

DENSITY OF POPULATION AS A REGULATING FACTOR,
IN THE REPRODUCTIVE POTENTIAL OF
SIGMODON HISPIDUS

By

Peter M. Green, O.S.B.

Bachelor of Science
St. Benedict's College
Atchison, Kansas
1952

Master of Science
Oklahoma State University
Stillwater, Oklahoma
1961

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Thesis Approved:

Ann Stebler

Thesis Adviser

H. Herbert Brunson

W. S. Newcomer

J. M. Boyce

Dean of the Graduate School

569570

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TABLE OF CONTENTS

| Chapter | Page |
|---|------|
| I. INTRODUCTION | 1 |
| Statement of Thesis | 1 |
| Density of Population and Rate of Recruitment | 5 |
| Density of Population and Mortality Rate. | 8 |
| <u>Sigmodon hispidus</u> | 19 |
| II. METHODS. | 22 |
| Study Areas and Field Techniques. | 22 |
| Grid Population | 22 |
| University Farm Population. | 23 |
| Penned Populations. | 24 |
| Caged Populations | 24 |
| Laboratory Analyses | 25 |
| Testicular Metabolism | 25 |
| Accessory Reproductive Organs | 25 |
| Adrenal Glands. | 25 |
| III. RESULTS. | 27 |
| Grid Population | 27 |
| Variations in Autumnal Breeding | 27 |
| Annual Changes in the Density of the Population | 32 |
| Seasonal Changes in Breeding Conditions | 32 |
| Seasonal Changes in Weight Classes. | 36 |
| Emigration and Immigration. | 36 |
| Penned Populations. | 36 |
| Pen 1 | 36 |
| Pen 2 | 39 |
| Pen 3 | 39 |
| Pen 4 | 39 |
| Population of the University Farm | 40 |
| Analyses of Adrenal Glands, Accessory Reproductive Organs, and Testes. | 40 |

| Chapter | Page |
|--|--------|
| Adrenal Weights. | 40 |
| Adrenal Sections | 44 |
| Accessory Reproductive Organs. | 50 |
| Metabolism of the Testes | 50 |
| IV. DISCUSSION | 65 |
| The Population on the Grid | 65 |
| Variations in Autumnal Breeding. | 65 |
| Annual Changes in the Density of the Population. | 67 |
| Seasonal Changes in Breeding Conditions. | 68 |
| Seasonal Changes in Weight Classes | 69 |
| Emigration and Immigration | 70 |
| Population at the University Farm. | 71 |
| Analyses of Adrenal Glands, Accessory Reproductive Organs, and Testes | 71 |
| Adrenal Weights. | 71 |
| Adrenal Sections | 75 |
| Accessory Reproductive Organs. | 79 |
| Metabolism of the Testes | 81 |
| Weight of the Testes | 82 |
| Percent Dry Weight | 82 |
| Uptake of Oxygen | 83 |
| Metabolism of Glucose. | 84 |
| The Production of Lactic Acid. | 85 |
| Protein Content. | 85 |
| Summation. | 86 |
| V. SUMMARY AND CONCLUSIONS. | 88 |
| LITERATURE CITED | 91 |
| APPENDIX | 99 |
| ADDENDUM | 100 |
| Management Implications. | 100 |

LIST OF TABLES

| Table | Page |
|--|------|
| I. Percent trapping success and breeding condition of male sigmodon during the fall months of 1959, 1960, 1961, and 1963 | 28 |
| II. Percent of trapping success and breeding condition of female sigmodon during the fall months of 1959, 1960, 1961, and 1963 | 29 |
| III. Percent breeding male sigmodon correlated with trapping success, average minimum temperature, average maximum temperature, lowest monthly temperature, and monthly precipitation. | 30 |
| IV. Percent breeding female sigmodon correlated with trapping success, average minimum temperature, average maximum temperature, lowest monthly temperature, and monthly precipitation | 31 |
| V. Estimates of the sigmodon population on the grid from June, 1963 to May, 1964. | 33 |
| VI. Breeding condition of male sigmodon in the population on the grid from June, 1963 to May, 1964 | 34 |
| VII. Breeding condition of female sigmodon in the population on the grid from June, 1963 to May, 1964 | 35 |
| VIII. Changes in weight classes of the sigmodon population on the grid, as measured in grams and expressed in percent. | 37 |
| IX. Number and location of newly marked sigmodon appearing on the grid from November, 1963 to May, 1964 | 38 |
| X. Percent of trapping success for the sigmodon population at the farm from October, 1963 to May, 1964. | 41 |
| XI. Comparison of trapping success between the sigmodon populations on the grid and at the farm from October, 1963 to May, 1964 | 41 |

| Table | Page |
|---|------|
| XII. Weights of the paired preputial glands, paired seminal vesicles, ventral prostate, and paired adrenal glands, expressed in milligrams percent of adult male sigmodon taken from the population on the grid. | 42 |
| XIII. Weights of the paired preputial glands, paired seminal vesicles, ventral prostate, and paired adrenal glands, expressed in milligrams percent, of adult male sigmodon taken from the population at the farm. | 43 |
| XIV. Weights of paired adrenal glands, expressed in milligrams, milligrams percent, and milligrams of the largest sample, of adult male sigmodon from all populations. | 45 |
| XV. Width of the <u>zona glomerulosa</u> and of the <u>zona fasciculata</u> , in microns, and the number of vacuoles per 12.5 microns of the <u>zona fasciculata</u> in the adrenal cortex of adult male sigmodon from the population on the grid | 46 |
| XVI. Width of the <u>zona glomerulosa</u> and of the <u>zona fasciculata</u> , in microns, and the number of vacuoles per 12.5 microns of the <u>zona fasciculata</u> in the adrenal cortex of adult male sigmodon from the population at the farm. | 47 |
| XVII. Width of the <u>zona glomerulosa</u> and of the <u>zona fasciculata</u> , in microns, of the adrenal cortex of adult male sigmodon from all populations. | 48 |
| XVIII. Average and greatest number of vacuoles per 12.5 microns of the <u>zona fasciculata</u> in the adrenal cortex of adult male sigmodon from all populations | 49 |
| XIX. Weights of the paired preputial glands, expressed in milligrams, milligrams percent, and milligrams of the largest sample, of adult male sigmodon taken from all populations | 51 |
| XX. Weights of the paired seminal vesicles, expressed in milligrams, milligrams percent, and milligrams of the largest sample, of adult male sigmodon taken from all populations | 52 |
| XXI. Weights of the ventral prostate glands, expressed in milligrams, milligrams percent, and milligrams of the largest sample, of adult male sigmodon taken from all populations | 53 |
| XXII. Body weight, testes weight, percent testicular dry weight, and uptake of oxygen from the testes of adult male sigmodon from the population on the grid. | 54 |

| Table | Page |
|--|------|
| XXIII. Body weight, testes weight, percent testicular dry weight, and uptake of oxygen from the testes of adult male sigmodon from the population at the farm. | 56 |
| XXIV. Utilization of glucose, production of lactic acid, protein content, and RNA and DNA content of testes of adult male sigmodon from the population on the grid. . . | 57 |
| XXV. Utilization of glucose, production of lactic acid, protein content, and RNA and DNA content of testes of adult male sigmodon from the population at the farm | 58 |
| XXVI. Testicular weight, expressed in grams, milligrams percent, and percent of dry weight, of adult male sigmodon from all populations. | 59 |
| XXVII. Testicular uptake of oxygen, expressed in microliters of oxygen per milligrams of tissue per hour, of adult male sigmodon from all populations. | 60 |
| XXVIII. Testicular utilization of glucose, expressed in micrograms of glucose per milligram of tissue per hour, of adult male sigmodon from all populations | 61 |
| XXIX. Testicular production of lactic acid, expressed in microliters of lactic acid per milligram of tissue per hour, with and without substrate of adult male sigmodon from all populations | 62 |
| XXX. Protein content, expressed in milligrams of protein per gram of testicular tissue, of adult male sigmodon from all populations. | 63 |
| XXXI. RNA and DNA content, expressed in milligrams of RNA and DNA per gram of testicular tissue of adult male sigmodon from all populations | 64 |

CHAPTER I

STATEMENT OF THESIS

A population of animals, unless it is hovering on the brink of extinction, potentially is capable of reproducing very rapidly. When the density of the population is comparatively low, this potentiality is actualized, and the rate of reproduction and recruitment proceeds rapidly; as the population becomes more dense, however, and approaches the carrying capacity of the environment, or upper symptome, losses to the population through death and emigration are compensated for by the gains which result from reproduction and immigration. At this stage the rate of increment balances the rate of decrement. A population may increase geometrically for a short time; but it must, and inevitably does, level off when the carrying capacity of the environment is approached.

The subject of this present report on research has to do with those processes by which the growth of a population of mammals is regulated. Populations commonly have been conceived as static, independent entities; consequently, the approach to the problems of growth and increase has been, more often than not, that of an economist rather than a trained biologist. This statement carries with it the implication that certain principles of economics, such as the law of supply and demand, have been translated from the world of economics to the world of living organisms, thereby completely neglecting the dynamism that is inherent in living beings and is implicit in evolutionary concepts.

Thomas Malthus (1830), writing about changes in human population, included as positive checks "all those causes which tend in any way prematurely to shorten the duration of human life, such as unwholesome occupation, severe labor, exposure to seasons, bad and insufficient food and clothing arising from poverty, bad nursing of children, excess of all kinds, great towns and manufactories, the whole train of common diseases and epidemics, wars, infanticide, plague, and famine." Following the same line of argument, ecologists could enumerate similar checks on the population of any species: increased predation, scarcity of food, lack of proper cover, and social intolerance. Such a rationale as this, however, is unsatisfying both aesthetically and intellectually for the reason that it ascribes too passive a role to living beings. This report on research is concerned, therefore, with a non-Malthusian theory of natural selection. Investigations which this paper records, in other words, were done from the viewpoint of a biologist, not an economist.

It is surely true that predators, parasites, and pathogens take an increased toll of individuals when the density of population rises, and environmental conditions become more severe. As the population increases, one may rightly expect an increase of those factors which will be harmful to the individuals of that population. Ordinarily, however, these extrinsic checks are incapable of imposing significant limitations on the expansion of the population. Moreover, if a population can be limited by intrinsic checks, there is no real reason for postulating checks which are extrinsic to the population itself. Again it is true that a population of a species could not exploit its habitat to the degree that the habitat could no longer support it. Food may be, and often is, the

ultimate limiting factor in expansion; to insist, however, that food is the proximate factor of limitation is to adopt a superficial view, for in the course of time the food supply itself would be depleted. If food were the proximate agent, the food supply would be plundered by an ever-increasing population; those animals which survived this exploitation would then be reduced to a state of semi-starvation in an exhausted environment.

Since the time of Claude Bernard, physiologists have explored the concept of dynamic equilibrium as a means of attaining stability of the internal environment of an individual organism. Physiological homeostasis, which may be defined as a state of internal dynamic balance, presumably has been perfected in the course of evolutionary history to enable animals to be comparatively independent of those destructive forces which may be found in their environment. Population homeostasis, it may be inferred, involves evolutionary adaptations which are equally complex and equally beneficial; it enables a population of organisms to adjust to its external environment without danger of over-exploitation.

In an homeostatic system there are two component processes. One brings about those changes which are required to restore balance when it has been upset, or when conditions external to the system have been altered; the system then adjusts to a new level. The other component process, which may be described here as a negative feedback process, elicits a corrective response when information about the state of balance or imbalance has been reported to it. Thus, when the balance sways in one direction, these negative feedback processes check and reverse such a trend so that the system returns to a state of equilibrium. It is possible to cite many examples of homeostasis on the physiological level. Although examples are not numerous, there seems to be

enough to warrant the transfer of this concept of homeostasis to the population level. If one grants the validity of such a transfer, the negative feedback component evaluates the capacity of the environment and adjusts its rate of recruitment accordingly. According to this hypothesis, the density of population is constantly being set at the optimum level of exploitation of available resources; the result is that a maximum population will be supported in a specific habitat, and the resources will not be irreparably damaged.

The actual control of the density of population of any species is effected by the regulation of the rates of recruitment and mortality. Homeostatic adaptations can enter any any stage: from that of fertilization to that of breeding adults. In mammals, embryos may be aborted or resorbed in the uterus. The size of the litter, moreover, can be varied. The number of litters per female during breeding season may be altered. The density of population may also affect such matters as the number of breeding adults, the length of breeding season, which may be either prolonged or shortened; and it even influences parental care and nourishment of the young. At any one of these levels, homeostatic restraints may be imposed. These restraints will result in an increase to the population which is consonant with the losses which are sustained during the non-breeding season and with the environmental carrying capacity.

Losses to a population may also be regulated by homeostasis, and here the flexibility of the system is a conditio sine qua non. The reason is obvious: the homeostatic process must be adjusted in a way that it will compensate for the losses to the population which result from predators, parasites, or pathogens.

The hypothesis of natural regulation of animal populations has been expressed thus far in the most general terms. It is now necessary to examine the evidence which has been gained from experimental observation in the laboratory as well as in field studies. The remaining portion of this introductory chapter, therefore, will be devoted to a rather detailed account of the various studies which have been made on this particular problem.

Density of Population and Rate of Recruitment

It is quite possible, because of homeostatic regulating processes, for a species of mammals, having once begun an active period of reproduction, to provide a rather small increment to the population as a whole. By virtue of a negative feedback component, the potential rate of reproduction is not actualized.

Strecker and Emlen (1958) found that the growth of population in wild house mice (Mus musculus) was stabilized by an involution of the reproductive organs in the female; in this manner did the process of homeostatic regulation work itself out. In this experiment, cover and water facilities were supplied in excess, but allotments of food were limited to 250 grams per day per colony.

Southwick (1955a) found that continued crowding causes a serious decline in the birth rate of house mice (Mus musculus), even though there was an unlimited supply of food and water. In two of his four populations the decline in birth rates could be attributed to the fact that fewer males were producing sperm and fewer females were ovulating. In the other two populations the decline was thought to be the result of such factors as excessive copulation pressure and failures in early embryonic life. In an extension of this type of experiment, Southwick (1955b) observed that aggressive activity and the mortality rate

of the litter increased as the density of the population increased. Forty-two young were born in boxes with no nests; none of these survived. Fifty-eight young were born in communal nests; none of these survived either.

Calhoun (1949) observed that socially dominant and socially inferior female rats (Rattus norvegicus) produced the same number of litters, but the litter mortality rate was different in the two groups: the socially dominant females weaned ten litters from 12 pregnancies, while the socially inhibited females weaned no more than one litter.

Davis (1951) studied Norway rats (Rattus norvegicus) in stationary, increasing, and decreasing populations in the residential areas of Baltimore. The increasing and decreasing populations contained a greater percentage of pregnant females than did the stationary populations. The actual increase in numbers in the increasing populations was thought to be the result of better survival of the young rats after weaning.

Patric (1962), in a study of red-backed mice (Clethrionomys), recorded low embryo counts during years of high density of population and high embryo counts during those years in which the density of population was not so high. Thus, only 18.4% of the adult females which were captured during a year of high density were pregnant, while 55.0% of the females were pregnant during a year of low density.

Hoffman (1958), in a study of voles (Microtus agrestis), noted that as density increases, the rate of ovulation and the size of the litter decreased.

