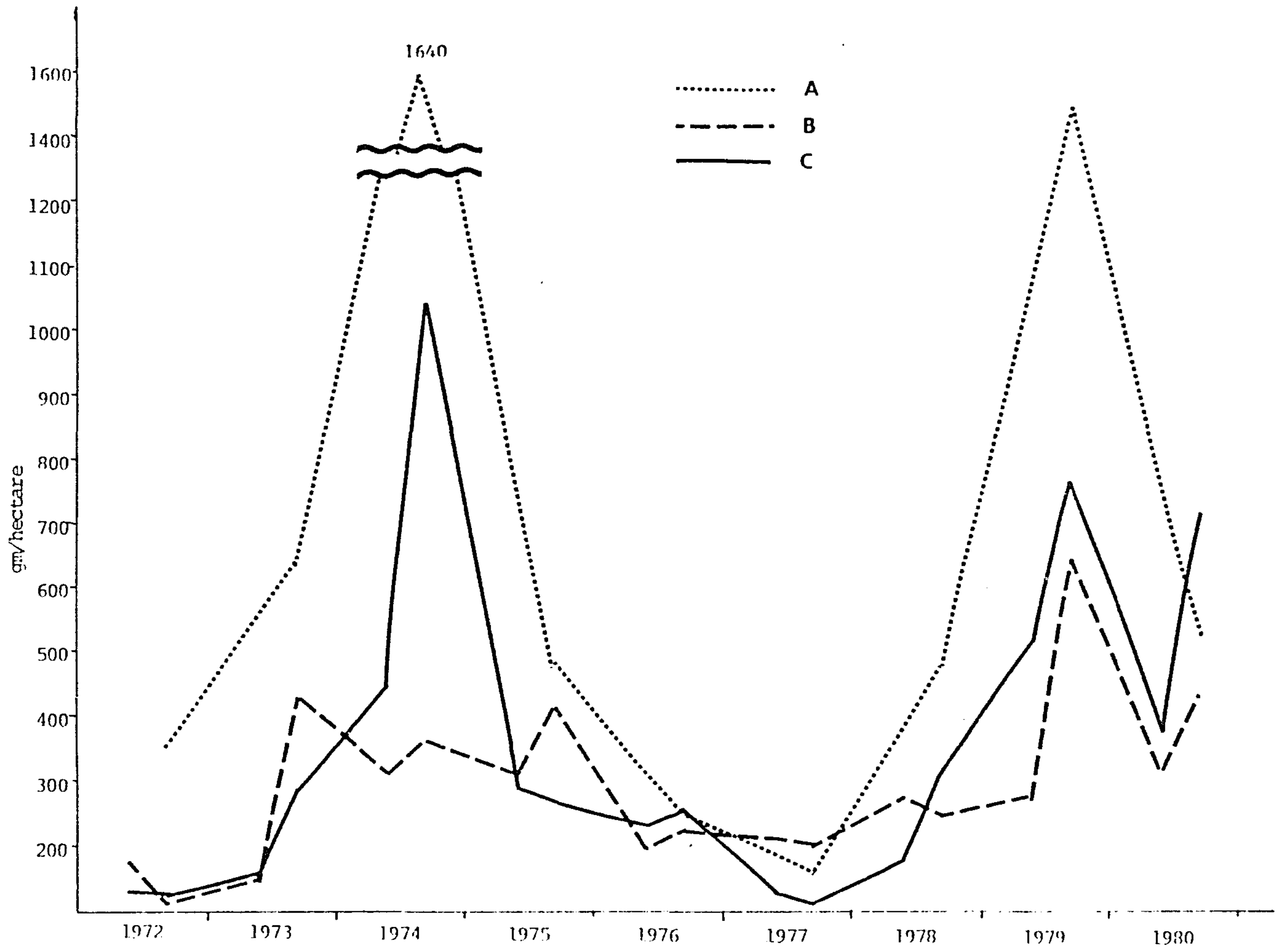

Figure 19. Perognathus baileyi Biomass on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

Dipodomys merriami

At the Silverbell site, D. merriami showed the same stretegy as did P. baileyi in the area; a gradual increase in 1973 with a much more rapid increase through that winter, reaching a peak in 1974 (Figure 20). The difference was in the time of year that the peak was reached. Where P. baileyi reached its peak in late summer, D. merriami reached it in May of the same year. A high of 778 g/hectare was reached with the population decreasing gradually from that point. The decrease was not near as rapid as with the other heteromyids.

There was only a gradual increase in biomass following the second rainfall phenomenon with a high of only 347 g/hectare recorded in September of 1980. This is less than half of the 1974 high.

The other two sites saw a very similar pattern for D. merriami. At Red Hill, a peak of 399 g/hectare was reached in 1975 and only 162 g/hectare in 1980. The SRER site registered a high of 720 g/hectare in May 1974, and 422 g/hectare in May of 1975. In the second period, only 410g/hectare was reached and this was in May 1980. In all three study sites, the biomass of D. merriami following the second rainfall phonomenon was approximately one half of that of the first.

Neotoma albigula

All three research sites had very similar sized populations of N. albigula. The response to the first wet period was a slight increase in biomass at all three sites. Silverbell reached a high of only 19 g/hectare in 1974. The pre-phenomenon biomass was less than 1g/hectare (Figure 21).

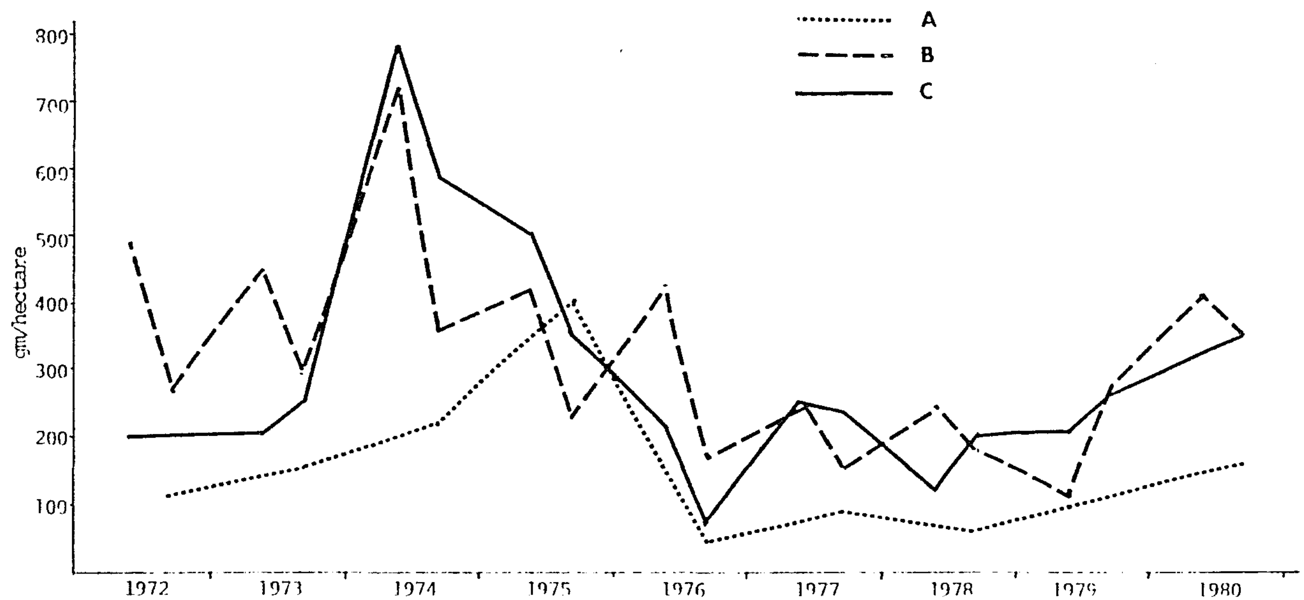

Figure 20. Dipodomys merriami Biomass on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