Clarke (1955), after a study of two vole (Microtus agrestis) populations, concluded that the breeding season may vary in length, the

length being determined by the density of the population. At the beginning of the experiment one population was four times larger than the other; the rate of growth of the larger population, however, was less than that of the smaller. In the course of time the two populations became nearly equal in size. In addition to the shorter breeding season, the larger population had fewer fertile females.

Errington (1956) pointed out that adult female muskrats (Ondatara zibethicus) gave birth to the usual maxima of four litters per season in those areas in which there was a low to moderate density, or when the females had lost a large portion of their young. On the other hand, females ceased breeding after giving birth to one or two litters when they found themselves in crowded conditions.

Buechner and Swanson (1955) found that more than 50% of the yearling elk females were pregnant in a population of low density, and they suggested that there is a negative correlation between density and pregnancy in this species.

Still another form of regulation can be obtained by suppressing early maturity in favor of a longer term of sterile adolescence. Breeding activity then would be limited to a smaller number of animals than the potential breeding stock, and there would be present in the population a reserve of non-breeding sub-adults. This class would thus serve as a buffer or stabilizer in the event of an emergency. Christian (1955) found that the seminal vesicles and preputial glands of male white rats exhibited a pronounced decline in weight when the population grew in size.

To summarize the evidence that has been presented up to this point: regulatory processes that are intrinsic to the population itself are able to govern the rate of increment to the population. The rate of growth of the population can be controlled at any of several stages from

ovulation to sub-adult, and the population can thereby be adjusted to the upper symptote of the environment.

Density of Population and Mortality Rate

Infectious disease and predation are unable to check the patterns of growth in populations, although both may increase as density of population increases. In a crowded condition, animals will have less suitable cover and move into marginal habitats, thus rendering themselves more liable to predation. Similarly, a pathogen will spread more rapidly when animals are in more frequent contact with one another. This fact, however, is not the complete explanation for the virulence of a pathogenic organism in a population of high density. Resistance to disease is an intrinsic, not extrinsic, phenomenon; and there is apparently some relation between resistance to disease and density of population.

Davis and Read (1958), using house mice (Mus musculus) in both isolated and crowded situations, found that 15 days after infection with Trichinella spiralis the mice in the group had from 16 to 51 parasites in the intestines, while only three of the mice in isolation had intestinal parasites. Continuing the experiment with other mice, they reported that after 13 days the mice in isolation had 1054 larvae per gram of muscle, while those in the group had an average of 1556.

Noble (1961) used the Unita ground squirrel (Citellus armatus) as an experimental animal in a series of stressful situations. The animals that were subjected to a variety of stresses, including that of crowding, had a cecal protozoa count 48% higher than that of the controls. As the cecal protozoa count increased, the white blood cell count decreased.

According to Tobach and Block (1952), an experiment with albino

white mice provided significant data in this matter of the relation between stress situations and pathogenic conditions. The mice which had been put together in a group and then infected with tubercule bacilli showed a greater resistance to tuberculosis than those mice which had been in isolation and then infected. When the mice which had been in isolation, and afterwards infected, were put into crowded conditions, they more quickly succumbed to tuberculosis than had the mice in the group.

Christian and Williamson (1958) induced subcutaneous granulomas in mice in a group and then into mice in isolation. The granulomas of the former weighed 19% less than those of the latter. These results were interpreted to mean that crowding had a suppressive effect on processes of inflammation.

Hence it is not unreasonable to expect that a pathogen will be more readily transmitted from host to host in crowded conditions. These experiments indicate, however, that resistance of an individual to disease is also a factor to be considered. More importantly, this resistance is related to the density of the population.

Populations of animals in nature do not invariably increase in geometric fashion until an upper limit is reached, and then level off at a constant value. Quite often there are fluctuations which are unusually extreme in maxima and minima. This fact is almost a matter of common observation, and a wealth of material can be found about these "cycles" of populations. Much of the literature is descriptive, presenting data from previous records in addition to the author's personal observations. There are two essential questions posed by this phenomenon: 1) How regular are the fluctuations in terms of numbers?

Are they truly cycles, even in the dictionary's definition of that word? Are they so regular and consistent that future events can be predicted after an analysis of the data? 2) What is the underlying cause of these changes in density? Is there some environmental factor that fluctuates or oscillates with the same periodicity as the density of population itself? If such be the case, what effect does the predator-prey relationship, food-supply, or disease vectors have on a population? Do these factors play some role which is secondary to extra-terrestrial events? Sunspots (Elton, 1924) and the lunar cycle (Siivonen and Koskimies, 1955) have been postulated as having some relation to or controlling the regularity of such cycles of population.

Palmgren (1949) chose a series of numbers by rolling dice and by drawing cards; then he compared the results with data on oscillation of populations. He concluded that "the short-term fluctuations of population densities in northern mammals and birds seem largely explainable as a compound result of random variables of some master factors, apparently climatic, and the influence of the population density of the previous year." Cole (1951) is of the same opinion and states that "the oscillations of any hypothetical factors determining population size need only be about as regular as would be expected of a random variable. . . . If, as is known to be the case, many factors operate separately to favor population change, we might expect the resultant of the many haphazard influences to appear as essentially random fluctuations." This paper is followed by a symposium on the subject, in which his theory is more fully elaborated (Cole, 1954).

Seton (1911) estimated that at the peak density, Alberta Province had a population of one hundred million "fat, white, bunnies". In a

period of weeks the rabbit population was decimated by some factor which he thought was an epidemic. "To explain the variations," he wrote, "we must seek not the reason for increase--that is normal, but for the destructive agency that ended the increase." Regardless of the periodicity of the fluctuations of populations, mentioned here only in passing, the physiological symptoms and behavioral characteristics of animals in their phase of decline show a clearly defined pattern of consistency.

The population "crash" of Norwegian lemmings (Lemmus lemmus) in Sweden in 1960 was not associated with either lack of food or excessive predation (Curry-Lindahl, 1962). Green, Larson, and Bell (1939) reported that there was no increase in resident predator population and no great influx of predators during a population "die-off" of snowshoe hares (Lepus americanus). Helminth and arthropod parasites, along with tularemia, were also eliminated as causative agents.

The sudden decrease of brown and varying lemmings (Lemmus trimucronatus and Dicrostonyx greenlandicus) of the central Canadian arctic, from 1959 to 1962, was not due to starvation or to malnutrition (Krebs, 1963). Chitty (1952) could observe no environmental conditions that would cause excessive mortality rates during the time of almost complete disappearance of voles (Microtus agrestis) from the Lake Vyrnwy area of Montgomeryshire. Elson, Ford, Baker, and Gardner (1931) examined a number of dead and dying wild house mice, using routine blood cultures as well as bacteriological and histological preparations. All results were negative.

The observations made by Godfrey (1955), while studying two isolated populations of field voles (Microtus agrestis), are representative of many field studies. "There was no evidence that food was short. The voles were known to be eating every species of grass on the areas, and

there was little sign of general damage to vegetation as frequently observed in periods of vole abundance. There was no evidence from body weight or general condition that the voles were starving during the peak year or following winter, and the crash itself proceeded throughout the growing seasons of the grasses. . . There is no reason to suppose that disease alone was sufficient to have killed the young. . . Unfavorable weather, such as extreme heat or cold, might have caused some of the deaths among newly-weaned young, but by itself it is unlikely to have eliminated the young on one area without affecting those on the other half a mile away."

MacLulich (1937), while investigating the causes of population "crashes" in the varying hare (Lepus americanus), observed that hares were lethargic and could almost be touched before they would sluggishly move away. After examining 160 specimens, he could not associate this condition with any particular disease vector. Some of the specimens had ample food in their stomachs, and in two instances there was no evidence of depletion of food supply.

Green and Larson (1938a) studied the "cycle" of the snowshoe hare (Lepus americanus), which occurs approximately every ten years in the Lake Alexandria region of Minnesota. Hares which appeared quite normal were suddenly stricken with convulsions and died in seizures. The convulsions were found to be associated with hypoglycemia, and death was caused by a low level of blood sugar. They then concluded: "So far as we can determine, the basis of the disease is degeneration of the liver. . . The liver degeneration is associated with a failure to store glycogen. When carbohydrate reserve in the liver reaches a low value, the hare leads a precarious existence. As excitement or exertion depletes the small glycogen reserve, the blood sugar drops below the normal range,

unconsciousness supervenes, and the hare dies. Routine technical procedures have shown that normal hares have an average liver glycogen value of 5.5%, while hares in shock have values from 0.02 to 0.18%. Investigating this matter further, Larson and Green (1938) reported that seven of 31 hares had microscopic lesions of the adrenal glands, 11 had hemorrhagic thyroid glands that were distended with large amounts of colloid, and 18 had congestion or hemorrhages of the liver. Chitty (1957) reported gross splenic hypertrophy, accompanied by a form of hemolytic anemia, occurred in dense breeding populations of voles (Microtus agrestis).

A. Howells, R.C.M.P., a correspondent of Chitty's and Elton's (1937), recorded observations made during a decimation of population: "Very scarce. Sudden decrease in April and May, 1936. Symptoms: disease of the liver -- spots and pimples. . . appear to have a stroke and die almost immediately. Previously noted on one or two occasions; around March and April, 1935, in the Herb Lake District especially. Symptoms: mucous discharge from the mouth, spots on liver; rabbits would run a short distance then drop over dead." It is of interest to compare this report with the observations made by Findlay and Middleton (1934) during a period of high mortality rate among wild voles (Microtus agrestis) in Scotland North Wales: "The first appearance of ill health was a slight sluggishness in movement, the eyes being less prominent than usual. This lethargic period was followed by one of convulsive activity. The voles exhibited head retraction, circular movements, hunching of the back, and frequently paralysis of the hind limbs, associated with periodic convulsive movements. Sometimes death occurred during these convulsions, more commonly the voles passed into a catatonic condition, followed after a short period by death".

Errington (1954) collected 509 specimens of muskrat (Ondatara zibethicus) which had died during two "cyclic highs" on his study area in Iowa. He could distinguish nine major syndromes or combinations of syndromes that caused death; and, of the 509 specimens, 460 had necrotic foci in the liver and occasionally in the spleen. Intestinal hemorrhages, particularly of the cecum and rectum were common.

Lechleitner (1958) followed a population of black-tailed jack rabbits (Lepus californicus) through a period of sudden decline. He attributed about 20% of the deaths to coccidiosis, but could not find a causative agent for the majority of the deaths. At necropsy, the carcasses showed mahogany-red livers, along with frequent hemorrhages about the enlarged adrenals. The behavior of one animal was described: "In the present study one hare was found lying on its side. It was extremely 'bug-eyed' and moribund, but occasionally made running motions with its feet. At the same time, there was a continuous raising and lowering of its head, accompanied by gasping. It died with its extremities extended, and rigor mortis set in almost immediately".

Evans (1949) studied the structure of a population of house mice (Mus musculus) in a granary at Davis, California. He began his study with a number of mice too great to estimate, but he noted that five traps were sprung within 10 minutes of setting and that mice could be heard rustling and squeaking on all sides. The date was January, 1942. By June of that year the population had completely died out. No necropsies were made but the investigator kept notes on all apparent abnormalities. "Most of the mice were already dead when the traps were opened; a few were moribund and incapable of maintaining equilibrium; in one case there was paralysis of the hind quarters. Other abnormal signs included pure white feces (? undigested rolled oats or flour) and dark brown (? bloody) urine."

Abstracting for the moment for the differences of species, the behavioral pattern during a decline in population is described in the following terms: sluggishness, eyes less prominent, "bug-eyed", lethargic manner of acting, paralysis of the hind limbs, and convulsions; immediate intestinal hemorrhages; splenic hemorrhages; splenic hypertrophy, enlargement and hemorrhages of the adrenal glands, bloody urine, and hypoglycemia. This type of behavior and these symptoms are not to be attributed to any known disease. Nor is it possible to lay the blame for the decline in population on predators. Nor, in the case just cited, was there an insufficiency in the supply of food. Before attributing such a decline in population to some kind of "shock disease", it is necessary to relate the observations which have been made to the general theory of regulating population. It is to that theory that attention must now be directed.

There is good reason to anticipate that those processes which regulate the density of a population will bring about continual adjustments which will equate the level of the population to the upper symptote of the environment. It may happen, however, that environmental changes will be so sudden that the homeostatic systems are over-taxed and are unable to make the necessary adjustments. After control of recruitment and emigration has proved to be inadequate, a "die-off" appears to be the final method of defense by which a population protects its available resources from exhaustion and depletion. This final measure is most often observed where the supply of food fluctuates abruptly with seasonal changes. The experience of the present writer in working with Sigmodon hispidus on the prairies of north central Oklahoma has shown that there is a correlation between the supply of food and density of the population. Such environmental changes, however, are extrinsic to the animal and cannot fully explain growth or decline of the population. Intrinsic factors must be given

careful consideration in order to shed some light on the question of density and its built-in controls.

Selye (1937) has developed a working hypothesis which directs attention to the pituitary and adrenal glands as homeostatic regulators. The syndrome which results from alteration of the pituitary-adrenocortical axis is referred to as the General Adaptation Syndrome. Selye later (1946) defined this syndrome as "the sum of all non-specific, systemic reactions of the body which ensure upon long continued exposure to stress". Stress itself may be induced by any number of damaging agents: cold, surgical shock, spinal shock, traumatic injuries, excessive muscular exercise, or drugs. Atrophine, morphine, adrenaline, vasopressin, and formaldehyde are the drugs most frequently used for this purpose. During the first stage of the syndrome, the alarm stage, the following morphological and physical changes occur: acute gastro-intestinal ulcers, a result of dissolution of the mucosa and often accompanied by inflammatory infiltrations of the sub-mucosa and muscularis; hyperplasia of the adrenal cortex and rapid loss of lipid granules from the cortical cells; discharge of the chromaffin cells in the adrenal medulla; decreased liver weight and occasional fatty degeneration or cloudy swelling of the liver; fecal necroses of the liver; hemoglobinuria and albuminuria; exophthalmos; increased lachrymation and salivation; cerebral hemorrhages caused by periarteritis nodosa of the brain, resulting in clonic seizures. Selye (1939) also pointed out that in the female rat there is inhibition of estrus and a decrease of ovarian weight. The loss of ovarian weight is attributed to a scarcity of mature follicles and corpora lutea, in addition to a marked involution of interstitial tissues.

The General Adaptation Syndrome has two further stages. During the

stage of resistance the organism acquires a tolerance toward the stress agent, and the symptoms disappear. If stress continues, resistance is diminished and the third stage, that of exhaustion, follows. This syndrome has been associated with the decimation of populations by a number of researchers: Green, Larson, and Bell (1939); Christian (1950); Lechleitner (1958); Louch (1955).

Whatever the causative agent, presumably there is an effect on the pituitary, which initiates an increase in the production and release of adrenocorticotrophic hormone (ACTH). Rosch (1957) has shown that ACTH stimulates the adrenal cortex to release glucocorticoids, but does not directly control the release of mineralocorticoids. The glucocorticoids, in addition to promoting glycogen formation, inhibit granuloma barriers and cause an involution of connective elements of tissue, thus decreasing the general resistance of the body.

During the time of stress, moreover, the primary and accessory reproductive organs become smaller and less active. Since the primary organs are stimulated by gonadotropic hormones which are of pituitary origin, it appears that the output of these hormones is diminished. Other bodily functions which depend on pituitary hormones are also affected. Young animals grow at a slower rate and lactating females produce less milk.

The basic rationale of the General Adaptation Syndrome is that during periods of stress the pituitary secretes a greater amount of ACTH, which has a direct effect on the adrenal cortex. The adrenal cortex, under this stimulus, secretes an increased quantity of glucocorticoids. According to Selye (1946), when the amount of ACTH reaches a higher level, there is a decrease in the secretion of somatotrophic hormone, lactogenic hormone, and gonadotropic hormones.

Christian and Ratcliffe (1952) cite 14 instances of death among captive wild animals which were attributable to shock disease. All of the animals died after being subjected to minor stresses, and 10 were observed to have died of convulsive seizures; rigor mortis set in immediately after death. At necropsy it was found that the lymphoid tissue was hyperplastic, the livers were reduced in size and were dark; the glycogen stores of the liver were depleted. Hypoglycemia was thought to be the immediate cause of death.

There are two criteria usually employed to measure the amount of stress to which an animal is subjected: one is the relative size and variation in weight of the adrenal glands, which is found to correlate positively with density of population (Christian and Davis, 1955; Louch, 1958); the other measurement is the size and weight of the primary and accessory reproductive organs (Christian, 1955). Christian and Davis (1955) found that a reduction of the density of population by removal of some of the animals resulted in decreased weights of the adrenal glands of Norway rats (Rattus norvegicus). Using the same experimental species, Christian and Davis (1956) observed that the adrenal glands of both sexes increased in weight as the population increased in density. They concluded that there is a density-dependent stimulus in the pituitary-adrenocortical system which operates in a quite independent fashion: independently, that is, of seasonal necessities brought about by the environment.

Christian (1956) pointed out that the adrenal weights of male house mice (Mus musculus) which came from high populations were 25% heavier than those which had been subjected to paired-isolated controls. Accompanying this change in adrenal weights, there was a delay in the development of preputial glands, seminal vesicles, and testes.

Louch (1956) says that high populations of confined meadow voles (Microtus pennsylvanicus) are accompanied by an increase of adrenocortical activity. According to Welch (1962) the adrenals of deer are larger on a densely populated range than they are on a sparsely populated one; and, on a single deer range, the size of the adrenals increased, parallel to the density of the population.

To cite Christian (1960) once again: when albino and wild stock mice are grouped together, there is a diminished uterine weight, suggesting thereby that a suppression of gonadal function and gonadotropic secretion has taken place. Furthermore, it has been suggested (Christian and Lemunyan, 1958) that crowding has an adverse effect on lactation. Christian (1959b) attributed the increase of adrenocortical activity and the decrease of reproductive activity to social competition. Such an attribution as this adds another dimension to the familiar concept of the upper symptote or carrying capacity of a particular environment.

By way of brief summary, then, it appears that such environmental factors as increases of social pressure and more frequent contacts between animals initiate a greater activity of the pituitary-adrenocortical system and depress the pituitary-gonadal system. By these processes the reproductive and mortality rates are altered, and the rate of growth of the population is regulated. Christian (1957, 1959b) has worked out a more extensive statement of this theory of the density of population and its effect on the endocrine system.

Sigmodon hispidus as an Experimental Animal

This introduction is broader in scope than the actual research which is to be reported; it is something of the nature of an apologia

disquisitione mea. It is the fond hope of the present writer that in pursuit of this course of action the data which have been obtained through research and the results of those data will provide some contribution to that theory of natural selection which places a premium on adaptability and flexibility of living organisms. It is further hoped that these studies, and the reports thereon, will suggest more experimentation and even further studies, particularly at Oklahoma State University, and with Sigmodon as an experimental animal.

One final word about Sigmodon hispidus as the experimental animal of these investigations and we will have done with the beginning. The cotton rat (Sigmodon hispidus) is a common field mammal of the southern United States and Mexico. Komarek (1937) and Mayer and Mayer (1944) think that it has frequent irruptions of population in cycles of four to five years. Stoddard (1944) noticed a high internal population of parasites among cotton rats during a 1934 irruption of population in Louisiana. Tissues were examined for tuleremia, but all results were negative except for three cases of severe coccidiosis. According to Schendel (1940) Oklahoma and Texas experienced an increase in cotton rats in 1939. Odum (1955) reports that in Georgia there were peaks of abundance during 1946, 1948, and 1952. Haines (1963) says that in Texas an outbreak lasted from 1958 to 1960, after which the population virtually disappeared. The reports of Goertz (1962) show that in Oklahoma, during late February and March, the population of cotton rats fell from 20 or 30 animals per acre to zero.

Mayer and Mayer (1944) have made laboratory studies of the cotton rats, and Clark (1946) has determined the estrous cycle of the female. Golley (1961) has investigated the zonation of the adrenal cortex.

The animal is found in relative abundance near Stillwater, Oklahoma, is not difficult to trap, and is comparatively gentle while being handled. For these reasons, over and above the enigma of sudden irruptions in populations, it has been chosen as the subject of the present research project.

CHAPTER II

METHODS

The animals used in this research project were selected from two non-contiguous field populations, as well as from stock which had been caged or penned for several months. The first section of this chapter describes the study areas and the methods used in field work, while the second section outlines the procedures used in laboratory analyses.

Study Areas and Field Techniques

Grid Population. The Oklahoma Cooperative Wildlife Research Unit has the use of 20 acres of upland prairie and open woodland on the west side of Oklahoma State Highway 86, about a half mile north of Stillwater Creek and the most westerly arm of Lake Carl Blackwell. A description of the vegetation and cotton rat habitat can be found in Goertz (1962). The 20 acres were surveyed and a line 20 chains long (1,230) on the east side was used as one reference line. The chain lengths on this line were numbered from 1 to 20. The reference line on the north extends for 10 chains (660 feet). The chain lengths on this line were lettered from A to J. There is a live-trap located at every point where a north-south chain intersects an east-west chain. This should give 200 trap sites, but only 171 traps were placed on the grid because the first chain line (line A) on the east and the first chain line (line 1) on the north were omitted. To illustrate, a point designated as D-15 is the point where the fifteenth chain from the north boundary intersects the fifth chain

from the east boundary. The traps are a quasi-permanent part of the study area, being left out between trapping periods. Each was covered with a quonset-shaped hood of roofing asphalt as protection from the elements. In addition to this, the traps were covered with loose vegetation during the summer and a handful of grass was placed in the trap for bedding purposes in the winter.

The traps were opened for five days each month, giving a total of 855 trap-nights monthly. Density of the population was estimated by the simple recapture method of Bailey (1951). By way of illustration, the application of this method to data from the month of January, 1964, is given in Appendix 1.

Rolled or crimped oats were used for bait. While operating the trap lines, animals were weighed on a dietitian's scale and field notes were taken about the reproductive condition of the animals. The field notes were later transferred to permanent filing cards. From these cards it is possible to tell at a glance how often an individual animal was trapped, its weight, the trap site(s) at which it was taken, and its reproductive condition. Field notes and data cards for the period from October, 1959 to December, 1961, were also available.

Five of the largest adult male cotton rats trapped on the east half of the grid were returned to the laboratory on the fourth day of a trapping period, and five adult males from the west half were returned on the fifth and final day of trapping. These animals were taken to the laboratory in the field traps to reduce additional sources of stress.

University Farm Population. Originally it was intended to chose a site close to the University for trapping animals to stock the pens and cages. This was found three miles west of the University Campus on McElroy Street, at a roadside area bordering a field similar to the grid. During

September and October, 1963, 149 animals were removed from this population and confined in either pens or cages. Since this population was so sharply reduced, samples of five adult males were taken to the laboratory in September and in October, to be compared to the grid samples for these months. The same procedure was followed from January to May, 1964, to determine whether reproductive activity would be initiated earlier in a population subjected to predation. All animals trapped during these periods were removed from the population. The relative density of this population can be compared to that of the grid by comparing the percentages of trapping success.

Penned Populations. A large pen, with outer dimensions of 100 feet by 80 feet, was constructed in an area densely covered with Bermuda grass. This pen was further subdivided into four pens of 50 feet by 40 feet each. Corrugated metal was used for fencing material, and one section was entrenched at least one foot into the ground with another section wired about this. The metal fence is thus about four feet in height.

During September and October, 1963, the pens were stocked with all of the animals trapped at the University Farm in the following numbers: 72 in pen 1; 41 in pen 2; 26 in pen 3; 10 in pen 4. It was planned to maintain these populations for two months, sample from all four pens, and allow the remaining animals to over-winter in the pens. The procedure had to be modified for reasons to be presented in the next chapter.

Caged Populations. Twenty cages for small mammals were constructed, using the design suggested by Dice (1929). These were placed on a rack that can best be described as a non-revolving, five-tiered "Lazy Susan". The cages were placed in a large open-air flight cage, where a study of cowbirds was in progress. The caged animals were thus exposed to the

weather, and with only an overhead shelter. Cages were stocked with isolated and grouped cotton rats, and it was planned to conduct laboratory studies after a period of two months. This procedure was partially modified, as will be seen in the presentation of data and results.

Laboratory Analyses

All of the laboratory studies were made with adult male cotton rats, the largest individuals obtainable from the sampled populations.

Testicular Metabolism. One testis was exised and chilled immediately to 0°C., after which the teased tubules were prepared for manometric studies. Uptake of oxygen was determined according to the method of Umbreit (1857). Utilization of glucose was measured following the method of Keston (1956) and production of lactic acid according to Summerson (1941).

The remaining testis tissue was homogenized in a ratio of 1:20 volumes of double distilled water with a Potter-Elvehjem homogenizer and aliquots were removed for the following chemical determinations: Protein, using the method suggested by Lowry (1951); deoxyribonucleic acid (DNA) and ribonucleic acid (RNA) as outlined by Schmidt and Thannhauser (1945).

Accessory Reproductive Organs. The preputial glands, seminal vesicles, and ventral prostate were dissected and weighed to the nearest milligram. Fresh organ weights are reported.

Adrenal Glands. The paired adrenals were dissected and fixed in 10% formalin solution. The fixed glands were then cleaned and weighed to the nearest milligram. This procedure was followed, rather than cleaning and weighing the fresh gland, because of the fragility of the gland and the toughness of the connective tissue covering.

One adrenal from each animal was sectioned and stained with hematoxylin and eosin.

This laboratory procedure was followed with the ten animals taken from the grid population each month, five or ten from the University Farm population each month, and all animals taken from the pens or cages.

CHAPTER III

RESULTS

Grid Population

Variations in Autumnal Breeding. The data on sigmodon, presented in Tables I and II, have been gleaned from field notes of previous years, as well as from the present year of study. The presumption is that there is a relationship between success in trapping and density of population. No attempt is made to estimate the density of the population per se. It is also presumed that these animals share an equal likelihood of being captured, regardless of their breeding condition; hence the number of animals captured and re-captured might be used to determine the percentage of trapping success. The percentage of success in trapping was obtained by dividing the number of trapped animals by the total number of traps and multiplying the quotient by 100. The breeding condition of the animals was ascertained in the field by the position of the testes and the orifice of the vulva, both of which are readily observed in this species.

Tables III and IV present the data in a different form, along with environmental factors which might have an effect on the length of the breeding season. Linear coefficients of correlation for the observed breeding condition, in addition to the percent of success in trapping and various climatic factors, are also to be found in these tables. Since the most significant coefficient of correlations is between

TABLE I

PERCENT TRAPPING SUCCESS AND BREEDING CONDITION OF MALE SIGMODON
DURING THE FALL MONTHS OF 1959, 1960, 1961, AND 1963

| Month | Total Trapped | Total Traps | Percent Success | Males Capt. and Recapt. | Testes Descended | Percent Testes Descended |
|-----------|---------------|-------------|-----------------|-------------------------|------------------|--------------------------|
| Oct. '59 | 565 | 963 | 58.67 | 235 | 9 | 3.83 |
| Nov. '59 | 773 | 1145 | 67.51 | 354 | 0 | 0 |
| Sept. '60 | 1 | 1710 | .0005 | 1 | 1 | 100.00 |
| Oct. '60 | 6 | 1710 | .0035 | 6 | 3 | 50.00 |
| Nov. '60 | 23 | 1710 | .0135 | 13 | 1 | 7.69 |
| Sept. '61 | 416 | 1710 | .2432 | 254 | 125 | 49.21 |
| Oct. '61 | 189 | 1197 | .1579 | 109 | 60 | 55.04 |
| Nov. '61 | 155 | 1197 | .1295 | 59 | 11 | 18.64 |
| Sept. '63 | 673 | 855 | 78.71 | 325 | 2 | 0.0006 |
| Oct. '63 | 713 | 855 | 83.40 | 367 | 6 | 0.016 |
| Nov. '63 | 684 | 855 | 80.00 | 339 | 0 | 0. |

TABLE II

PERCENT TRAPPING SUCCESS AND BREEDING CONDITION OF FEMALE SIGMODON
DURING THE FALL MONTHS OF 1959, 1960, 1961, AND 1963

| Month | Yr. | Total Trapped | Total Traps | Percent Success | Females Capt. and Recapt. | Vulva Open | Percent Vulva Open |
|-------|-----|---------------|-------------|-----------------|---------------------------|------------|--------------------|
| Oct. | '59 | 565 | 963 | 58.67 | 330 | 58 | 17.57 |
| Nov. | '59 | 773 | 1145 | 67.51 | 419 | 39 | 10.74 |
| Sept. | '60 | 1 | 1710 | .0005 | 0 | 0 | 0 |
| Oct. | '60 | 6 | 1710 | .0035 | 0 | 0 | 0 |
| Nov. | '60 | 23 | 1710 | .0135 | 10 | 3 | 30.00 |
| Sept. | '61 | 416 | 1710 | .2432 | 162 | 45 | 27.78 |
| Oct. | '61 | 189 | 1197 | .1579 | 80 | 44 | 55.00 |
| Nov. | '61 | 155 | 1197 | .1295 | 96 | 25 | 38.40 |
| Sept. | '63 | 673 | 855 | 78.71 | 318 | 81 | 25.50 |
| Oct. | '63 | 713 | 855 | 83.40 | 367 | 31 | 8.30 |
| Nov. | '63 | 684 | 855 | 80.00 | 342 | 10 | 2.97 |