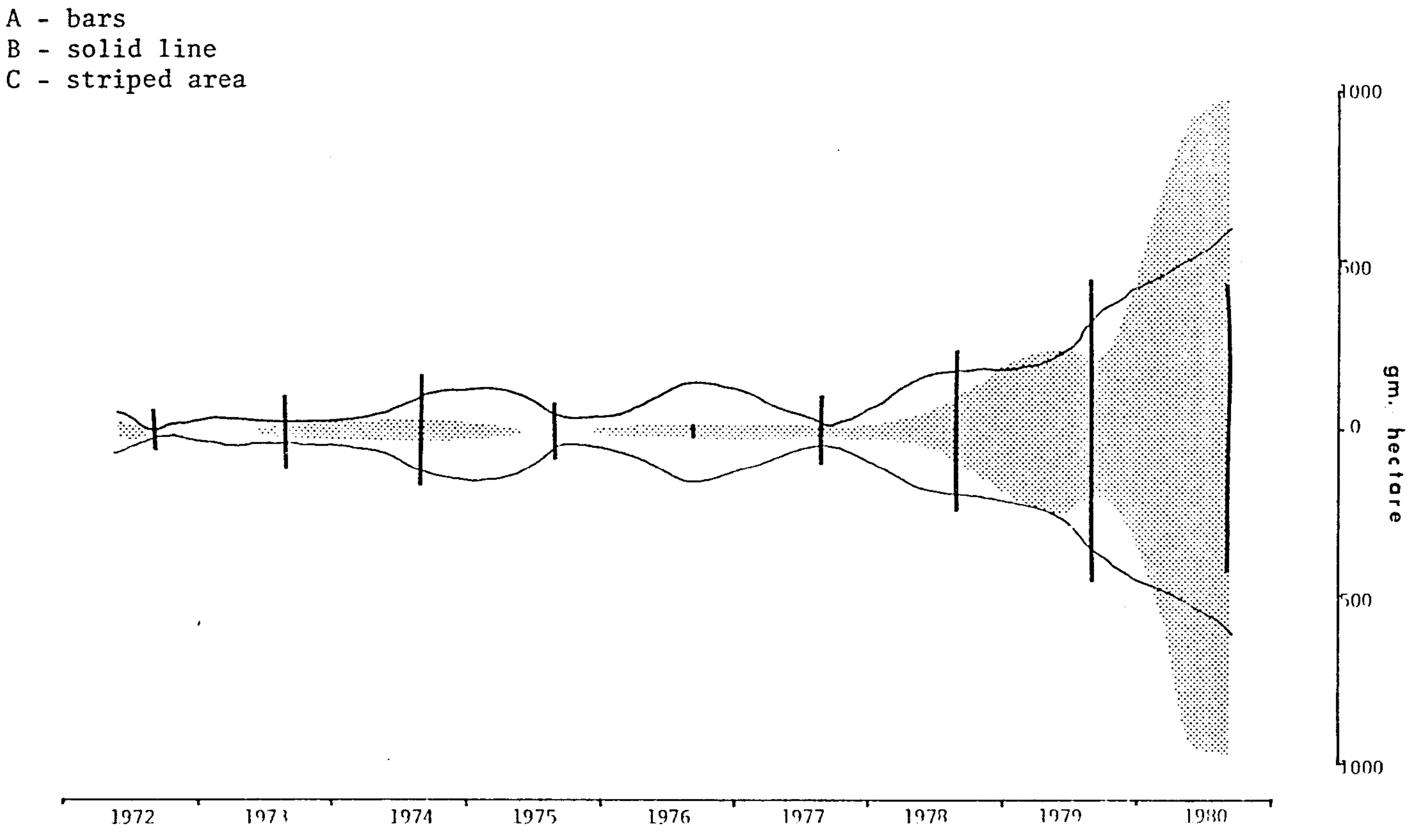

Figure 21. Neotoma albigula Biomass on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

At Red Hill, a peak of 332 g/hectare was reached in 1974, up from around 200 g/hectare that spring. The SRER site registered 238 g/hectare in September of 1974, up from only 59 g/hectare the previous year.

The combination of weather circumstances in 1977-78 had a profound impact on the *Neotoma* populations in all areas. At the Silverbell site, *N. albigula* biomass took a tremendous leap to 1947 g/hectare by September of 1980. The other two sites had peaks of 874 g/hectare (Red Hill) and 1190 g/hectare (SRER). It is interesting to note that Silverbell, with the highest biomass at this time, has the lowest biomass of *N. albigula* among the three areas for most of the other years.

The reason for the phenomenal increase in *N. albigula* may be attributed to the combination of high fall and early spring rains followed by a tremendous rainfall in 1978. This did not happen in 1972-73. At that time, the high annual rainfall occurred in 1972 followed by high autumnal-early spring rains. Although the annual rainfall of 1972 was abundant, it did not approach that of 1978.

Neotoma albigula consumes much more of the woody and succulent plants than do the heteromyids. In addition, these plants are utilized in den construction. Higher densities of these plants would be conducive for pack rat inhabitation (Vorhies and Taylor, 1940; Brown, Lieberman, and Dengler, 1972; and Olsen, 1973).

A combination of high ephemeral production followed by exceptional perennial production would maximize the benefits for *N. albigula* in food material, den sites, and construction materials.

CHAPTER 8

DISCUSSION

Breeding and Triggering Mechanism

It is apparent then, that good herbaceous growth and seed production stimulates the population densities of nocturnal rodents. Initially, for the heteromyids, as well as the cricitids, it seems that population levels attained is dictated primarily by breeding potential rather than survivorship. Conley, Nichols, and Tipton (1976) also noted that survival increased while natality decreased with an increase of effective precipitation.

Predators such as raptors, snakes, and carnivorous mammals, would remove part of the population but since their population size is consigned to a much reduced population, their efforts should be minimal at this time.

Due to more than adequate food supply and a relatively low density of predators, survivorship should be extremely high in the offspring. The number of offspring per litter and number of litters per breeding season would determine the rate and degree of population increase.

With *P. amplus*, the males emerge in March followed by the females a couple of weeks later. Young of the year, generally, do not appear above ground until May. Yet the population may closely follow an exponential growth curve in a very short period of time- May through

August (Figure 22). This suggests that females may have multiple litters through the summer and that young females of the first litters are capable of breeding the same summer. French et al. (1974) found a positive correlation between increasing litter size and increasing breeding rates, also that under most favorable conditions, young of the year and offspring from the first breeding period, also reproduced.

Figure 23 shows the theoretical breeding potential of *P. amplus* and *P. penicillatus*, utilizing these arguments. This scheme, coupled with low mortality due to an abundance of food and low predators, make it relatively easy for these rodents to reach the densities attained in this study.

The larger heteromyid species reach peak population numbers at a later date than the smaller ones. This is due, in part, to a slower breeding strategy. For *D. merriami*, the mean litter size is slightly over two, which is approximately half of that for smaller rodents (Alcorn, 1941; Chew, 1958; Chew and Butterworth, 1959; Reynolds, 1960; Eisenberg, 1963; and Bradley and Mauer, 1971). Although *D. merriami* may have two reproductive peaks per year, these are usually at different times of the year (Reynolds, 1960; Van De Graaff, 1975). I have found no indication of multiple litters occurring back to back.

The mechanism necessary for the rapid acceleration of reproductive output must be fairly immediate and affecting the population on a large scale. In normal years some reproduction generally occurred, but it was restricted and apparently limited to a very small percentage of the total females. From monthly data collected at the SRER site,