TABLE III

PERCENT BREEDING MALE SIGMODON CORRELATED WITH TRAPPING SUCCESS,
AVERAGE MINIMUM TEMPERATURE, AVERAGE MAXIMUM TEMPERATURE,
LOWEST MONTHLY TEMPERATURE, AND MONTHLY PRECIPITATION

| Month | Yr. | Percent Testes Descended | Percent Trapping Success | Average Maximum Temp. (°F.) | Average Minimum Temp. | Total Precipitation (Inches) | Monthly Low Temp. (°F.) |
|-------|-----|--------------------------------|--------------------------------|-----------------------------------|-----------------------------|------------------------------------|----------------------------|
| Sept. | '60 | 100.00 | .0005 | 88.2 | 61.2 | 0.74 | 48 |
| Oct. | '61 | 55.04 | .1579 | 75.8 | 50.7 | 1.27 | 28 |
| Oct. | '60 | 50.00 | .0035 | 79.1 | 51.1 | 6.30 | 30 |
| Sept. | '61 | 49.31 | .2432 | 81.5 | 59.8 | 9.43 | 44 |
| Nov. | '61 | 18.64 | .1259 | 58.5 | 38.1 | 3.56 | 24 |
| Nov. | '60 | 7.69 | .0135 | 66.5 | 38.9 | 0.65 | 19 |
| Oct. | '59 | 3.83 | 58.67 | 72.0 | 46.1 | 12.08 | 32 |
| Oct. | '63 | 0.02 | 83.40 | 86.1 | 53.4 | 2.07 | 32 |
| Sept. | '63 | 0.01 | 78.71 | 87.5 | 62.3 | 3.03 | 39 |
| Nov. | '59 | 0. | 67.51 | 58.1 | 29.7 | 0.40 | 8 |
| Nov. | '63 | 0. | 80.00 | 65.1 | 36.9 | 1.69 | 21 |

| | |
|--|---------|
| Correlation coefficient between testes descended and trapping success | -0.7182 |
| Correlation coefficient between testes descended and average maximum temperature | 0.4524 |
| Correlation coefficient between testes descended and average minimum temperature | 0.5318 |
| Correlation coefficient between testes descended and average total precipitation | 0.0202 |
| Correlation coefficient between testes descended and lowest temperature | 0.6057 |

TABLE IV

PERCENT BREEDING FEMALE SIGMODON CORRELATED WITH TRAPPING SUCCESS,
 AVERAGE MAXIMUM TEMPERATURE, AVERAGE MINIMUM TEMPERATURE,
 LOWEST MONTHLY TEMPERATURE, AND MONTHLY PRECIPITATION

| Month | Yr. | Percent Vulva Open | Percent Trapping Success | Average Maximum Temp. | Average Minimum Temp. | Total Precipitation (Inches) | Monthly Low Temp. |
|-------|-----|--------------------------|--------------------------------|-----------------------------|-----------------------------|------------------------------------|-------------------------|
| Oct. | '61 | 55.00 | .1579 | 75.8 | 50.7 | 1.27 | 28.0 |
| Nov. | '61 | 38.40 | .1295 | 58.5 | 38.1 | 3.56 | 24 |
| Nov. | '60 | 30.00 | .0135 | 66.5 | 38.9 | 0.65 | 19 |
| Sept. | '61 | 27.78 | .2432 | 81.5 | 59.8 | 9.42 | 44 |
| Sept. | '63 | 25.50 | 78.71 | 87.5 | 62.3 | 3.03 | 39 |
| Oct. | '59 | 17.57 | 58.67 | 72.0 | 46.1 | 12.08 | 32 |
| Nov. | '59 | 10.74 | 67.51 | 58.1 | 29.7 | 0.40 | 8 |
| Oct. | '63 | 8.30 | 83.45 | 86.1 | 53.4 | 2.07 | 32 |
| Nov. | '63 | 2.97 | 80.00 | 65.1 | 36.9 | 1.69 | 21 |

| | |
|--|---------|
| Correlation coefficient between vulva open and trapping success | -0.8067 |
| Correlation coefficient between vulva open and average maximum temperature | 0.5596 |
| Correlation coefficient between vulva open and average minimum temperature | 0.4510 |
| Correlation coefficient between vulva open and total precipitation | -0.0311 |
| Correlation coefficient between vulva open and lowest monthly temperature | 0.0234 |

success in trapping and presumed breeding condition (negative in both male and female), the formulae for lines of regression were also calculated. The formula for the regression line of the percent of the descended testes and percent of success in trapping is $Y = -0.84X + 40.92$. The formula for the regression line of the percent of open vulvae and the percent of success in trapping is $Y = -1.95X - 87.84$.

Annual Changes in Density of Population. The monthly estimate of the density of population, the reliability of the estimate, and the percent of success in trapping -- all these data are to be found in Table V. Data for the two months of July and August could not be obtained because the road to the trapping site was blocked off for repairs. When the road block was by-passed for two days in July in order to open the traps, it was discovered that the summer weather had caused a high mortality rate among the animals which had been trapped. Eighty-eight animals were trapped on the first day, of which 42 were dead in the traps. On the second day 67 animals were trapped, and 17 were dead. Since mortality due to heat exhaustion was so high (47.7% and 25.4% on those two days) and since driving conditions were hazardous, the traps were closed for these two months. Because of the snow and ice in December, trapping was also suspended after the first two days. Contrary to expectation, there was no mortality during these two days.

Seasonal Changes in Breeding Condition. The breeding conditions of both male and female sigmodon, as observed in the field, are tabulated in Tables VI and VII. Since pregnancy in the early stages and lactation in the later stages of nursing were not as easily determined as were the position of the testes and condition of the vulvae, these observations are not as reliable. The number of individual animals, not the total number of those trapped and re-trapped, is recorded in these two tables.

TABLE V.

ESTIMATES OF THE SIGMODON POPULATION ON THE GRID
FROM JUNE, 1963 TO MAY, 1964

| Month | Population Estimate | Variance | Coefficient of variation | Percent Trapping Success |
|-----------|---------------------|----------|--------------------------|--------------------------|
| June | 222 | 19.42 | 8.74 | 33.9 |
| September | 1043 | 101.58 | 9.73 | 78.7 |
| October | 786 | 55.77 | 7.09 | 83.4 |
| November | 705 | 52.52 | 7.45 | 80.0 |
| January | 454 | 20.70 | 4.83 | 80.1 |
| February | 212 | 12.81 | 6.06 | 41.1 |
| March | 81 | 16.28 | 20.10 | 10.9 |
| April | 9 | 5.20 | 57.77 | 1.8 |
| May | 8 | 2.31 | 28.87 | 2.0 |

TABLE VI

BREEDING CONDITION OF MALE SIGMODON IN THE POPULATION
ON THE GRID FROM JUNE, 1963 TO MAY, 1964

| Month | Number of Males | Percent of Males | Number of males with testes descended | Percent of males with testes descended |
|-----------|-----------------|------------------|---------------------------------------|--|
| June | 98 | 54.4 | 18 | 18.4 |
| September | 265 | 48.2 | 2 | 0.8 |
| October | 268 | 51.4 | 6 | 2.2 |
| November | 231 | 49.6 | 0 | 0 |
| January | 185 | 49.9 | 0 | 0 |
| February | 88 | 46.3 | 0 | 0 |
| March | 19 | 36.5 | 0 | 0 |
| April | 4 | 44.4 | 1 | 25.0 |
| May | 4 | 50.0 | 2 | 50.0 |

TABLE VII

BREEDING CONDITION OF FEMALE SIGMODON IN THE POPULATION
ON THE GRID FROM JUNE, 1963 TO MAY, 1964

| Month | Number of Females | Percent of Females | Number Lactating | Percent Lactating | Number Pregnant | Percent Pregnant | Number Vulva Open | Percent Vulva Open |
|-----------|-------------------|--------------------|------------------|-------------------|-----------------|------------------|-------------------|--------------------|
| June | 82 | 45.6 | 25 | 30.5 | 28 | 34.2 | 49 | 59.7 |
| September | 247 | 51.8 | 94 | 38.8 | 26 | 10.5 | 63 | 25.5 |
| October | 253 | 48.6 | 65 | 25.7 | 7 | 2.8 | 21 | 8.3 |
| November | 235 | 50.4 | 11 | 4.7 | 0 | 0 | 7 | 2.9 |
| January | 186 | 50.1 | 0 | 0 | 0 | 0 | 3 | 1.6 |
| February | 102 | 53.7 | 0 | 0 | 0 | 0 | 0 | 0 |
| March | 33 | 63.5 | 0 | 0 | 0 | 0 | 1 | 3.3 |
| April | 5 | 55.6 | 0 | 0 | 0 | 0 | 1 | 20.0 |
| May | 4 | 50.0 | 0 | 0 | 1 | 25.0 | 2 | 50.0 |

Season Changes in Weight Classes. A dietitian's scale was used for weighing the animals in the field. On rainy days, the cloth sack in which the animals were weighed would gain in weight; adjustments, however, were continually made during the course of the day. Animals which were returned to the laboratory were weighed under better conditions and on more accurate scales; the weight usually did not vary more than five grams from the weight in the field. The percent of animals in each weight class for each month is summarized in Table VIII, where the animals in the lowest of the classes of weight are presumed to be the youngest.

Emigration and Immigration. There was no possible way in this field study to estimate the number of animals that had emigrated from the grid, as opposed to those that had died or for some reason or other had not been re-captured. By the end of October, however, 897 animals had been marked in a population that was estimated to have been 705 in November. Although this large number had been marked, 145 unmarked animals were trapped in November. This fact suggested, as only one possible explanation, that immigration onto the grid had been taking place. Table IX gives the number of the unmarked animals which had been trapped in each row of the grid after November, after which time most of the population was thought to have been marked. It should be borne in mind that immigration could occur at each end of the grid and that this possibility is not presented in the table. The letters in this table refer to the trap row, with B and J as the two outside rows.

Penned Populations

Pen 1. 74 animals were released into Pen 1 during the last week of September and the first two weeks of October, 1963. In December

TABLE VIII

CHANGES IN WEIGHT CLASSES OF THE SIGMODON POPULATION ON THE GRID,
AS MEASURED IN GRAMS AND EXPRESSED IN PERCENT

| Month | 10-29 | 30-49 | 50-69 | 70-89 | 90-109 | 110-129 | 130-149 | 150-169 | 170-189 | 190-209 |
|-----------|-------|-------|-------|-------|--------|---------|---------|---------|---------|---------|
| June | 1.66 | 14.44 | 17.77 | 17.22 | 10.56 | 10.00 | 11.11 | 7.22 | 8.33 | 1.66 |
| September | 8.89 | 22.13 | 18.38 | 18.18 | 11.66 | 8.11 | 6.72 | 3.16 | 2.17 | 1.19 |
| October | 3.84 | 13.24 | 29.37 | 23.61 | 18.69 | 8.45 | 2.30 | 0.39 | 0.19 | 0 |
| November | 3.00 | 12.23 | 21.67 | 32.62 | 19.96 | 8.58 | 1.93 | 0 | 0 | 0 |
| January | 0 | 12.93 | 55.26 | 26.42 | 5.39 | 0 | 0 | 0 | 0 | 0 |
| February | 0 | 17.37 | 61.05 | 17.37 | 3.68 | .52 | 0 | 0 | 0 | 0 |
| March | 0 | 5.78 | 69.22 | 25.00 | 0 | 0 | 0 | 0 | 0 | 0 |
| April | .0 | .0 | 22.22 | 77.77 | 1.11 | 0 | 0 | 0 | 0 | 0 |
| May | 0 | 0 | 37.50 | 37.50 | 25.0 | 0 | 0 | 0 | 0 | 0 |

TABLE IX
 NUMBER AND LOCATION OF NEWLY MARKED SIGMODON APPEARING
 ON THE GRID FROM NOVEMBER, 1963 TO MAY, 1964

| Month | Grid Line | | | | | | | | |
|----------|-----------|------|------|-----|-----|-----|-----|------|------|
| | B | C | D | E | F | G | H | I | J |
| November | 24 | 13 | 21 | 13 | 12 | 12 | 17 | 14 | 19 |
| December | 3 | 3 | 6 | 6 | 1 | 1 | 0 | 1 | 0 |
| January | 8 | 7 | 1 | 1 | 4 | 3 | 2 | 9 | 10 |
| February | 4 | 3 | 1 | 1 | 2 | 2 | 0 | 2 | 3 |
| March | 6 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| April | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| May | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| Total | 46 | 26 | 31 | 21 | 22 | 18 | 20 | 26 | 32 |
| Percent | 19.0 | 10.7 | 12.8 | 8.7 | 9.1 | 7.4 | 8.3 | 10.7 | 13.3 |

there were three survivors. In January, eight more animals were released into Pen 1. There were no surviving animals in February, as indicated by 40 unsuccessful trap-nights.

Pen 2. This pen was stocked with 41 animals in September and October. There were 15 animals remaining in December, of which three were taken to the laboratory. In January, 12 animals made up the entire population. After 40 unsuccessful trap-nights in February, it was presumed that the population had been extinguished.

Pen 3. Twenty-three animals were released into Pen 3 during September and October. Five of these were trapped and taken to the laboratory for analyses in December. In January, there were seven males and six females left; of these one of the females had an open vulva. Again after 40 unsuccessful trap-nights in February, the population was presumed to be extinct.

Pen 4. In October, this pen was stocked with 10 animals. In December there were five females, two of which were with open vulvae. During January, eight more animals were released into the pen. There were no survivors here either, after the usual 40 trap-nights in February.

The original plan had been to take samples from four populations of different densities at various time-intervals. Such a plan had to be abandoned. The small amount of data which had been obtained from these penned populations is integrated on a monthly basis with the data from the populations on the grid and on the University farm.

Caged Populations

Seven males were isolated in cages, and eight males were paired in four separate cages in October. It was planned to leave the animals in

cages with abundance of food, water, and cover for two months. Two of the males would not occupy the same cage. In one instance, necropsy revealed that the dead animal had a broken back and that its hind quarters were lacerated with teeth marks. Nor would animals readily survive when isolated in cages. Of the seven with which the experiment began, only three survived until December. The data from these cages are also incorporated with the data from the grid and from the farm.

Populations of the University Farm

Data could have been obtained from the University Farm during the month of November; at that time, however, more emphasis was being placed on caged and penned populations. All of the 179 animals which had been confined in pens and cages were obtained from the University Farm; the result is that the population was depleted more than Table X would indicate. Even after the experiments in the pen and cage had been completed, all the animals which had been trapped from this population were removed. Table XI presents, on a monthly basis, a comparison with success in trapping on the grid and at the University Farm.

Analyses of Adrenal Glands, Accessory Reproductive Organs, and Testes

Adrenal Weights. Tables XII and XIII summarize the data obtained from accessory sex organs and the adrenal glands of male cotton rats which had been taken from the populations on the grid and the University Farm. As the result of an oversight, the seminal vesicles and ventral prostates from the sample on the grid were not weighed in the month of June. The adrenal glands from the population on the University Farm, which had been taken during the month of February, were also discarded by accident.

TABLE X

PERCENT OF TRAPPING SUCCESS FOR THE SIGMODON POPULATION
AT THE FARM FROM OCTOBER, 1963, TO MAY, 1964

| Month | Number of Traps | Number of Animals Trapped and Removed | Percent Trapping Success |
|----------|-----------------|---------------------------------------|--------------------------|
| October | 150 | 60 | 40.0 |
| January | 150 | 30 | 20.0 |
| February | 150 | 12 | 8.0 |
| March | 180 | 3 | 1.7 |
| April | 300 | 2 | 0.6 |
| May | 150 | 2 | 1.3 |

TABLE XI

COMPARISON OF TRAPPING SUCCESS BETWEEN THE SIGMODON POPULATIONS
ON THE GRID AND AT THE FARM FROM OCTOBER, 1963 TO MAY, 1964

| Month | Grid | University Farm |
|----------|------|-----------------|
| October | 83.4 | 40.0 |
| January | 80.1 | 20.0 |
| February | 41.1 | 8.0 |
| March | 10.9 | 1.7 |
| April | 1.8 | 0.6 |
| May | 2.0 | 1.3 |

TABLE XII

WEIGHTS OF THE PAIRED PREPUTIAL GLANDS, PAIRED SEMINAL VESICLES, VENTRAL PROSTATE, AND
 PAIRED ADRENAL GLANDS, EXPRESSED IN MILLIGRAMS PERCENT, OF ADULT MALE SIGMODON
 TAKEN FROM THE POPULATION ON THE GRID

| Month | N | Preputial (mg%) | N | Seminal Vesicles (mg%) | N | Ventral Prostate | N | Adrenals (mg%) |
|-------|----|--------------------|----|---------------------------|----|------------------|----|-------------------|
| June | 10 | 152.8±10.72 | | --- | | --- | 10 | 24.80±1.53 |
| Sept. | 10 | 202.4±19.47 | 10 | 1007.25±65.00 | 10 | 186.30±37.34 | 10 | 17.89±0.97 |
| Oct. | 8 | 51.6± 5.89 | 7 | 45.72± 7.43 | 10 | 31.36± 8.31 | 10 | 24.02±1.74 |
| Nov. | 10 | 31.4± 2.55 | 10 | 1.68± 0.58 | 10 | | 10 | 22.50±1.06 |
| Jan. | 10 | 32.3± 4.49 | 10 | 11.54± 4.38 | 10 | | 10 | 29.41±1.67 |
| Feb. | 9 | 33.8± 3.91 | 10 | 5.32± 1.65 | 10 | | 8 | 33.32±1.64 |
| March | 5 | 20.7± 2.50 | 5 | 3.27± 0.23 | 5 | | 5 | 26.70±1.11 |
| April | 3 | 53.6± 7.43 | 3 | 137.50±17.19 | 3 | 49.01±19.27 | 3 | 33.19±3.34 |
| May | 3 | 193.3±20.31 | 3 | 898.63±107.70 | 3 | 264.2±71.40 | 3 | 32.11±1.97 |

TABLE XIII

WEIGHTS OF THE PAIRED PREPUTIAL GLANDS, PAIRED SEMINAL VESICLES, VENTRAL PROSTATE, AND
 PAIRED ADRENAL GLANDS, EXPRESSED IN MILLIGRAMS PERCENT, OF ADULT MALE SIGMODON
 TAKEN FROM THE POPULATION AT THE FARM

| Month | N | Preputial (mg%) | N | Seminal Vesicles (mg%) | N | Ventral Prostate (mg%) | N | Adrenals (mg%) |
|-------|---|--------------------------|---|---------------------------|---|---------------------------|---|-------------------------|
| Sept. | 5 | 224.8 [±] 15.71 | 5 | 936.7 [±] 174.80 | 5 | 284.7 [±] 50.85 | 5 | 19.60 [±] 1.16 |
| Oct. | 8 | 86.9 [±] 17.73 | 5 | 402.7 [±] 92.44 | 5 | 107.9 [±] 32.28 | 5 | 25.66 [±] 1.58 |
| Jan. | 5 | 27.9 [±] 10.90 | 5 | 5.8 [±] 1.51 | 5 | | 5 | 26.30 [±] 2.84 |
| Feb. | 5 | 19.7 [±] 3.11 | 5 | 20.2 [±] 7.62 | 5 | | | --- |
| March | 0 | | 0 | | 0 | | 0 | |
| April | 0 | | 0 | | 0 | | 0 | |
| May | 2 | 158.2 [±] 9.60 | 2 | 977.4 [±] 18.55 | 2 | 286.6 [±] 64.31 | 2 | 22.38 [±] 1.09 |

After November, the ventral prostates were not visible. Standard error is given after the mean weights in these and the following tables, wherever it is applicable.

Because it is thought that there are two factors (climatic conditions and density of population) which influence the parameters which are being estimated, the data are presented in two different forms. First, there is a separate monthly tabulation for each population in order to show more clearly the climatic relationship. Then, in the second place, there is the grouping of the different populations under each month in order to demonstrate the effects of the density of the population in two different populations during the same time-interval. This procedure will also be followed wherever it is applicable.

Table XIV presents the unadjusted mean weight, in milligrams, of the paired adrenal glands; the weight adjusted for body weight, and the weight, also in milligrams, of the largest of the paired adrenal glands in the entire sample.

Adrenal Sections. A total of 119 adrenal glands were sectioned and stained with haemotoxylin and eosin. Many of the first sections were lacking medullae; therefore, the paraffin blocks were shaved with a scalpel under a dissecting microscope and additional slides were made. Since the sections without medullae often did show the boundaries between zones of the cortex, they were also included in the results which are tabulated in Tables XV to XVIII. Of the 119 sections, 49 had centric medullae; 11 had acentric medullae; 9 had islets of medullary tissue; and 50 were without medullae. These data may give some indication of the relative size of the adrenal medulla in sigmodon.

The widths of the zona glomerulosa and the zona fasciculata were measured with an ocular scale under low power magnification; and this

TABLE XIV

WEIGHTS OF PAIRED ADRENAL GLANDS, EXPRESSED IN MILLIGRAMS, MILLIGRAMS PERCENT
AND MILLIGRAMS OF THE LARGES SAMPLE OF ADULT MALE SIGMODON
FROM ALL POPULATIONS

| Month | Population | Paired Adrenals (mg.) | Paired Adrenals (mg.%) | Largest Sample (mg.) |
|-------|---------------|--------------------------|---------------------------|-------------------------|
| June | Grid | 30.61±2.05 | 24.80±1.53 | 44.3 |
| Sept. | Grid | 26.05±3.32 | 17.89±0.97 | 41.0 |
| Sept. | Farm | 20.00±1.48 | 19.60±1.16 | 23.0 |
| Oct. | Grid | 23.20±2.00 | 24.02±1.74 | 34.0 |
| Oct. | Farm | 31.00±2.51 | 25.66±1.58 | 45.0 |
| Oct. | Cage (3 days) | 29.40±4.07 | 23.10±1.36 | 39.0 |
| Nov. | Grid | 24.10±1.28 | 22.50±1.06 | 34.0 |
| Dec. | Pen 2 | 21.33±0.91 | 27.04±2.34 | 23.0 |
| Dec. | Pen 3 | 25.50±0.77 | 30.30±2.37 | 29.0 |
| Dec. | Cage (2 mos.) | 27.67±4.11 | 31.20±3.16 | 29.0 |
| Jan. | Grid | 26.10±1.67 | 29.41±1.67 | 34.0 |
| Jan. | Farm | 22.60±2.04 | 26.30±2.84 | 30.0 |
| Feb. | Grid | 27.50±1.32 | 33.32±1.64 | 33.0 |
| Feb. | Farm | --- | --- | -- |
| March | Grid | 24.40±1.86 | 26.70±1.11 | 30.0 |
| March | Farm | --- | --- | -- |
| April | Grid | 20.00±4.51 | 33.19±3.34 | 29.0 |
| April | Farm | --- | --- | -- |
| May | Grid | 31.66±10.02 | 32.11±1.97 | 42.0 |
| May | Farm | 28.50± 0.50 | 22.38±1.09 | 29.0 |

TABLE XV

WIDTH OF THE ZONA GLOMERULOSA AND OF THE ZONA FASCICULATA IN MICRONS, AND THE NUMBER OF VACUOLES PER 12.5 MICRONS OF THE ZONA FASCICULATA IN THE ADRENAL CORTEX OF ADULT MALE SIGMODON FROM THE GRID POPULATION

| Month | N | Zona glomerulosa width (microns) | N | Zona fasciculata width (microns) | N | Average number of vacuoles per 12.5 microns | Greatest number of vacuoles per 12.5 microns |
|-------|----|-------------------------------------|-----|-------------------------------------|----|--|---|
| June | 6 | 56.0 [±] 0 | --- | --- | 6 | 0.16 | 1 |
| Sept. | 15 | 59.9 [±] 2.1 | 12 | 170.5 [±] 8.9 | 15 | 3.86 | 10 |
| Oct. | 16 | 56.9 [±] 3.0 | 13 | 180.8 [±] 10.9 | 16 | 4.19 | 10 |
| Nov. | 15 | 70.5 [±] 3.0 | 11 | 167.6 [±] 8.4 | 15 | 4.87 | 15 |
| Jan. | 11 | 74.7 [±] 6.4 | 8 | 182.8 [±] 5.9 | 11 | 2.91 | 14 |
| Feb. | 9 | 59.9 [±] 16.7 | 6 | 183.7 [±] 13.2 | 11 | 4.33 | 9 |
| March | 5 | 69.7 [±] 6.6 | 3 | 198.8 [±] 9.0 | 5 | 2.60 | 4 |
| April | 3 | 51.9 [±] 3.7 | 2 | 161.1 [±] 27.8 | 3 | 2.33 | 4 |
| May | 3 | 37.3 [±] 12.7 | 1 | 222.2 | 3 | 0.33 | 1 |

TABLE XVI

WIDTH OF THE ZONA GLOMERULOSA AND OF THE ZONA FASCICULATA, IN MICRONS,
VACUOLES PER 12.5 MICRONS OF THE ZONA FASCICULATA
 IN THE ADRENAL CORTEX OF ADULT MALE SIGMODON
 FROM THE POPULATION AT THE FARM

| Month | N | <u>Zona glomerulosa</u> width (microns) | N | <u>Zona fasciculata</u> width (microns) | N | Average number of vacuoles per 12.5 microns | Greatest number of vacuoles per 12.5 microns |
|-------|----|--|---|--|----|--|---|
| Sept. | 5 | 65.2 [±] 8.3 | 4 | 196.9 [±] 23.5 | 5 | 5.60 | 10 |
| Oct. | 10 | 59.6 [±] 10.4 | 9 | 199.9 [±] 10.4 | 10 | 2.80 | 8 |
| Jan. | 7 | 77.2 [±] 8.3 | 5 | 144.0 [±] 10.9 | 7 | 1.43 | 3 |
| Feb. | | | | | | | |
| March | | | | | | | |
| April | | | | | | | |
| May | 2 | 27.8 [±] 15.1 | 1 | 166.6 | 2 | 1.5 | 2 |

TABLE XVII

WIDTH OF THE ZONA GLOMERULOSA AND OF THE ZONA FASCICULATA,
IN MICRONS, OF THE ADRENAL CORTEX OF ADULT MALE SIGMODON
FROM ALL POPULATIONS

| Month | Population | Zona glomerulosa width (microns) | Zona fasciculata width (microns) |
|-------|---------------|-------------------------------------|-------------------------------------|
| June | Grid | 56.0 [±] 0 | --- |
| Sept. | Grid | 59.9 [±] 2.1 | 170.5 [±] 8.9 |
| Sept. | Farm | 65.2 [±] 8.3 | 196.9 [±] 23.5 |
| Oct. | Grid | 56.9 [±] 3.0 | 180.8 [±] 10.9 |
| Oct. | Farm | 59.6 [±] 10.4 | 199.9 [±] 10.4 |
| Oct. | Cage (3 days) | 56.0 [±] 0 | 200.0 [±] 0 |
| Nov. | Grid | 70.5 [±] 3.0 | 167.6 [±] 8.4 |
| Dec. | Pen 2 | 56.0 [±] 0 | 198.7 [±] 16.3 |
| Dec. | Pen 3 | 59.9 [±] 9.9 | 202.5 [±] 12.9 |
| Jan. | Grid | 74.7 [±] 6.4 | 182.8 [±] 5.9 |
| Jan. | Farm | 77.2 [±] 8.3 | 144.0 [±] 10.9 |
| Feb. | Grid | 59.9 [±] 16.7 | 183.7 [±] 13.2 |
| Feb. | Farm | --- | --- |
| March | Grid | 69.7 [±] 6.6 | 198.8 [±] 9.0 |
| March | Farm | --- | --- |
| April | Grid | 51.9 [±] 3.7 | 161.1 [±] 27.8 |
| April | Farm | --- | --- |
| May | Grid | 37.3 [±] 12.7 | 222.2 |
| May | Farm | 27.8 [±] 15.1 | 166.6 |

TABLE XVIII

AVERAGE AND GREATEST NUMBER OF VACUOLES PER 12.5 MICRONS
 OF THE ZONA FASCICULATA IN THE ADRENAL CORTEX OF ADULT
 MALE SIGMODON FROM ALL POPULATIONS

| Month | Population | Greatest number for one gland | Average number of vacuoles per 12.5 microns |
|-------|---------------|----------------------------------|---|
| June | Grid | 0.16 | 1 |
| Sept. | Grid | 3.86 | 10 |
| Sept. | Farm | 5.60 | 10 |
| Oct. | Grid | 4.19 | 10 |
| Oct. | Farm | 2.80 | 8 |
| Oct. | Cage (3 days) | 6.0 | 9 |
| Nov. | Grid | 4.87 | 15 |
| Dec. | Pen 2 | 3.0 | 5 |
| Dec. | Pen 3 | 4.33 | 7 |
| Jan. | Grid | 2.91 | 14 |
| Jan. | Farm | 1.43 | 3 |
| Feb. | Grid | 4.33 | 9 |
| Feb. | Farm | | |
| March | Grid | 2.60 | 4 |
| March | Farm | | |
| April | Grid | 2.33 | 4 |
| April | Farm | | |
| May | Grid | 0.33 | 1 |
| May | Farm | 1.5 | 2 |

scale was later calibrated with a stage micrometer, allowing the results to be expressed in microns. The zona glomerulosa, a narrow concentric band under the capsule, was quite constant in width and clearly distinguishable from the underlying zona fasciculata. The zona fasciculata, however, frequently varied in width, and the division between it and the zone central to it was not always clear. Generally speaking, however, the zona fasciculata had larger and lighter staining cells with intracellular vacuoles.

In order to count the number of vacuoles in the zona fasciculata under high power magnification, one end of the etching of the ocular scale was placed on the edge of the zona glomerulosa in the area where the most vacuoles were found, and the number of vacuoles touching the scale were counted. Usually the vacuoles were more numerous near the periphery of the zone and decreased toward the center of the gland.

It was not possible to measure the width of the zone inside the zona fasciculata for the reason that, even if the medulla were present in the center of the section, the width of this zone varied from one part of the slide to the other so much that the measurement would be purely arbitrary.

Accessory Reproductive Organs. Since the seasonal variation in weights of the accessory glands appeared to be so great, the data which are presented in Tables XIX, XX and XXI are organized on a monthly basis. Following the format of Table XIV, the weights are expressed in milligrams, milligrams percent, and milligrams of the largest individual in the sample.