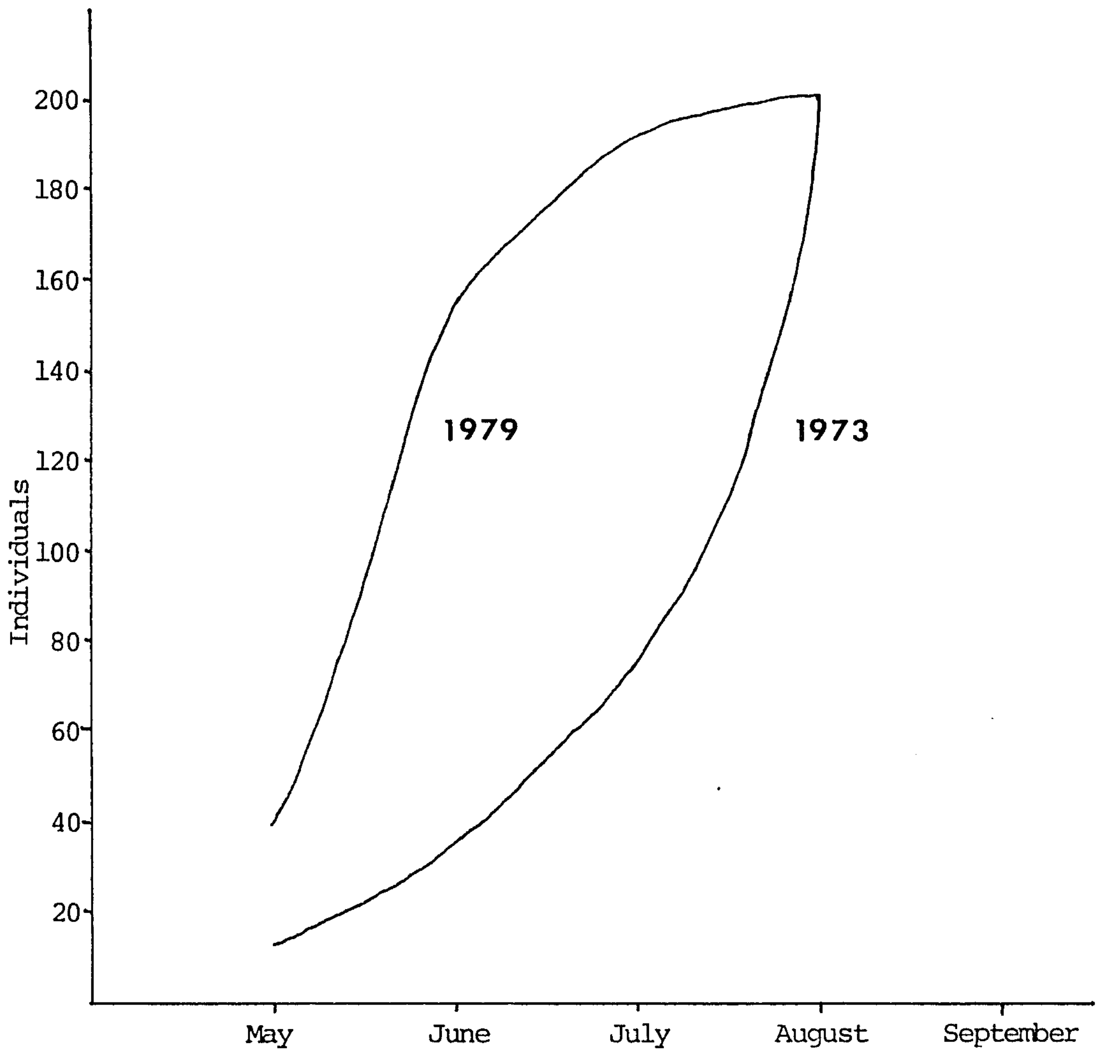

Figure 22. Population Increase of *Perognathus amplus* at the Santa Rita Experimental Range for 1973 and 1979.

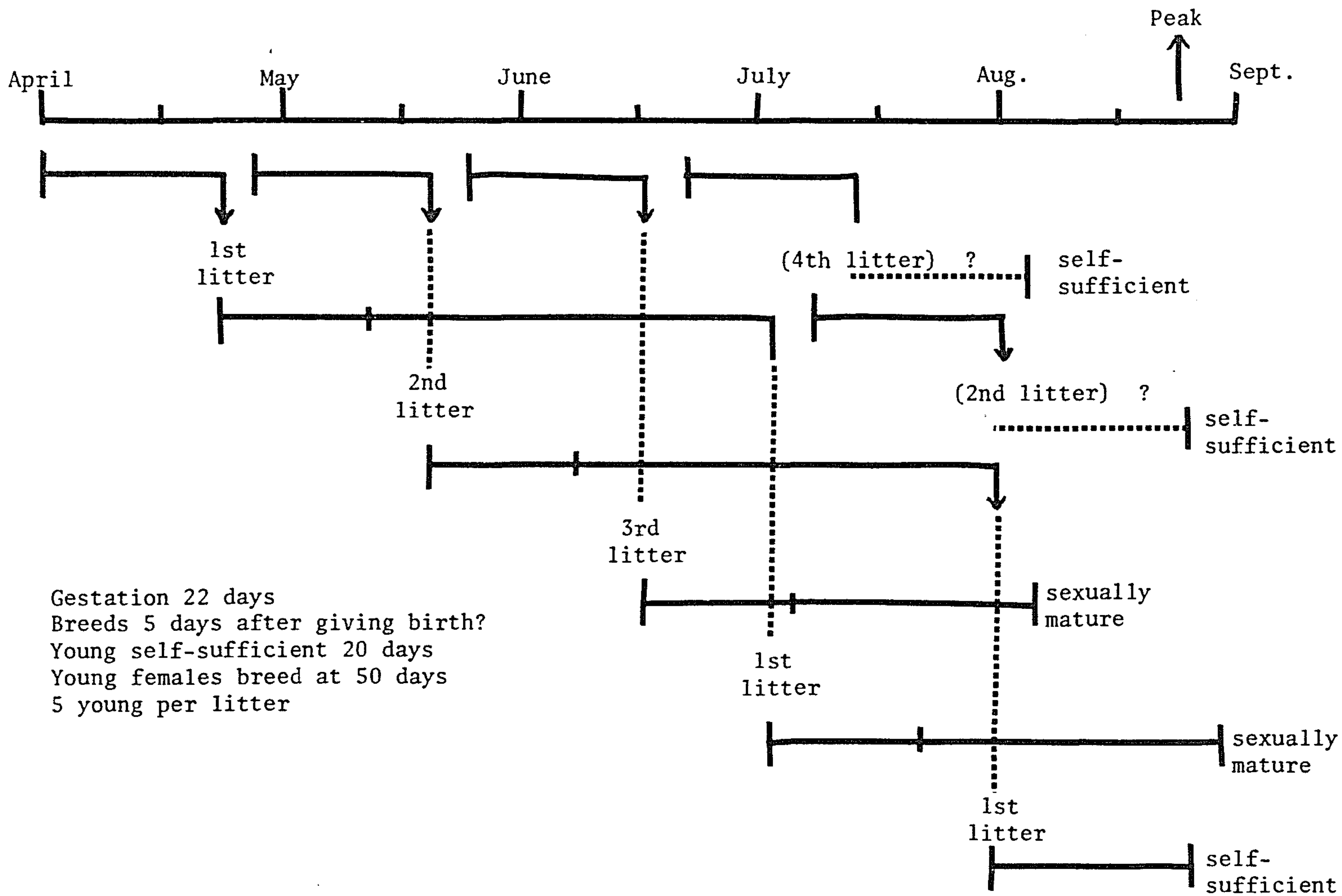

Figure 23. Theoretical Maximal Production of Young for Perognathus amplus and Perognathus penicillatus.

it appears that males generally are reproductively active essentially every year during the same period of time. It seems that the females determine whether breeding occurs in any particular year.

During the drier years, breeding itself may be restricted or other factors prevent a substantial increase in numbers such as reabsorption of embryos, death of young due to inadequate lactation, or low survivorship of young in nest or shortly after weaning due to inadequate food supply. For a female to continue producing young when conditions are not favorable would be a tremendous output of energy for very little genetic return.

During "wet" periods any restrictions or inhibitors of reproduction are apparently non-existent, if in fact there are "inhibitors." It may well be that it is more of a lack of "stimuli" during drier years that prevents breeding.

Many investigators have suggested that rodent reproduction may be triggered by a profusion of green plant material in the environment (Reynolds, 1960; Beatley, 1969; Bradley and Mauer, 1973; and Smith, Gentry, and Binder, 1974). Van De Graaf and Balda (1973) compared an area at Silverbell having good growth of winter annuals- *Plantago*, *Pectocarya*, *Allionia*, *Erodium*, and *Tridens*, with an area near Phoenix that was depauperate of these plants. They found 95% of *D. merriami* males and 92% of the females were sexually active. In contrast, the Phoenix site had only 14% of the males sexually active and none of the females. The Silverbell area received nearly three times more rain then did the Phoenix site, with 83% of it occurring in the last five months of 1971.

Hungerford (1960) studying Gambel quail populations, found that large quantities of vitamin A and carotene were needed for normal hormone production. It appeared that these provided the stimuli necessary to accelerate reproduction. He found that natural occurring populations received these substances from green plant matter.

Something very similar may be true for the desert rodents. It must be noted that for some of the rodent populations to reach the numbers they do by August of the same year, reproduction would have to be stimulated on a massive scale prior to the time that large numbers of seeds are dropped by the ephemerals.

Indications are that the initial reproductive surge is not so much a function of abundant food resource as it is a possible prolific consumption of green plant material, possibly of flower parts also, that stimulates sex hormone production.