Metabolism of the Testes. Table XXII contains the following information about the population on the grid: the weight of the testes in milligrams,

TABLE XIX

WEIGHTS OF THE PAIRED PREPUTIAL GLANDS, EXPRESSED IN MILLIGRAMS,
MILLIGRAMS PERCENT, AND MILLIGRAMS OF THE LARGEST SAMPLE,
OF ADULT MALE SIGMODON TAKEN FROM ALL POPULATIONS

| Month | Population | Paired Adrenals (mg.) | Paired Adrenals (mg.%) | Largest Sample (mg.) |
|-------|----------------|---------------------------|---------------------------|-------------------------|
| June | Grid | 185.22 [±] 8.99 | 152.80 [±] 10.72 | 245.5 |
| Sept. | Grid | 294.60 [±] 13.43 | 202.48 [±] 19.27 | 512.0 |
| Sept. | Farm | 227.40 [±] 13.53 | 224.80 [±] 15.71 | 252.0 |
| Oct. | Grid | 48.55 [±] 7.86 | 51.64 [±] 5.89 | 91.0 |
| Oct. | Farm | 112.75 [±] 29.11 | 86.93 [±] 17.73 | 266.0 |
| Oct. | Cage (3 days) | 257.20 [±] 19.19 | 208.60 [±] 18.13 | 293.0 |
| Nov. | Grid | 33.70 [±] 3.16 | 31.35 [±] 2.55 | 52.0 |
| Dec. | Pen 2 | 6.66 [±] 1.47 | 8.26 [±] 1.53 | 293.0 |
| Dec. | Pen 3 | 23.40 [±] 8.27 | 24.94 [±] 6.20 | 55.0 |
| Dec. | Cage (2 mos.) | 9.33 [±] 3.54 | 10.30 [±] 3.33 | 16.0 |
| Jan. | Grid | 28.20 [±] 3.58 | 32.29 [±] 4.49 | 54.0 |
| Jan. | Farm | 25.40 [±] 11.14 | 27.93 [±] 10.90 | 68.0 |
| Feb. | Grid | 28.00 [±] 3.53 | 33.80 [±] 3.91 | 39.0 |
| Feb. | Farm | 19.60 [±] 4.51 | 19.74 [±] 3.11 | 32.0 |
| March | Grid | 18.80 [±] 2.28 | 20.71 [±] 2.50 | 28.0 |
| March | Farm | --- | --- | -- |
| April | Grid | 32.33 [±] 6.71 | 53.61 [±] 7.43 | 40.0 |
| April | Farm | --- | --- | -- |
| May | Grid | 186.3 [±] 14.17 | 193.3 [±] 20.31 | 210.0 |
| May | Farm | 186.0 [±] 6.00 | 158.2 [±] 9.60 | 203.0 |

TABLE XX

WEIGHTS OF PAIRED SEMINAL VESICLES, EXPRESSED IN MILLIGRAMS, MILLIGRAMS PERCENT, AND WEIGHT OF THE LARGEST SAMPLE, OF ADULT MALE SIGMODON TAKEN FROM ALL POPULATIONS

| Month | Population | Seminal Vesicles (mg.) | Seminal Vesicles (mg.%) | Largest Sample (mg.) |
|-------|---------------|----------------------------|----------------------------|-------------------------|
| Sept. | Grid | 1497.9 [±] 267.84 | 1007.25 [±] 65.00 | 2835.0 |
| Sept. | Farm | 1016.6 [±] 236.34 | 936.70 [±] 174.8 | 1553.0 |
| Oct. | Grid | 43.1 [±] 6.80 | 45.72 [±] 7.43 | 77.0 |
| Oct. | Farm | 506.5 [±] 149.25 | 402.73 [±] 92.44 | 1400.0 |
| Oct. | Cage (3 days) | 1267.4 [±] 116.20 | 1016.20 [±] 68.26 | 1520.0 |
| Nov. | Grid | 1.8 [±] 0.63 | 1.68 [±] 0.58 | 7.0 |
| Dec. | Pen 2 | 2.6 [±] 0.29 | 3.38 [±] 0.48 | 3.0 |
| Dec. | Pen 3 | 32.2 [±] 12.07 | 23.46 [±] 11.34 | 78.0 |
| Dec. | Cage (2 mos.) | 24.0 [±] 22.06 | 24.65 [±] 22.23 | 68.0 |
| Jan. | Grid | 8.7 [±] 4.02 | 11.54 [±] 4.38 | 45.0 |
| Jan. | Farm | 6.4 [±] 0.38 | 5.75 [±] 1.51 | 7.0 |
| Feb. | Grid | 4.8 [±] 1.32 | 5.32 [±] 1.65 | 14.0 |
| Feb. | Farm | 23.8 [±] 13.54 | 20.21 [±] 7.62 | 78.0 |
| March | Grid | 3.0 [±] 0.32 | 3.27 [±] 0.23 | 4.0 |
| March | Farm | --- | --- | ---- |
| April | Grid | 83.67 [±] 18.78 | 137.50 [±] 17.19 | 109.0 |
| April | Farm | --- | --- | ---- |
| May | Grid | 864.0 [±] 106.63 | 898.63 [±] 107.70 | 979.0 |
| May | Farm | 1218.5 [±] 13.50 | 977.40 [±] 18.55 | 1232.0 |

TABLE XXI

WEIGHTS OF THE VENTRAL PROSTATE GLANDS, EXPRESSED IN MILLIGRAMS, MILLIGRAMS PERCENT,
AND MILLIGRAMS OF THE LARGEST SAMPLE, OF ADULT MALE SIGMODON TAKEN FROM ALL
POPULATIONS

| Month | Population | Ventral Prostate (mg.) | Ventral Prostate (mg.%) | Largest Sample (mg.) |
|-------|---------------|---------------------------|----------------------------|-------------------------|
| Sept. | Grid | 269.8 [±] 20.30 | 186. 3 [±] 37.34 | 788.0 |
| Sept. | Farm | 309.2 [±] 73.36 | 284. 7 [±] 50.85 | 493.0 |
| Oct. | Grid | 28.8 [±] 7.49 | 31. 4 [±] 8.31 | 66.0 |
| Oct. | Farm | 150.1 [±] 52.41 | 107. 9 [±] 32.28 | 447.0 |
| Oct. | Cage (3 days) | 386.6 [±] 68.70 | 299. 0 [±] 30.98 | 560.0 |
| Nov. | Grid | | | |
| Dec. | Pen 2 | | | |
| Dec. | Pen 3 | | | |
| Dec. | Cage (2 mos.) | | | |
| Jan. | Grid | | | |
| Jan. | Farm | | | |
| Feb. | Grid | | | |
| Feb. | Farm | | | |
| March | Grid | | | |
| March | Farm | --- | --- | --- |
| April | Grid | 29.66 [±] 11.26 | 49.01 [±] 19.27 | 49.0 |
| April | Farm | --- | --- | -- |
| May | Grid | 238. 3 [±] 43.24 | 264. 2 [±] 71.40 | 289.0 |
| May | Farm | 360.0 [±] 91.01 | 286. 6 [±] 64.31 | 451.0 |

TABLE XXII

BODY WEIGHT, TESTES WEIGHT, PERCENT TESTICULAR DRY WEIGHT, AND UPTAKE OF OXYGEN FROM THE TESTES OF ADULT MALE SIGMODON FROM THE POPULATION ON THE GRID

| Month | N | Body Weight (gms.) | Testes Weight (mg.%) | N | Percent Dry Weight | N | Oxygen Uptake No. Substrate (ul/mg/hr) | Oxygen Uptake Substrate (ul/mg/hr) |
|-------|----|-----------------------|-------------------------|----|-----------------------|----|--|--|
| June | 10 | 126.30 \pm 8.42 | 2124.83 \pm 54.66 | 10 | 14.31 \pm 0.19 | 10 | 5.80 \pm 0.58 | 8.70 \pm 0.63 |
| Sept. | 10 | 141.49 \pm 11.53 | 2318.42 \pm 169.64 | 10 | 14.04 \pm 0.13 | 10 | 6.99 \pm 0.50 | 8.44 \pm 0.85 |
| Oct. | 10 | 96.19 \pm 3.56 | 1820.34 \pm 403.95 | 1 | 15.7 | 9 | 6.34 \pm 1.20 | 5.06 \pm 0.39 |
| Nov. | 10 | 107.35 \pm 3.00 | 73.59 \pm 7.48 | -- | --- | 7 | 6.51 \pm 0.67 | 5.51 \pm 0.56 |
| Jan. | 10 | 88.81 \pm 3.65 | 125.81 \pm 18.51 | -- | --- | 6 | 7.21 \pm 1.03 | 5.61 \pm 0.23 |
| Feb. | 10 | 84.15 \pm 3.47 | 146.85 \pm 16.88 | 1 | 12.2 | 5 | 11.12 \pm 0.87 | 8.64 \pm 0.53 |
| March | 5 | 91.03 \pm 5.65 | 286.10 \pm 64.51 | 3 | 17.03 \pm 1.04 | 4 | 8.58 \pm 0.48 | 8.57 \pm 0.86 |
| April | 3 | 60.17 \pm 11.12 | 1873.71 \pm 251.71 | -- | --- | 3 | 7.98 \pm 0.38 | 10.55 \pm 0.51 |
| May | 3 | 97.66 \pm 13.86 | 2031.60 \pm 21.75 | 3 | 13.46 \pm 0.01 | 3 | 5.95 \pm 0.63 | 5.46 \pm 0.34 |

the percent of dry weight, and the oxygen uptake, with and without substrate. Table XXIII contains the same information for the population which had been taken from the University Farm. Table XXIV gives this information about the population from the grid: the utilization of glucose, the production of lactic acid, the content of protein, and the content of RNA and DNA. Table XXV gives the same information for the population on the University Farm. Following the method of presentation of earlier data, Table XXVI gives the weight of the testes in grams, milligrams percent, and the percent dry weight; this information includes both populations. Also to be found in Table XXVI are the data taken from studies of both the pen and the cage. Table XXVII presents the rate of oxygen uptake, expressed in microliters of oxygen per milligram of tissue per hour, of all populations. The rate of the utilization of glucose expressed in micrograms of glucose per milligrams of tissue per hour, is to be found in Table XXVIII. The production of lactic acid, with and without substrate, is contained in Table XXIX. Table XXX gives the content of protein of the testes in milligrams of protein per gram of tissue. In Table XXXI are found the RNA and DNA content of the testes, expressed in milligrams of RNA and DNA per gram of tissue.

These data were tabulated in two forms in order to show more clearly the effects of climatic conditions on each population (as in Tables XXII to XXV), and the monthly differences between the two populations (as in Table XXVI to XXXI). The total number of animals in each sample is listed in the first column of Table XXII. In cases where there was insufficient tissue to carry out all of the tests, the number of animals which make up the sample is found in the column which preceded the mean and standard error of the parameter.

TABLE XXIII

BODY WEIGHT, TESTES WEIGHT, PERCENT TESTICULAR DRY WEIGHT, AND UPTAKE OF OXYGEN
FROM THE TESTES OF ADULT MALE SIGMODON FROM THE POPULATION AT THE FARM

| Month | N | Body Weight (gms.) | Testes Weight (mg.%) | N | Percent Dry Weight | N | Oxygen Uptake No Substrate (ul/mg/hr) | Oxygen Uptake Substrate (ul/mg/hr) |
|-------|---|---------------------------|-----------------------------|----|-------------------------|---|---|--|
| Sept. | 5 | 104.92 [±] 13.59 | 2245.75 [±] 63.18 | 5 | 14.40 [±] 0.46 | 5 | 5.74 [±] 0.78 | 10.54 [±] 0.39 |
| Oct. | 8 | 123.49 [±] 11.19 | 1118.35 [±] 230.54 | 7 | 14.92 [±] 0.70 | 7 | 7.05 [±] 0.36 | 7.91 [±] 1.31 |
| Jan. | 5 | 85.90 [±] 3.73 | 102.42 [±] 9.45 | -- | --- | 3 | 5.94 [±] 0.57 | 7.55 [±] 0.63 |
| Feb. | 5 | 96.60 [±] 13.73 | 444.36 [±] 64.31 | -- | --- | 5 | 8.09 [±] 0.92 | 7.42 [±] 1.05 |
| March | 0 | --- | --- | 0 | --- | 0 | --- | --- |
| April | 0 | --- | --- | 0 | --- | 0 | --- | --- |
| May | 2 | 124.75 [±] 3.75 | 1323.45 [±] 26.45 | | 12.50 [±] 0.40 | 2 | 4.03 [±] 0.18 | 6.03 [±] 0.28 |

TABLE XXIV

UTILIZATION OF GLUCOSE, PRODUCTION OF LACTIC ACID, PROTEIN CONTENT, AND RNA
AND DNA CONTENT OF TESTES OF ADULT MALE SIGMODON FROM THE POPULATION
AT THE FARM

| Month | N | Glucose Utilization (ug/mg/hr) | N | Lactic Acid No. Substrate (ug/ng/hr) | Lactic Acid Substrate (ul/mg/hr) | N | Protein Content (mg./gm.) | N | RNA Content (mg/gm) | DNA Content (mg/gm) |
|-------|----|--------------------------------------|----|--|--|----|---------------------------------|----|---------------------------|---------------------------|
| June | 10 | 96.98 \pm 10.22 | 9 | 1.17 \pm 0.55 | 27.33 \pm 3.47 | 10 | 74.70 \pm 2.33 | 10 | 3.00 \pm 0.06 | 6.20 \pm 0.37 |
| Sept. | 10 | 70.28 \pm 3.54 | 10 | 2.61 \pm 0.92 | 29.77 \pm 1.48 | 7 | 77.73 \pm 1.84 | 10 | 2.83 \pm 0.15 | 5.78 \pm 0.22 |
| Oct. | 9 | 136.96 \pm 43.20 | 9 | 18.81 \pm 2.25 | 62.28 \pm 9.70 | 1 | 74.38 \pm 4.19 | 7 | 2.40 \pm 0.21 | 1.10 \pm 1.71 |
| Nov. | 6 | 96.04 \pm 15.76 | -- | --- | | 5 | 53.85(N=1) | 3 | 2.70 \pm 0.06 | 4.80 \pm 0.56 |
| Jan. | 6 | 83.48 \pm 13.56 | 5 | 5.12 \pm 1.16 | 26.22 \pm 1.84 | 5 | 69.92 \pm 3.74 | 5 | 3.50 \pm 0.05 | 8.49 \pm 0.12 |
| Feb. | 5 | 116.25 \pm 21.50 | 4 | 1.41 \pm 0.50 | 28.49 \pm 5.67 | 4 | 9.62 \pm 0.70 | 5 | 5.36 \pm 0.11 | 5.60 \pm 0.40 |
| March | 4 | 104.41 \pm 15.71 | 2 | 11.54 \pm 7.20 | 21.98 \pm 2.56 | | 6.27 \pm 0.94 | 4 | 5.56 \pm 0.46 | 4.22 \pm 0.30 |
| April | 3 | 61.73 \pm 7.05 | 3 | | 15.32 \pm 2.66 | 3 | 86.80 \pm 3.97 | 3 | 5.87 \pm 0.13 | 7.15 \pm 0.22 |
| May | 3 | 96.39 \pm 30.65 | 3 | | 10.51 \pm 3.88 | 3 | 61.31 \pm 10.21 | 3 | 4.79 \pm 0.42 | 9.09 \pm 1.75 |