Bradely and Mauer (1971) found that _D. merriami_ may have up to 36% of its diet in green plant matter, mostly from February to May and again in August. I have also observed green plant matter in the cheek pouches of heteromyids during May, August, and September. Two cases of _D. merriami_ eating prickly pear fruit, as noted by their red-stained chin and chest, were observed in early fall. This, though, may have been due to the consumption of seeds from freshly fallen fruit rather than eating of the pulp itself.

In all probability, propagation is held in check by a number of restraints during the drier non-productive years when seed resources and green vegetation are low. These restraints may be related to body metabolism such as reduced body fat, low amounts of essential vitamins and minerals necessary for production of reproductive hormones, and lack of added environmental free water possibly needed for milk production, in addition to shortage of energy supplies via seeds.

Adequate greenery coupled with ample seed resources could provide the criteria needed for accelerated propagation and survivorship for a period of time.

Population Growth Curve

Of interest and possibly adding to the evidence for density dependency during peak population is the population growth curve for *P. amplus* at the SRER site. Here the population of *P. amplus* reached the same densities during both peak periods.

In May 1973, the base population for *P. amplus* numbered six individuals/hectare. A population high of 95 ind./hectare was reached by August of that same year (Figure 24). In 1979, from a base of 25 ind./hectare, the peak population was essentially reached by July of that same year (see Figure 22). Once the density of 95 ind./hectare was approached, any increase all but ceased.

The question arises as to why, considering it was a bonus plant production year and there was the presence of a large *P. amplus* breeding base, did not the population of 1979 surpass that of 1973? The initial rate of increase was the same for both periods.

It could be argued, that in 1973, the peak density of 95 ind./hectare was not surpassed for a number of reasons: 1) the breeding season was coming to a close (approach of cooler weather) therefore energies would have to be channelled into seed gathering and storage;

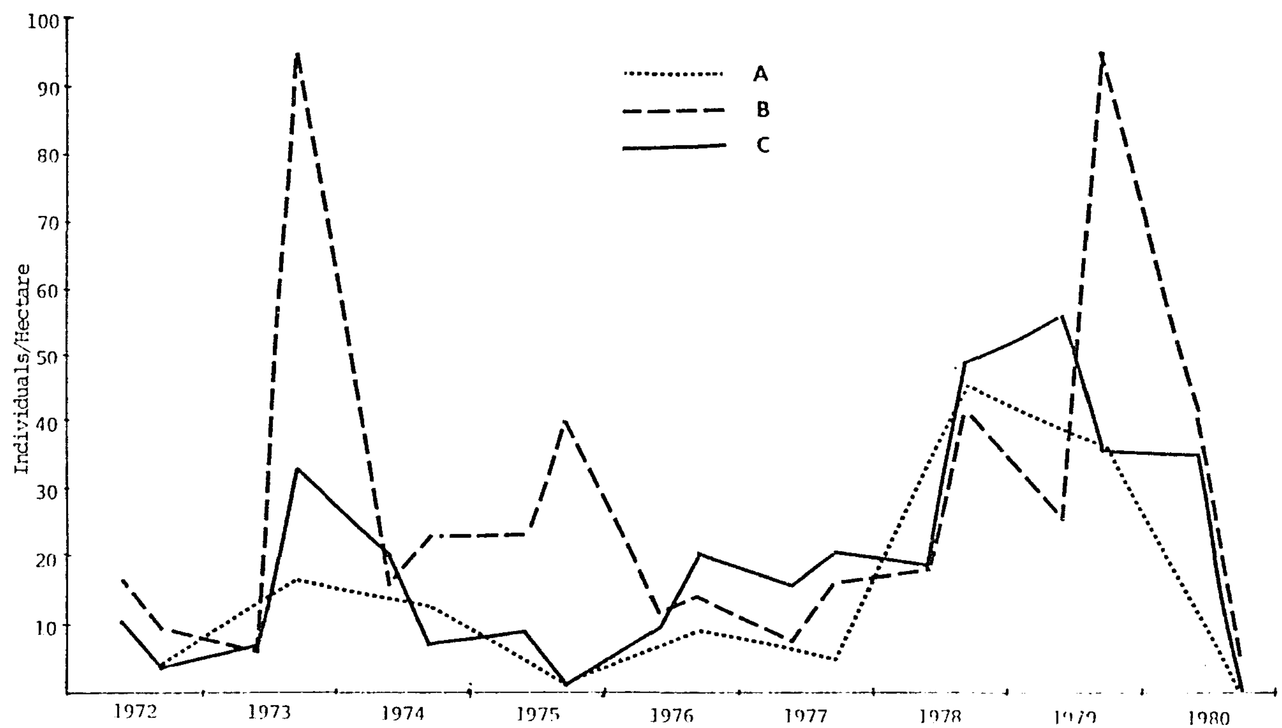

Figure 24. Perognathus amplus Densities on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.

2) easily available food resources became diminished after a summer of foraging by an assortment of seed predators; 3) a predetermined density of plants can only produce a finite number of seeds- once that is removed it takes infinitely more energy to find the seeds that were overlooked due to burial, etc.

Each of these factors, as concerning both peak periods, should be examined. First, if only the 1973 peak was considered, argument #1 could possibly be valid. Perognathus amplus do curtail their above ground activity in fall and winter (see Figure 13). Seed reserves would have to be stored by late summer if survival through the winter is to be enhanced. This is especially true for the young produced in late summer litters. They have very little time to cache seeds before the onslaught of colder weather.

In 1979 the same principle should apply. Although there was ample time to continue producing young, population size essentially stabilized by the end of July, one full month earlier than in 1973. It would seem that population growth should continue throughout late July and early August as it did in 1973, if only the need for storage of seeds is considered.

The same is true of argument #2. It is not likely that food resources diminished more rapidly in 1979 than they did in 1973. The densities of seed predators were essentially the same for the two time periods. Bonus years for plant production were 1978-79. During the second wet period the conditions seemed to be even more favorable for heteromyid production since the total biomass attained was higher than in 1973. This would point to a greater production of food resources.

In addition, the second good year of rains in 1979 would restock, to some extent, the depleted seed resource of 1978. This along with the great production of 1978 would point to food resources being in greater quantities in 1978-79. Surely, by all indications, they would be no less than those of 1973-74.

There is no doubt that there is an ultimate level of seeds that may be produced by a finite number of plants (argument #3). It must be recognized, though, that in any grouping of plants, there are different strategies involved in production. There are winter annuals, spring annuals, late summer annuals, perennials that bloom in spring, and others that bloom and seed in the fall. All of these types are found in the three areas of this study. Whether all types are equally stimulated by these special rains was not documented in this study.

The data presented in this study indicates that the plant response, although similar, was not equal between the two periods. The rodent populations provide indices to plant production. The greater heteromyid biomass attained in 1979 as well as the phenomenal increase of N. albigula at that time, suggests greater plant production following the rainfall phenomenon of 1977-78.

Also consider the rainfall pattern of 1977-79, where good winter rains were followed by exceptional annual rainfall of 1978, which in turn was followed by excellent winter rains. In 1972-73, a good annual rainfall of 1972 was followed by exceptional winter rains. This in turn was followed by a very dry year. In addition, the annual rainfall of 1978 was the highest recorded in the last 57 years. Thus, the rainfall pattern would indicate a potentially higher plant production in 1978-79.

Yet, P. amplus having a greater breeding base, a greater food supply, sufficient time, and essentially the same number of seed competitors, did not surpass the 1973 level. This evidence leads me to believe that at these periods of time, populations may become density dependent rather than resource limited.

This is not to say this situation lasts for a prolonged period of time. Very soon, the smaller heteromyids decrease their activity for the winter. The larger heteromyids, along with other seed predators, continue to forage throughout the winter months, depleting the seed resources even further.

By the next spring, with a greatly reduced seed supply due to removal by predation and burial by rain and winds, resource limitation probably becomes the determining force in population densities.

At the Silverbell and Red Hill sites a similar pattern developed for the P. amplus. The heteromyids at Silverbell reached 121.5 ind./hectare in 1974 and 124.3 ind./hectare in 1979 (Table 3). Although the total number between the two periods is very similar, the number contributed by each species differs greatly between periods (Table 4).

Perognathus amplus reached a peak of 33 ind./hectare in September of 1973 compared to 55.2 ind./hectare in 1979. The biomass was 425 and 795 g/hectare, almost twice that of 1973. Similar results were recorded for Red Hill.

Table 3. Total Heteromyid Number/Hectare on Three Sites.