TABLE XXV

UTILIZATION OF GLUCOSE, PRODUCTION OF LACTIC ACID, PROTEIN CONTENT, AND RNA
AND DNA CONTENT OF TESTES OF ADULT MALE SIGMODON FROM THE
POPULATION AT THE FARM

| Month | N | Glucose Utilization (ug/mg/hr) | N | Lactic Acid No Substrate (ug/ml/hr) | Lactic Acid Substrate (ul/mg/hr) | N | Protein Content (mg./gm.) | N | RNA Content (mg/gm) | DNA Content (mg/gm) |
|-------|---|--------------------------------------|---|---|--|---|---------------------------------|---|---------------------------|---------------------------|
| Sept. | 4 | 62.32 [±] 9.85 | 5 | 7.17 [±] 6.16 | 18.55 [±] 6.56 | 3 | 64.44 [±] 13.68 | 5 | 4.64 [±] 0.47 | 7.66 [±] 0.75 |
| Oct. | 7 | 124.98 [±] 27.77 | 7 | 6.36 [±] 1.81 | 49.78 [±] 11.02 | 7 | 83.91 [±] 5.00 | 7 | 2.79 [±] 0.04 | 5.66 [±] 0.37 |
| Jan. | 3 | 48.51 [±] 5.76 | 3 | --- | 10.58 [±] 2.11 | 2 | 1.34 [±] 0.51 | 2 | 4.22 [±] 0.77 | --- |
| Feb. | 5 | 39.77 [±] 7.54 | 4 | 0.71 [±] 0.20 | 11.31 [±] 1.28 | 5 | 8.15 [±] 0.49 | 5 | 6.24 [±] 0.49 | 10.45 [±] 0.60 |
| March | 0 | --- | 0 | --- | --- | 0 | --- | 0 | --- | --- |
| April | 0 | --- | 0 | --- | --- | 0 | --- | 0 | --- | --- |
| May | 2 | 113.09 [±] 14.33 | 0 | --- | 9.65 [±] 0.005 | 2 | 93.24 [±] 6.02 | 2 | 5.32 [±] 0.009 | 12.12 [±] 0.32 |

TABLE XXVI

TESTICULAR WEIGHT, EXPRESSED IN GRAMS, MILLIGRAMS PERCENT, AND PERCENT OF DRY WEIGHT, OF
ADULT MALE SIGMODON FROM ALL POPULATIONS

| Month | Population | Testes (gms.) | Testes (mg.%) | Percent Dry Weight |
|-------|---------------|--------------------------|-----------------------------|-------------------------|
| June | Grid | 2.64 [±] 0.16 | 2124.83 [±] 54.66 | 14.31 [±] 0.19 |
| Sept. | Grid | 3.15 [±] 0.17 | 2318.42 [±] 169.64 | 14.40 [±] 0.19 |
| Sept. | Farm | 2.36 [±] 0.33 | 2245.75 [±] 63.18 | 14.40 [±] 0.46 |
| Oct. | Grid | 1.83 [±] 0.37 | 1820.34 [±] 403.95 | 15.7 [±] (N=1) |
| Oct. | Farm | 1.14 [±] 0.36 | 1118.35 [±] 230.54 | 14.92 [±] 0.70 |
| Oct. | Cage (3 days) | 2.75 [±] 0.25 | 2210.22 [±] 90.48 | 14.14 [±] 0.08 |
| Nov. | Grid | 0.079 [±] 0.009 | 73.59 [±] 7.48 | --- |
| Dec. | Pen 2 | 0.060 [±] 0.004 | 75.20 [±] 1.63 | --- |
| Dec. | Pen 3 | 0.104 [±] 0.034 | 110.69 [±] 26.57 | --- |
| Dec. | Cage (2 mos.) | 0.095 [±] 0.047 | 102.47 [±] 22.03 | --- |
| Jan. | Grid | 0.105 [±] 0.019 | 125.81 [±] 18.51 | --- |
| Jan. | Farm | 0.089 [±] 0.011 | 102.42 [±] 9.45 | --- |
| Feb. | Grid | 0.125 [±] 0.018 | 146.58 [±] 16.88 | 12.20 (N=1) |
| Feb. | Farm | 0.432 [±] 0.044 | 444.36 [±] 64.31 | --- |
| March | Grid | 0.258 [±] 0.059 | 286.10 [±] 65.41 | 17.03 [±] 1.04 |
| March | Farm | --- | --- | --- |
| April | Grid | 1.072 [±] 0.058 | 1873.71 [±] 251.71 | --- |
| April | Farm | --- | --- | --- |
| May | Grid | 1.940 [±] 0.170 | 2031.6 [±] 217.50 | 13.46 [±] 0.01 |
| May | Farm | 1.639 [±] 0.281 | 2643.9 [±] 264.5 | 12.50 [±] 0.40 |

TABLE XXVII

TESTICULAR UPTAKE OF OXYGEN, EXPRESSED IN MICROLITERS OF OXYGEN
PER MILLIGRAMS OF TISSUE PER HOUR, OF ADULT MALE SIGMODON
FROM ALL POPULATIONS

| Month | Population | N | Without Substrate (ul/mg/hr) | With Substrate (ul/mg/hr) |
|-------|---------------|----|---------------------------------|------------------------------|
| June | Grid | 10 | 5.80 [±] 0.58 (N=8) | 8.70 [±] 0.63 |
| Sept. | Grid | 10 | 6.99 [±] 0.50 | 8.44 [±] 0.85 |
| Sept. | Farm | 5 | 5.74 [±] 0.78 | 10.54 [±] 0.39 |
| Oct. | Grid | 9 | 6.34 [±] 1.20 | 5.06 [±] 0.39 |
| Oct. | Farm | 7 | 7.05 [±] 0.36 | 7.91 [±] 1.31 |
| Oct. | Cage (3 days) | 4 | 6.39 [±] 0.58 | 9.81 [±] 0.84 |
| Nov. | Grid | 9 | 6.51 [±] 0.67 | 5.51 [±] 0.56 |
| Dec. | Pen 2 | 4 | 4.52 [±] 0.48 | 3.17 [±] 0.36 |
| Dec. | Pen 3 | 4 | 2.99 [±] 0.60 | 3.37 [±] 0.41 |
| Dec. | Cage (2 mos.) | 3 | 5.61 [±] 0.52 | 3.81 [±] 0.16 |
| Jan. | Grid | 6 | 7.21 [±] 1.03 | 5.61 [±] 0.23 |
| Jan. | Farm | 3 | 5.94 [±] 0.57 | 7.55 [±] 0.63 |
| Feb. | Grid | 5 | 11.12 [±] 0.87 | 8.64 [±] 0.53 |
| Feb. | Farm | 5 | 8.09 [±] 0.92 | 7.42 [±] 1.05 |
| March | Grid | 4 | 8.58 [±] 0.48 | 8.57 [±] 0.86 |
| March | Farm | 0 | --- | --- |
| April | Grid | 3 | 7.98 [±] 0.38 | 10.55 [±] 0.51 |
| April | Farm | 0 | --- | --- |
| May | Grid | 3 | 5.95 [±] 0.63 | 5.46 [±] 0.34 |
| May | Farm | 2 | 4.03 [±] 0.18 | 6.03 [±] 0.28 |

TABLE XXVIII

TESTICULAR UTILIZATION OF GLUCOSE, EXPRESSED IN MICROGRAMS
OF GLUCOSE PER MILLIGRAM OF TISSUE PER HOUR OF ADULT
MALE SIGMODON FROM ALL POPULATIONS

| Month | Population | N | Glucose Uptake (ug/mg/hr) |
|-------|---------------|----|------------------------------|
| June | Grid | 10 | 96.98±10.22 |
| Sept. | Grid | 10 | 70.28±3.54 |
| Sept. | Farm | 4 | 62.32±9.85 |
| Oct. | Grid | 9 | 136.96±43.20 |
| Oct. | Farm | 7 | 124.98±27.77 |
| Oct. | Cage (3 days) | 5 | 59.61±7.05 |
| Nov. | Grid | 6 | 96.04±15.76 |
| Dec. | Pen 2 | 3 | 93.46±11.60 |
| Dec. | Pen 3 | 4 | 138.93±32.30 |
| Dec. | Cage (2 mos.) | 3 | 106.70±30.73 |
| Jan. | Grid | 6 | 83.48±13.56 |
| Jan. | Farm | 3 | 48.51±5.76 |
| Feb. | Grid | 5 | 116.25±21.50 |
| Feb. | Farm | 5 | 39.77±7.54 |
| March | Grid | 4 | 104.41±15.71 |
| March | Farm | 0 | --- |
| April | Grid | 3 | 61.73±7.05 |
| April | Farm | 0 | --- |
| May | Grid | 3 | 96.39±30.65 |
| May | Farm | 2 | 113.09±14.33 |

TABLE XXIX

TESTICULAR PRODUCTION OF LACTIC ACID, EXPRESSED IN MICROLITERS
OF LACTIC ACID PER MILLIGRAM OF TISSUE PER HOUR, WITH AND
WITHOUT SUBSTRATE, OF ADULT MALE SIGMODON FROM ALL
POPULATIONS

| Month | Population | N | Lactic acid without Substrate (ul/mg/hr) | Lactic acid with Substrate (ul/mg/hr) |
|-------|---------------|----|--|---|
| June | Grid | 10 | 1.17±0.55 (N=9) | 27.33±3.47 |
| Sept. | Grid | 10 | 2.61±0.92 | 29.77±1.48 |
| Sept. | Farm | 7 | 7.17±6.16 | 18.55±6.56 |
| Oct. | Grid | 9 | 18.81±2.25 | 62.28±9.70 |
| Oct. | Farm | 7 | 6.36±1.81 | 49.78±11.02 |
| Oct. | Cage (3 days) | 5 | 0.21±0.19 | 25.97± 6.63 |
| Dec. | Grid | 5 | 6.23±(N=1) | 25.97±6.63 |
| Dec. | Farm | 3 | 4.78±0.50 (N=2) | 22.29±3.67 |
| Jan. | Grid | 6 | 5.12±1.16 | 26.22±1.84 |
| Jan. | Farm | 3 | --- | 10.58±2.11 |
| Feb. | Grid | 5 | 1.41±0.50 (N=4) | 28.49±5.67 |
| Feb. | Farm | 5 | 0.71±0.20 (N=4) | 11.31±1.28 |
| March | Grid | 5 | 11.54±7.20 (N=2) | 21.98±2.56 |
| March | Farm | 0 | --- | --- |
| April | Grid | 3 | --- | 15.32±2.66 |
| April | Farm | 0 | --- | --- |
| May | Grid | 3 | --- | 10.51±3.88 |
| May | Farm | 2 | --- | 9.65±0.005 |

TABLE XXX

PROTEIN CONTENT, EXPRESSED IN MILLIGRAMS OF PROTEIN PER GRAM OF TESTICULAR TISSUE,
OF ADULT MALE SIGMODON FROM ALL POPULATIONS

| Month | Population | N | Protein Content (mg/gm) |
|-------|---------------|----|----------------------------|
| June | Grid | 10 | 74.70 [±] 2.33 |
| Sept. | Grid | 10 | 77.73 [±] 1.84 |
| Sept. | Farm | 3 | 64.44 [±] 13.68 |
| Oct. | Grid | 7 | 74.38 [±] 4.19 |
| Oct. | Farm | 7 | 83.91 [±] 5.00 |
| Oct. | Cage (3 days) | 5 | 66.50 [±] 13.86 |
| Nov. | Grid | 1 | 53.85 |
| Dec. | Pen 3 | 2 | 63.85 [±] 1.64 |
| Jan. | Grid | 4 | 69.92 [±] 3.74 |
| Jan. | Farm | 2 | 1.34 [±] 0.51 |
| Feb. | Grid | 5 | 9.62 [±] 0.70 |
| Feb. | Farm | 5 | 8.15 [±] 0.49 |
| March | Grid | 4 | 6.27 [±] 0.94 |
| March | Farm | 0 | --- |
| April | Grid | 3 | 86.80 [±] 3.97 |
| April | Farm | 0 | --- |
| May | Grid | 3 | 61.31 [±] 10.21 |
| May | Farm | 2 | 93.24 [±] 6.02 |

TABLE XXXI

RNA AND DNA CONTENT, EXPRESSED IN MILLIGRAMS OF RNA AND
DNA PER GRAM OF TESTICULAR TISSUE OF ADULT MALE
SIGMODON FROM ALL POPULATIONS

| Month | Population | N | RNA Content (mg/gm) | DNA Content (mg/gm) |
|-------|---------------|----|------------------------|------------------------|
| June | Grid | 10 | 3.00±0.06 | 6.20±0.37 |
| Sept. | Grid | 10 | 2.83±0.15 | 5.78±0.22 |
| Sept. | Farm | 5 | 4.64±0.47 | 7.66±0.75 |
| Oct. | Grid | 6 | 2.40±0.21 | 1.10±1.71 |
| Oct. | Farm | 7 | 2.79±0.04 | 5.66±0.37 |
| Oct. | Cage (3 days) | 5 | 2.86±0.21 | 6.38±0.37 |
| Nov. | Grid | 3 | 2.70±0.06 | 4.80±0.56 |
| Dec. | Pen 3 | 2 | 2.17±0.09 | 6.51±(N=1) |
| Jan. | Grid | 5 | 3.50±0.05 | 8.49±0.12 |
| Jan. | Farm | 2 | 4.22±0.77 | --- |
| Feb. | Grid | 5 | 5.36±0.11 | 5.60±0.40 |
| Feb. | Farm | 5 | 6.24±0.49 | 10.45±0.60 |
| March | Grid | 3 | 5.56±0.46 | 4.22±0.30 |
| March | Farm | 0 | --- | --- |
| April | Grid | 3 | 5.87±0.13 | 7.15±0.22 |
| April | Farm | 0 | --- | --- |
| May | Grid | 3 | 4.79±0.42 | 9.09±1.75 |
| May | Farm | 2 | 5.32±0.009 | 12.12±0.32 |

CHAPTER IV

DISCUSSION

The Population on the Grid

Variations in Autumnal Breeding. Sigmodon hispidus is surely a seasonal breeder, although the summer breeding season can be terminated in late August and early September, or it can be extended into November.

Sigmodon may also breed throughout the winter (Goertz, 1962). For some animals, such as the female ferret (Donovan and Harris, 1956) and the male starling (Burger, 1953), the breeding season is reported to be controlled by the amount of light, but this factor is seemingly of little consequence in either male or female cotton rats. In September, for example, the percent of males with descended testes varied from 100% to 0.006%, and in November the percent of females with open vulvae ranged from 38.40% to 2.97%, as the data in Tables I and II clearly show.

The validity of these two criteria (descended testes and open vulva) for determining reproductive competence apparently varies from species to species. For instance, Jameson (1950) found that scrotal testes are of limited usefulness as an indicator of reproductive condition in Peromyscus. He suggested that one should look for changes in seminal vesicles and in the prostate glands; moreover, he thought such a plan as this is not feasible, if one wishes to mark and release animals. Anthony (1953) was of the opinion that the presence of palpable testes in the prairie dog (Cynomys ludovicianus) was an indicator of gonadal function.

As far as the present study is concerned, it is clear that in sigmodon, atrophy of the testes follows upon ascent of the testes at the termination of the breeding season (Tables XX and XXIII).

Since no females were examined in the laboratory during the course of this study, the opening of the vulva is not as firmly established as being indicative of capacity for reproduction. The estrus cycle in the domestic rat does lengthen with exposure to cold (Bohanan, 1939), and there is a winter anestrus period which is related to the closing of the orifice of the vagina by epithelial fusion; at least such is true for the bank vole (Evotomys glareolus), (Brambell and Rolands, 1936). A thorough study of the winter anestrus period in the cotton rat under wild conditions is still to be undertaken; until that time, the assumptions made here lie on somewhat uneasy ground.