	1973 or 1974	1979
Silverbell	121.5	124.3
Red Hill	106.4	122.2
SRER	131.5	135.9

Table 4. Percent Contributed by Each Species to Total Heteromyid Number/Hectare on Three Sites.

	1973	1974		1979		
	SRER	Silverbell	Red Hill	SRER	Silverbell	Red Hill
Perognathus amplus	71.6	5.8	12.0	69.2	28.8	29.0
Perognathus penicillatus	14.1	54.9	15.4	13.0	43.7	17.8
Perognathus intermedius	-	1.3	9.4	-	3.2	14.8
Perognathus baileyi	8.1	25.4	57.5	12.9	19.1	36.1
Dipodomys merriami	5.6	12.5	5.6	4.9	5.1	2.3

The other heteromyids did not reach the levels of 1973-74 (Figure 25), even though they had similar or higher breeding bases in 1978 and conditions were as favorable. The initial rates of increase were the same for both periods as were the levels reached during the first surge in population numbers. Yet, in 1978-79 none but the P. amplus reached the levels realized in 1973-74, although the total number of heteromyids increased from the first period to the second.

This is possibly an indication of breeding inhibition brought on by high densities of heteromyids, primarily P. amplus. This does not imply that P. amplus out competes or is dominant over other heteromyids. It merely states that stress produced by the presence of such large numbers of individuals is detrimental to reproduction at full capacity.

I have observed many field encounters among heteromyids and inevitably P. amplus is the subordinate. Congdon (1974) observed the same thing for P. longimembris. But it must be stressed, that the other rodents must take the time and energies to chase the P. amplus away.

It is also well known that heteromyids, in general, are not a gregarious lot. They are difficult to breed in captivity and often do not get along well together in confinement. Eisenberg and Isaac (1963), and Hayden, Gambino, Lindberg (1966) noted the extreme aggressiveness of heteromyids to each other. Chew (1958) and Butterworth (1961) had limited success in breeding heteromyids as did Eisenberg and Isaac (1963).

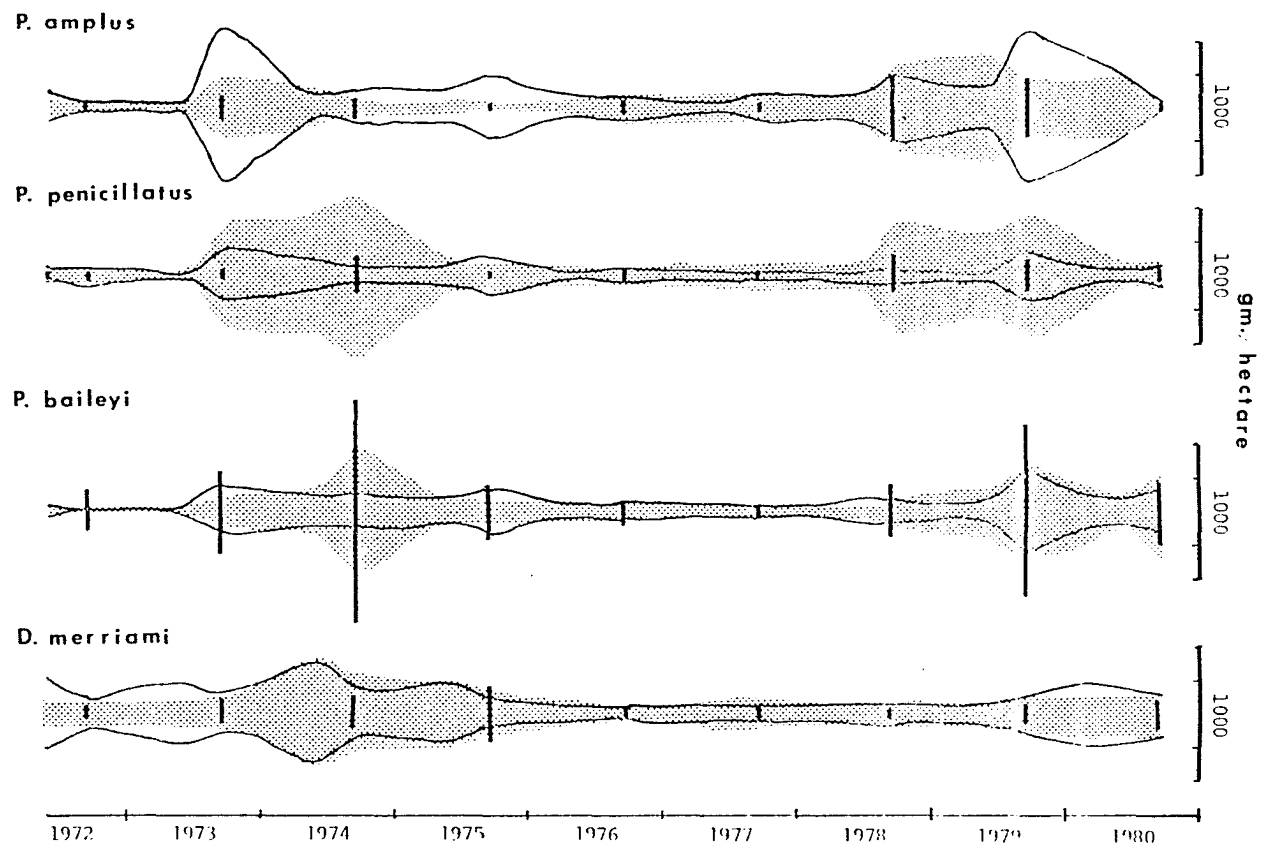

Figure 25. Annual Heteromyid Biomass, by Species, on Three Sites: A. Red Hill; B. Santa Rita Experimental Range; C. Silverbell.
A = bar; B = Line; C = Shaded Area

Thus, stress produced by constant confrontation, although minor, could very easily be detrimental to pronounced breeding. This inability to cope with other individuals in a limited space may explain why heteromyids never reach the densities reported for other groups of rodents.

In this study the highest individual species number per hectare reached was 94.1 for *P. amplus* at SRER. The other highs were much lower than this- *P. penicillatus*, 66.7 at Silverbell; *P. intermedius*, 18.1 at Red Hill; *P. baileyi*, 61.2 at Red Hill; and *D. merriami*, 19.3 at Silverbell. Packard (1971) found densities of 9.42/hectare for *P. flavus* and 52.54/hectare for *D. ordii*. Reynolds (1960) working at the SRER found maximum densities of 18.29/hectare for *D. merriami* which is very similar to this study with 18.1/hectare at the SRER.

Peak numbers for cricetids seem to be much higher. Packard (1972) reported densities of 76.81/hectare for *P. maniculatus* while Barrett (1968) found *S. hispidus* in densities of 237.22/hectare. Myers and Krebs (1974) report populations of *Microtus pennsylvanicus* attaining maximum densities of up to 740/hectare, with "normal" high densities of over 200/hectare.

The reported high densities for some of the rodents other than heteromyids may provide circumstantial evidence pointing to large densities having an inhibitory effect on the population of heteromyids in general. It must be kept in mind, though, that the dietary regime of *Sigmodon* and *Microtus* is vastly different than that of most heteromyids; but possibly under the conditions of high plant production that factor is eliminated.

The question arises as to why the P. amplus at the Silverbell and Red Hill sites reach such greater densities in 1978, and why the decrease following the peak was much slower than during 1974.

I believe the reason for the greater numbers produced in 1978 is related to the larger breeding stock present in 1977 as compared to 1972. Given an allotted amount of time for propagation, the more animals present initially, the larger the resultant population.

In May of 1973, before the breeding season, there were 6.8 ind./hectare at Silverbell. This base population produced 33.0 ind./hectare at its peak- nearly a five-fold increase. In 1978, a base population of 18.2 ind./hectare increased to a peak of 55.2 ind./hectare- a three-fold increase. But if only the females of the base population are considered, 3.8 females in 1973 produced the peak population of 33.0 ind./hectare, which is an increase of x8.68. In 1978, a base of 6.4 females resulted in a peak of 55.2 ind./hectare, an increase of x8.63.

This eight - fold increase in number over the females base indicates that breeding potential and strategy were similar in both periods. For the P. amplus population to build beyond the levels recorded, it would take either a greater female base or a longer breeding season, or a combination of both, if density allowed it.

Whether the optimal number of P. amplus capable for the ecosystem was reached in 1978 is not known. To have an indication of this, would encompass a similar rainfall phenomenon occurring, with the P. amplus female base surpassing that of May, 1978.

Why a greater number survived or possibly more young were produced, in 1979 then in 1974 may have been due to the occurrence of another winter rain phenomenon in 1979. This possibly stimulated more seed production which created an easily available food resource for the P. amplus in spring and summer of 1979. This may give credence to Reichman and Oberstein (1977) who observed that P. amplus was not as proficient at foraging deeper placed seeds.

Regardless, P. amplus was present in greater densities following the rainfall of 1977-78. Conditions for the other heteromyids appeared just as favorable, yet they did not increase in numbers to the extent they did in 1974. The arguments set forth point to influence of density pressures on population numbers during highs, in this case an inter-specific one.

Due to the ability of P. amplus and P. penicillatus to increase rapidly, they are first to reach high densities. As conditions change the P. amplus is not able to cope- whether with the environmental changes or competition- and rapidly decline in numbers. If conditions remain favorable, they are able to maintain their numbers for a longer time even in the face of possible competition from larger heteromyids. The effect of P. amplus in large numbers, seems to be an inhibitory one on other heteromyids.

Carrying Capacity

Regardless of the mechanism whether resource or density dependent limiting population numbers during peak times, it seems the carrying capacity of heteromyid rodents for the system was being approached. For all three areas to reach essentially the same densities in the same time frame (Table 3) was quite unexpected, considering the areas and techniques. It would be difficult to imagine a more favorable sequence of rainfall patterns occurring than did during this study period.

In reviewing the past climatic history, exceptional rainfall in early fall-early spring coupled with high total yearly rainfall is a rarity. In addition, having the highest annual rainfall recorded in the last five decades occurring during the study period, would add even more validity to the speculation that conditions during the study were as favorable as possible for heteromyid propagation. It is only emphasized by the seldom, widespread carpeting of the desert floor by wildflowers.

For rodents dependent on seeds, this prolific production of seeds would provide the opportunity for acceleration of many of the more subtle ramifications of population survival- increase and dispersal of genetic material, invasion of new territories, and establishment and imprinting of social behavior. Normally fettered to simply surviving, a profusion of food resources would allow the population to channel expenditure of energy into high levels of reproduction.

Viewed in this context, the rodents are not all that different from the desert plants they depend on. The population is in a more-or-less dormant state throughout a prolonged period of time with only a few individuals active genetically. When conditions are favorable, and in this environment these periods are rare, the population blossoms;

dispersing a tremendous amount of genetic material to be selected for in the ensuing "drought."

A prevailing observation in both ephemeral plants and animals in this environment is the paucity of any intermediate levels in numbers. It is either very low or exceedingly high. Only at the SRER did levels ever reach an "intermediate" state and that was in 1975. This was again due directly or indirectly to favorable rainfall in 1974. The SRER is more a grassland association than a true desert, though.

In the lower desert it stands to reason, when conditions are favorable, the most must be made of the bounty for the next chance may be a long time in coming. Selective forces would favor the individuals that could rapidly take advantage of such conditions. Viewed from this standpoint, it is not so surprising to see population numbers for the three areas reach similar levels during favorable conditions. What the plants do, so do the rodents.

The combination of rains were as varied as any observed during the last 41 years. These conditions should insure that a multitude of flowering combinations took place thus attaining the best possible level of food resource available to rodents in a natural situation. Only with a greater production of seeds beyond the 1973 and 1978 levels or by augmenting seed production through addition of commercial seed during another favorable period, will the question of whether carrying capacity was reached during this study be answered.

Attention must be brought to the fact that the base line or "maintenance" population of heteromyids remained fairly constant. The pre-1973 population was approximately 30 ind./hectare in all areas.

The post-1974 and pre-1978 populations were maintained at essentially the same level.

Although there was never a prolonged drought as in 1947-50, with rainfall in the Tucson basin measuring 155, 189, 187, and 236 mm for those years, there were very lean years in 1973, 1975, and 1976 with 192, 179, and 200 mm of annual rainfall. Very little rain fell in the fall and winter months of these years. Yet the populations remained at the above mentioned levels. It may well be, though, that a rare period of prolonged drought would depress the population below this level.

Dispersal

During high density periods it would be expected to find species invading new areas due to population pressures. This was the case in this study.

The most dramatic invasion into new areas was accomplished by *Neotoma albigula*. Beginning in 1978, *N. albigula* was captured in areas not previously occupied by them any time during the nine-year study. It was not until they reached extremely high densities that they did so.

At Silverbell, *Perognathus intermedius*, normally found only along the larger washes, was frequently trapped on creosote flats when populations were higher. The same was true at Red Hill.

Olding and Cockrum (1977), reported the re-establishment of the Red Hill site by a large number of rodents within three weeks after initial trapping removed all rodents from the 5.06 hectare grid. From September 1 through 11, 1974, initial trapping removed 768 rodents.

Trapping was conducted again from October 3rd through the 5th of 1974. This period produced an additional 238 rodents. This is a phenomenal rate of reinvasion that points to tremendous population pressures in the region beyond the grid.

If the surrounding area is given dimensions similar to that of the grid, an area of 25.3 hectares containing 3,650 rodents would encompass the grid. This is assuming similar densities occur outside the grid. This created dispersal sink would, in a matter of three weeks, account for 6.5% of the surrounding population. Stickel (1946), Van Vleck (1968), and Smith, Maza and Wiener (1980) found that other species responded similarly to voids created by removal trapping.

Other incidences pointing to dispersion during the wet periods are the appearance of *Mus musculus*, *Sigmodon arizonae* and *Onychomys torridus*. In these cases, it may not be so much population pressures which forced these individuals into these areas as it is to the habitat changes instigated by rainfall which made the environment more favorable. It could well be that food resources are temporarily more plentiful in the bajada areas.

On the SRER site, although no *M. musculus* were captured during the study period, *S. arizonae* were captured in small numbers during the population highs. *Sigmodon* is quite common in the higher elevations of the SRER and it may be that here it is also a case of population pressures forcing young *S. arizonae* into the lower less grassy areas.

Comparison of Heteromyids of Three Areas

The nine-year average peak standing crop of heteromyids was highest at the Silverbell site (Table 5), although the SRER had the highest heteromyid numbers during peak periods (Table 3). Red Hill had a mean of 1.06 kg/hectare compared to the high of Silverbell of 1.34 kg/hectare.

The most *Perognathus amplus* contributed to the heteromyid biomass was 33.8% at SRER while it contributed only 15.3% at Red Hill (Table 6). These figures are totals for the nine years. *Perognathus penicillatus* comprised 32.0% of the total biomass at Silverbell for its greatest contribution. At Red Hill, *Perognathus baileyi* comprised 53.5% of the heteromyid biomass, while *Dipodomys merriami* contributed the highest amount at SRER with 32.9% closely followed by Silverbell with 24.8%.

It is interesting to note, if the biomasses of all three areas are combined for the nine-year period, each species contributed approximately one fourth of the total biomass. This is only true if *P. penicillatus* and *P. intermedius* are treated as one. Apparently, if the areas are considered as a whole, each species contributes equally.

If numbers/hectare are considered, of all the *P. amplus* captured, 52.9% were captured at SRER. Of the *P. penicillatus*, 62.7% were captured at Silverbell, while 51.7% of the *P. baileyi* were trapped at Red Hill. *Dipodomys merriami* were more prevalent at Silverbell with 41.0% captured. These figures encompass only the late summer populations since Red Hill is not monitored in the spring.

Table 5. Mean Heteromyid Biomass for Three Sites (1972-1980).

	kilograms/hectare	
	Spring	Late Summer
Silverbell	1.03	1.34
SRER	0.84	1.10
Red Hill	----	1.06

Table 6. Species Composition (%) of Total Heteromyid Biomass for Nine Years in Three Areas.

	SRER	Silverbell	Red Hill	Average
P. amplus	33.8	20.8	15.3	24.4
P. penicillatus	13.3	32.0	9.9	20.9
P. intermedius	----	1.3	6.9	2.0
P. baileyi	20.0	21.1	53.5	27.0
D. merriami	32.9	24.8	14.4	25.7

Apparently, from this data, *P. amplus* prefers the more "closed" habitat of SRER while *P. penicillatus* and *D. merriami* prefer the more "open" bajada areas of Silverbell. *Perognathus intermedius* and *P. baileyi* seem to prefer the rockier area of Red Hill.

CHAPTER 9

SUMMARY AND CONCLUSIONS

Rainfall, specifically high autumnal rain followed by high early spring rains, triggers a pronounced bloom of desert annuals. The perennials seem to respond more to high annual rainfall of the previous year. These deviate rains are fairly rare in occurrence.

Of the three study areas, the lower desert areas of Silverbell and Red Hill are dominated by ephemeral blooms, while the SRER site is dominated by perennial growth and seeding.

The plant growth, flowering, and seed production influence the population size of nocturnal rodents. These, dominated by heteromyids, also show a corresponding jump in numbers which lags behind that of the plants. It is apparent that the presence of green plant material in large quantities as well as enlarged food reserves, stimulate and maintain high levels of rodents for up to a year.

The smaller rodents increase in number rapidly and reach peak populations earlier than the larger ones. In the two periods of population highs, all nocturnal rodents increased in number. The amount contributed by each species varied, though, between the periods.

Decrease in population numbers is usually rapid and complete, reaching biomasses of approximately 600 g/hectare. This low level is maintained until the next rainfall phenomenon.

Very similar levels of population numbers were reached in the two peaks following excellent rains, suggesting environmental restraints of some sort limiting the upper level that can be attained.

Neotoma albigula reacted only slightly to the first bloom but dramatically to the second, suggesting a difference in plant production between the two periods.

Considering the data recorded during this study, several predictions are possible, (1) Unusually high rainfall (twice or better) in the autumn followed by high rainfall in late winter-early spring, will produce a prolific flowering of annuals. This will be followed by a substantial increase in the heteromyid population; (2) Areas dominated by perennials react more to high annual rainfall of the preceding year. If these rains are 1/3 greater than the mean, rodent populations will be stimulated to reach peak levels; (3) In areas dominated by heteromyid rodents, peak population number of heteromyids will probably not surpass 138 ind./hectare.

APPENDIX A

LIVE WEIGHT BIOMASS AND NUMBER PER HECTARE OF HETEROMYID RODENTS ON SRER

	1972				1973				1974				1975			
	May		Sept		May		Sept		May		Sept		May		Sept	
Species	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h
Dip mer	12.4	494	6.7	267	11.3	450	7.4	295	18.1	720	8.9	354	10.6	422	5.7	227
Per pen	5.3	98	7.1	131	1.8	33	18.6	342	10.6	195	6.6	121	8.4	155	13.8	254
Per amp	16.5	195	9.4	111	6.1	72	94.1	1120	16.0	189	23.1	273	23.4	276	39.4	465
Per bai	2.5	77	.4	12	1.6	49	10.6	382	6.9	213	8.5	263	6.9	213	10.2	315
Total	36.7	864	23.6	521	20.8	604	131.5	2085	51.6	1317	47.1	1011	49.3	1066	69.1	1261

	1976				1977				1978				1979			
	May		Sept		May		Sept		May		Sept		May		Sept	
Species	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h
Dip mer	10.6	422	4.3	171	6.0	239	3.9	155	6.0	239	4.6	183	2.9	115	6.7	267
Per pen	1.8	33	4.8	88	3.1	57	3.1	57	3.1	57	4.5	83	3.6	66	17.7	326
Per amp	11.8	139	14.1	166	7.6	89	16.0	189	18.4	217	40.4	477	25.4	300	94.0	1109
Per bai	3.2	99	4.1	127	3.7	114	3.2	99	5.7	176	4.9	151	5.7	176	17.5	541
Total	27.4	693	27.3	552	20.4	499	26.2	500	33.2	689	54.4	894	37.6	657	135.9	2243

	1980			
	May		Sept	
Species	N	G/h	N	G/h
Dip mer	10.3	410	8.5	338
Per pen	5.7	105	6.6	121
Per amp	40.9	483	4.7	55
Per bai	6.9	213	10.6	328
Total	63.8	1211	30.4	842

APPENDIX B

LIVE WEIGHT BIOMASS AND NUMBER PER HECTARE OF HETEROMYID RODENTS ON SILVERBELL

	1972				1973				1974				1975			
	May		Sept		May		Sept		May		Sept		May		Sept	
Species	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h
Dip Mer	5.3	204	5.1	205	4.6	204	6.4	251	19.3	778	15.2	586	12.5	504	9.5	353
Per pen	4.0	57	3.8	65	2.2	40	44.1	739	41.3	813	66.7	1187	14.9	256	11.1	157
Per amp	10.7	118	3.6	42	6.8	105	33.0	425	19.8	279	7.1	90	8.8	110	1.3	12
Per bai	1.1	32	1.1	27	1.4	57	6.3	182	12.4	348	30.9	940	6.5	192	6.3	170
Per int	0	0	0	0	.2	4	.6	7	.7	7	1.6	19	.8	9	2.0	3
Total	21.1	411	13.6	339	15.2	410	90.4	1604	93.5	2225	121.5	2822	43.5	1071	30.2	695

	1976				1977				1978				1979			
	May		Sept		May		Sept		May		Sept		May		Sept	
Species	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h
Dip mer	5.2	216	1.7	70	6.2	249	6.5	235	2.9	125	5.0	197	4.9	205	6.4	258
Per pen	9.0	152	10.3	156	10.8	181	14.6	207	9.2	161	47.0	803	29.7	598	54.3	880
Per amp	9.4	117	20.1	216	15.8	205	20.4	198	18.2	214	48.9	632	55.2	795	35.8	418
Per bai	4.9	131	6.0	129	1.1	33	.6	10	4.4	79	8.8	206	12.9	416	23.8	666
Per int	.3	3	.6	7	1.8	24	.8	10	1.3	22	2.4	40	2.2	32	4.0	49
Total	38.8	619	38.7	578	35.7	692	42.9	660	36.0	601	112.1	1878	104.9	2046	124.3	2271

	1980			
	May		Sept	
Species	N	G/h	N	G/h
Dip mer	7.5	319	8.7	347
Per pen	10.3	175	15.4	227
Per amp	34.8	450	1.2	17
Per bai	9.0	277	22.9	616
Per int	1.6	20	2.6	34
Total	63.2	1241	50.8	1241

APPENDIX C

LIVE WEIGHT BIOMASS AND NUMBER PER HECTARE
OF HETEROMYID RODENTS ON RED HILL

Species	1972 Sept N	1972 Sept G/h	1973 Sept N	1973 Sept G/h	1974 Sept N	1974 Sept G/h	1975 Sept N	1975 Sept G/h	1976 Sept N	1976 Sept G/h	1977 Sept N	1977 Sept G/h	1978 Sept N	1978 Sept G/h
Dip mer	3.1	115	4.1	152	6.0	220	10.7	399	1.6	51	2.3	91	1.6	65
Per pen	1.5	21	2.2	29	16.4	222	1.7	20	5.0	70	5.3	66	18.4	252
Per amp	4.2	48	16.6	187	12.8	145	.8	8	8.7	92	4.8	46	44.7	519
Per bai	9.6	258	20.2	540	61.2	1640	15.0	379	6.6	150	2.4	59	13.4	379
Per int	3.7	45	3.0	36	10.0	120	1.9	19	1.2	16	4.8	56	7.8	107
Total	22.1	487	46.1	944	106.4	2347	30.1	825	23.1	379	19.6	318	85.9	1322

Species	1979 Sept N	1979 Sept G/h	1980 Sept N	1980 Sept G/h
Dip mer	2.8	111	4.1	162
Per pen	21.8	210	4.0	53
Per amp	35.4	407	.3	3
Per bai	44.1	1247	16.5	432
Per int	18.1	215	3.9	44
Total	122.2	2190	28.8	694

APPENDIX D

LIVE WEIGHT BIOMASS AND NUMBER PER HECTARE OF *NEOTOMA ALBIGULA* ON ALL SITES

	1972				1973				1974				1975			
	May		Sept		May		Sept		May		Sept		May		Sept	
Site	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h
SRER	.8	118	0	0	.4	59	.4	59	.8	118	1.6	238	1.6	238	.4	59
Silverbell	.3	21	0	0	0	0	.2	38	.7	54	0	0	0	0	0	0
Red Hill			.8	119			1.4	213			2.2	332			1.2	160

	1976				1977				1978				1979			
	May		Sept		May		Sept		May		Sept		May		Sept	
Site	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h	N	G/h
SRER	1.2	178	2.0	297	.8	118	.4	59	2.3	357	2.3	357	3.1	476	4.7	714
Silverbell	.3	21	.3	21	.3	26	.3	30	.7	90	2.4	245	3.1	483	2.7	390
Red Hill			.2	26			1.7	194			3.1	480			5.7	887

	1980			
	May		Sept	
Site	N	G/h	N	G/h
SRER	6.6	1011	7.8	1190
Silverbell	12.4	1856	11.3	1947
Red Hill			5.2	874

LITERATURE CITED

Alcorn, J.R. 1941. Counts of embryos in Nevadan kangaroo rats (Genus Dipodomys). J. Mammal. 22:88-89.

Barrett, G.W. 1968. The effects of an acute insecticide stress on a semi-enclosed grassland ecosystem. Ecology 49:1019-1035.

Beatley, J.C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology 50:721-724.

Beatley, J.C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856-863.

Bradley, W.G. and R.A. Mauer. 1971. Reproduction and food habits of Merriam's kangaroo rat, Dipodomys merriami. J. Mammal. 52: 479-507.

Bradley, W.G. and R.A. Mauer. 1973. Rodents of a creosote bush community in Southern Nevada. Southwest. Nat. 17:333-344.

Brown, J.H., G.A. Lieberman, and W.F. Dengler. Woodrats and cholla: dependence of a small mammal population on the density of cacti. Ecology 53:310-313.

Brown, J.H. and G.A. Lieberman. 1973. Resource utilization and co-existence of seed-eating desert rodents in sand dune habitats. Ecology 54:788-797.

Butterworth, B.B. 1961. A comparative study of growth and development of the kangaroo rat; Dipodomys deserti, Stephens, and Dipodomys deserti, Merns. Growth 25:127-128.

Chew, R.M. 1958. Reproduction by Dipodomys merriami in captivity. J. Mammal. 39:597-598.

Chew, R.M. and B.B. Butterworth. 1959. Growth and development of Merriam's kangaroo rat, Dipodomys merriami. Growth 23:75-95.

Christopher, E.A. 1973. Sympatric relationships of the kangaroo rats, Dipodomys merriami and Dipodomys agilis. J. Mammal. 54:317-327.

Chudoba, S. and S. Huminski. 1980. Estimating numbers of rodents and edge effect using a modified version of the standard minimum method. Acta Theriol. 25:365-376.

Congdon, J. 1974. Effect of habitat quality in distributions of three sympatric species of desert rodents. J. Mammal. 55:659-662.

Conley, W., J.D. Nichols, and A.R. Tipton. 1976. Reproduction strategies in desert rodents. J. Mammal. 57:193-215.

Eisenberg, J.F. 1963. A comparative study of sand bathing behavior in heteromyid rodents. Behavior 22:16-23.

Eisenberg, J.F. and D.E. Isaac. 1963. The reproduction of heteromyid rodents in captivity. J. Mammal. 44:61-66.

French, N.R., B.G. Maza, and A.P. Aschwander. 1966. Periodicity of desert rodent activity. Science 154:1194-1195.

French, N.R., B.G. Maza, H.O. Hill, A.P. Aschwander, and H.W. Kaaz. 1974. A population study of irradiated desert rodents. Ecol. Monogr. 44:45-72.

Grdzinski, W., Z. Pucek, and L. Ryszkowski. 1966. Estimation of rodent numbers by means of prebaiting and intensive removal. Acta Theriol. 11:29-314.

Hayden, P., J.J. Gambino, and R.G. Lindberg. 1966. Laboratory breeding of the little pocketmouse, Perognathus longimembris. J. Mammal. 47:412-423.

Hoffmeister, D.F. 1964. Unusual sex ratios in winter and spring taken pocket mice in the Southwest. Southwest. Nat. 9:252-254.

Hungerford, C.R. 1960. The factors affecting the breeding of Gambel's quail, Lophortyx gambelii gambelii, in Arizona. Ph.D. dissertation, University of Arizona, 97 pp.

Kenagy, G.L. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201-1219.

Lowe, C.H. 1964. The vertebrates of Arizona. The University of Arizona Press, Tucson, Arizona, 270 pp.

Maza, B.G., N.R. French, and A.P. Aschwanden. 1973. Home range dynamics in a population of heteromyid rodents. J. Mammal. 54:405-426.

Myers, J.H. and C.J. Krebs. 1974. Population cycles in rodents. Sci. Am. 230:38-46.

O'Farrell, M.J. 1974. Seasonal activity patterns of rodents in a sagebrush community. J. Mammal. 55:809-824.

O'Farrell, N.J. and G.T. Austin. 1978. A comparison of different trapping configurations with the assessment line technique for density estimations. J. Mammal. 59:866-868.

O'Farrell, M.J., D.W. Kaufman, and D.W. Lundahl. 1977. Use of live-trapping with the assessment line method for density estimation. J. Mammal. 58:575-583.

Olding, R.J. and E.L. Cockrum. 1977. Estimation of desert rodent populations by intensive removal. J. Ariz. Acad. Sci. 12:94-108.

Olsen, R.W. 1973. Shelter-site selection in the white-throated woodrat, Neotoma albigula. J. Mammal. 54:594-610.

Orions, G.H. and O.T. Solbrig. 1977. Convergent Evolution in Warm Deserts. Dowden, Hitchinson, and Ross, Inc. Strauasburg, Penn., 333 pp.

Packard, R.L. 1971. Small mammal survey on the Jornada and Pantex sites. U.S. IBP Grassland Biome Tech. Report (114):1-48.

Packard, R.L. 1972. Small mammal studies on the Jornada and Pantex sites. U.S. IBP Grassland Biome Tech. Report (188):1-78.

Reichman, O.J. and K.M. Van De Graaff. 1973. Seasonal activity and reproductive patterns of five species of Sonoran Desert rodents. Am. Mid. Nat. 90:118-126.

Reichman, O.J. and D. Oberstein. 1977. Selection of seed distribution types by Dipodomys merriami and Perognathus amplus. Ecology 58:636-643.

Reynolds, H.G. 1958. The ecology of the Merriam Kangaroo rat (Dipodomys merriami, Mearns) on the grazing lands of Southern Arizona. Ecol. Mongr. 28:111-127.

Reynolds, H.G. 1960. Life history notes on Merriam's kangaroo rat in Southern Arizona. J. Mammal. 41:48-58.

Rosenzweig, M.L. and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50:558-572.

Rosenzweig, M.L. and P.W. Sterner. 1970. Population ecology of desert rodent communities: body size and seed-husking as bases for heteromyid coexistence. Ecology 51:217-224.

Rosenzweig, M.L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology 54:111-117.

Schroder, G.D. and M.L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between Dipodomys ordii and Dipodomys merriami. Oecologia. 19:9-28.

Smigel, B.W. and M.L. Rosenzweig. 1974. Seed selection in Dipodomys merriami and Perognathus penicillatus. Ecology 55:329-339.

Smith, M.H., J.B. Gentry, and J. Pinder. 1974. Annual fluctuations in a small mammal population in an eastern hardwood forest. J. Mammal. 55:231-234.

Smith, M.L., B.G. Maza, and J.G. Wiener. 1980. Social interaction and spatial distribution in a desert rodent. J. Mammal. 61:113-116.

Stickel, L.F. 1946. The source of animals moving into a depopulated area. J. Mammal. 27:301-307.

Turkowski, F.J. and J.R. Vahle. 1977. Desert rodent abundance in Southern Arizona in relation to rainfall. USDA Forest Service Research Note RM-346, pp. 1-4.

Turnage, W.V. and T.D. Mallery. 1941. An analysis of rainfall in the Sonoran Desert and adjacent territory. Carnegie Institution of Washington, Publication 529, Washington, D.C.

Van De Graaff, K.M. and R.P. Balda. 1973. Importance of green vegetation for reproduction in kangaroo rat, Dipodomys merriami merriami. J. Mammal. 54:509-512.

Van De Graaff, K.M. 1975. Reproductive ecology of some Sonoran Desert rodents. Ph.D. Dissertation. Northern Arizona University, Flagstaff, Arizona, 174 pp.

Van Vleck, D.B. 1968. Movements of Microtus pennsylvanicus in relation to depopulated areas. J. Mammal. 49:92-103.

Vorhies, C.T. and W.P. Taylor. 1940. Life history and ecology of the white-throated wood rat, Neotoma albigula albigula Hartly, in relation to grazing in Arizona. Agric. Tech. Bull., University of Arizona, 86:453-529.