Patterns of seasonal breeding also seem to vary from species to species among small mammals. Thus, male brown rats (Rattus norvegicus) were fertile throughout the year when they were in a comparatively sheltered habitat (Perry, 1945; Davis and Hall, 1948). Roof rats (Rattus rattus) also bred throughout the year, although there were maxima in February and in May (Davis, 1947). In those species that breed seasonally it has often been observed that the breeding season may vary in length, and that this capacity cannot be correlated with the severity of the climatic conditions. Neither in Apodemus sylvaticus nor in Evotymus glareolus was there any relationship between the extent of breeding activity and the severity of the winter (Baker, 1930). Hamilton (1941), in his study of the field vole (Microtus pennsylvanicus), concluded that the mean temperatures at which mice breed are the same as those temperatures at which they do not breed. Temperature, therefore, appears not to be a factor in determining patterns of reproduction

in these species. Hamilton further eliminated the amount of light and other climatic conditions as having little influence on the length of the breeding season. Newson (1962) reported that, during one winter, wild voles (Clethrionomys glareolus) continued to breed and grow at almost the summer level. Curry-Lindahl (1963) made similar observations about winter breeding in the lemming (Lemmus lemmus).

The data of Tables III and IV accord with these observations, namely that there is no apparent correlation between the length of the breeding season and any single climatic factor. The correlation between the length of the breeding season and the descent of the testes, however, is -0.7182 . Here is clear indication that males will continue to breed late in autumn, if the late summer population has been low. The correlation between success in trapping and open vulvae is also high and negative: -0.8067 . This high negative coefficient of correlation suggests that the females are capable of breeding later in the fall, if the late summer population has been at a low density. Conversely, breeding activity ceases in late August, regardless of climatic conditions, if the late summer population has been at a high density.

Annual Changes in Density of Population. During this study, the population on the grid increased rapidly from June to September, even though 59 animals were lost as a result of mortality in trapping during July. With the virtual cessation of breeding in September, and with the attrition which always is in operation, the population began to decrease rather early in the fall. The month of October was so warm that 25 animals succumbed, presumably to heat, while in the traps. Yet, in spite of the summer-like weather, the greatest monthly loss to the population was between September and October. To all apparent indications, predation was not a factor in this severe loss to the population.

The population on the grid reached a maximum density of 1,043 animals in September (Table V), and then declined sharply. Neither lack of suitable cover, inadequate supply of food, nor known predation could account for a loss of 257 animals during this month.

It also appears from Table V that, if the population numbered 450 or more animals, success in trapping remained about 80%; on the other hand, as the population decreased below this number the percent of success in trapping likewise decreased. That there was no more than 80% success in trapping, regardless of the density of population, was not unexpected, for some of the traps were in wooded areas with little ground cover. These areas were unattractive to sigmodon. In the more suitable areas on the grid it was not uncommon to find two, three, and occasionally four animals in the same trap. In low densities there appeared to be a positive correlation between success in trapping and density of population, thus allaying somewhat the uneasy assumption upon which Tables I to IV are based.

The only explanation for a coefficient of variation of 20.10% in March, and higher coefficients of variation in April and May, is that the adult males were removed from a comparatively small population early in the trapping week, not on the last two days of trapping, in order to obtain a monthly sample for laboratory examination.

Seasonal Changes in Breeding Conditions. There was constant attrition to the population during the winter months. This appeared, however, to be equal for both sexes until February, as is shown in Tables VI and VII. Not until this month did the ratio of the sexes show a lesser number of males on the grid; in March only 36.5% of the population were males. The drop in numbers from September to October (a loss of 257 animals) was not selective in terms of sex; the attrition which began in January,

however, does appear to have affected males more than females. Whether this fact is due to less vitality of the males or to intraspecific strife prior to the establishment of territory for the breeding season, or to some other causes, can be conjectured only.

To refer again to Tables VI and VII: in November there were no males with descended testes, although there were seven females with open vulvae. Moreover, the first indication of the start of the breeding season in the following spring was the presence of one sigmodon with an open vulva in March, at which time no males were as yet capable of breeding. This suggests, therefore, that the male may determine the length of the breeding season in sigmodon. Conversely, Davis and Hall (1948) found that the seasonal changes in reproductive rates depended on the female among Norway rats, and Baker (1930) observed that the females controlled the length of the breeding season in Apodemus sylvaticus.

Seasonal Changes in Classes of Weight. The summary of the data found in Table VIII lends itself to some conclusions about the winter survival of animals in different weight groups. During the entire winter period, until April, certain of the juvenile animals weighed less than 50 grams, which points toward a retarded rate of growth. The lowest weight class had no occupants after January. Presumably those which had been born in late fall, no later than November, weighed 30 grams or more at the end of two months. Also, there was little gain, and possibly some loss, in weight among animals which weighed more than 50 grams. Christian (1962) reported a loss of weight during winter months among woodchucks (Marmota monax) and suggested that for this reason the weight of the body is a poor measure with which to equate adrenal weight.

Attrition to the population was greater among the animals which weighed more than 90 grams (Table VIII). This may be related to population

turnover, the older animals being replaced by the younger. In June, there were ten different weight groups; in the following March there were only three groups, 69.22% of the population weighing between 50 and 69 grams. In April, however, 77.77% of the animals weighed between 70 and 89 grams, suggesting that there was a gain in weight with the appearance of spring vegetation.

Emigration and Immigration. During the period of trapping in November, the animals could be seen scurrying about more than in the months before and after. They appeared to be less fearful of people and readily left cover to feed at traps within minutes after setting and baiting. Several of the traps had been sprung before all were baited. Since 145 unmarked animals were trapped during this month, in a population that was decreasing and was later estimated to have only 705 animals, the possibility of immigration was explored.

Between September and October the population fell from 1,043 to 786; between October and November it fell from 786 to 705 (Table V). This estimate of 705 includes the 145 unmarked animals already mentioned. If these were excluded, the estimate would have been 580. It appeared that the population decreased more than the estimate for November indicated. In addition to this, the greatest number of unmarked animals were found in the outside rows of the grid (Table IX). Immigrants moving in from the surrounding areas may have masked a greater loss to the population than the estimate for November indicated.

Two events seems to have taken place, either simultaneously or the one following the other. First, there was an unexplained (and as yet inexplicable) loss of 483 animals (from 1,043 to 560) during September and October, when there seemed to be suitable cover and no extensive

predation; and second, this loss was associated with immigration from peripheral areas. This observation parallels that of Evans (1942), namely that the survival of a population from a period of high density to one of low density appears to be greatest in those habitats which normally maintain a low density of population. Briefly, it seemed that the population dropped abruptly in the more densely populated and more suitable habitat, and that this drop in population was associated with immigration.

All of the animals, with the exception of two females trapped in March, appeared to be in good health during these periods of trapping. One of these two was apparently paralyzed and unable to move except for jerking motions; the other moved slowly, lethargically, and without coordination.

Population at the University Farm

Since that part of the experiment with captive animals did not fulfill its expectations, it was planned to compare two wild populations: that on the grid and that at the farm. All the animals which had been trapped on the farm were removed from the population in order to determine whether breeding could be extended further into the fall or initiated earlier in the spring in a less dense population. Table XI shows that the grid was more densely populated than the farm.

Analyses of the Adrenal Glands, Accessory Reproductive Organs, and Testes

Adrenal Weights. In order to eliminate differences in sex and age, each monthly sample of adrenal glands was taken from the largest adult males in the populations. Table XVIII gives the mean body weight of these animals. The weight of the body was used as a criterion for determining

whether an animal was an adult or a juvenile; animals exceeding 70 grams were considered as adults (Odum, 1955).

There was a frustratingly wide variation in the adrenal weights within each monthly sample, a fact which was also noted by Barnett (1958) in wild rats. He suggested that this difference was due in part to genetic variability and in part due to the conditions of life of different individuals. Davis and Christian (1957) found a significant relationship between adrenal weights and social rank in "wild strain" mice. In a monthly sample which is taken from a wild population, it is of course quite impossible to tell which cotton rats are socially dominant and which are socially inferior. One must leave room, therefore, for the possibility that differences in adrenal weight are a result of differences in social status.

Golley (1961), in his experiments with sigmodon, found that those animals which had been trapped and released had larger adrenal glands than those which had not been previously trapped. In his opinion, this enlargement was due to the stress which came from live-trapping. During the year of trapping with which this present report is concerned, there were no external signs to indicate that confinement to a live trap was a source of stress to the animal involved. The only exceptions to this rule were the two females whose cases were cited earlier. In point of fact, it could be argued that the contrary was true. Thus, in September, after the closing of the traps in July, the success in daily trapping for five days was as follows: 64.9%, 74.9%, 78.9%, 85.4%, and 89.5%. As the animals became more and more aware of the traps, there was a notable increase of success in capturing them. Compare these figures with those of October: 79.5%, 84.2%, 81.3%, 88.3%, and 81.9%. It is possible that the rats, for all practical purposes, used the trap sites as feeding

stations, rather than avoided them as stressful situations.

The purpose in obtaining the adrenal weights in this study was to determine whether the stress induced by a crowded condition had any effect on the pituitary-adrenocortical axis which would be reflected by changes in this parameter. If there were such an effect, it would be positively correlated with the social stress that followed the increase in the density of the population. On the basis of a monthly comparison, the population of the grid was more dense than that at the farm, and reached its maximum density in the month of September. At this time the males from the grid had larger adrenal glands, one pair weighing as much as 41.0 mg. (Table XIV), whereas the largest adrenal glands from the population on the farm weighed only 23.0 mg. (Incidentally, this difference is masked in the adjustment for body weight.) The largest adrenal glands were obtained in June, however, when the population was still quite low. Moreover, the adrenal glands from the sample at the farm in October were larger (31.0 mg.) than those which had been taken from the animals on the grid (23.2 mg.) during the same month. One conclusion which may be drawn (albeit rather tenuously) from these data is that the adrenals appear to be heavier in the summer and fall than in the spring and winter. In the cases of the field vole (Microtus agrestis), Chitty (1961) found that the adrenal weights increased from low values in fall and winter to high values in mid-summer. Zalensky (1934) also reported that there is a significant increase in adrenal weight during the breeding season of the thirteen-lined ground squirrel (Citellus tridecemlineatus). The adrenals of the male Norway rat (Rattus rattus), however, averaged about 50% heavier in winter than in summer (Roger and Richter, 1948), and Anthony (1953) could find no seasonal trend in his analysis of adrenal weights in the male prairie dog (Cynomys ludovicianus). In the case of sigmodon,

at least on the basis of the data accumulated in this study, it is impossible to establish that there is a clear-cut, definite correlation between adrenal weights and the season of the year.

Studies of caged laboratory mice (Bullough, 1952; Christian, 1954, 1956a, 1959b) and meadow voles (Louch, 1956) have indicated that there is a direct relationship between the weight of the adrenal glands and the stress which had been induced by crowded conditions. In wild populations of field voles, Chitty (1961) could find no consistent relationship between the mean standardized adrenal weights and the trend of the population; the only exception to this generality was that females from expanding populations tended to have the heaviest adrenals. The weights of the adrenal glands of the Norway rat, however, did increase regularly as the population increased in density (Christian and Davis, 1956), and the adrenal weights of the meadow vole also increased in proportion to the density of the population (Louch, 1958). In the present study, these conclusions cannot be drawn from the evidence at hand about the relationship between changes in the density of the population and changes in adrenal weights.

Evidence of any correlation between adrenal weight and population density is lacking, whether one takes into account unadjusted adrenal weights, weights adjusted for body weight, or the weight of the largest pair of glands. During the annual changes in density of the population on the grid, there is no direct correlation; and there is no correlation in this respect between the animals at the farm and those on the grid, when one compares these on a monthly basis. Presumably there are other variables present in the environment and other sources of stress to which the individuals react as they would to the social stress induced by an increase in the density of the population. One such factor which must

be given consideration is the width of the X zone of the adrenal cortex. Adrenal weights may not be an accurate indicator of the amount of stress because of the absence or presence of this zone (Christian, 1956).

Adrenals Sections. The width of the zona glomerulosa could be measured with some degree of accuracy, since it is clearly separated from the zona fasciculata; it is also uniform in width over the entire section. This zone reached its maximum width during the month of January both on the grid and at the farm, 74.7 and 77.2 respectively, as is shown in Tables XV, XVI, and XVII. It is also evident from these tables that the zone is wider during other winter months. In the population on the grid, for which more data were available, there was a sudden increase from October to November (56.9 to 70.5 microns); and, except for February, the zone retained this width until March. The standard error for February, it should be noted, is inordinately large.

The hormones which regulate mineral balance within the body are synthesized in the zona glomerulosa (Greep and Deane, 1947; Deane, Shaw, and Greep, 1948; Stachenko and Giroud, 1959a). Furthermore, this zone does not appear to be under the direct influence of the anterior pituitary (Stachenko and Giroud, 1959b).

In the light of these observations about the functional zonation of the glomerulosal area of the cortex and its role in the synthesis of mineral regulating hormones, the data in Tables XV, XVI, and XVIII suggest two conclusions. First, the change in width is not mediated via the pituitary gland, because ACTH apparently has no direct effect on the zone. Therefore, this change is not due to the stress of crowding, if the reaction to this stress is to release a greater amount of ACTH. Second, there is possibly a change in the sodium-potassium balance of the cotton rat diet, associated with a change in the width and activity of this zone,

during the winter months. This fact may be attributed to a lower level of salt consumption during the non-growing season. Mosier (1957) suggests that, in the wild Norway rat, there is a compensation for a low salt diet by hyperplasia of the zona glomerulosa. The result produces an optimum balance of sodium and potassium in the presence of an intake of low sodium. Increased width of the zona glomerulosa can be caused by an increased intake of potassium or decreased intake of sodium, since either will upset the equilibrium. Deane, Shaw, and Greep (1948) have demonstrated that the depression of sodium-potassium ratio caused increased secretion by the cells of the zona glomerulosa, while elevation of this ratio caused decreased secretion by this zone.

Hence, it is suggested that the greater width of the zona glomerulosa, which is indicative of increased activity during the winter months, is due to a nutritional change rather than to changes in density of population. This nutritional change could be either an increased intake of potassium or a decreased intake of sodium. Cruickshank and Elliot (1926) found that the level of potassium showed only slight annual fluctuations, while the level of sodium in pasture grasses reached peaks at both the beginning and at the end of summer.

In examining the adrenal sections, it was almost impossible to distinguish between the zona fasciculata and the zona reticularis. For this reason, some of the slides were not used to obtain the data about the width of the zona fasciculata. It will be noticed in Tables XV, XVI and XVII that the size of the sample is smaller for an estimate of this parameter. There does not appear to be a consistent pattern in the width of the zona fasciculata from month to month in either population, or does there seem to be any basis for comparison between populations. This zone, for instance, reached its greatest width (199.9 microns) at the

farm in October, and on the grid in March (198.8 microns). It was expected that there would be some correlation between environmental stresses, particularly those due to density of population, and the width of this zone of the adrenal cortex. This expectation, however, was not realized.

The growth and function of the zona fasciculata cells is controlled by ACTH (Stachenko and Giroud, 1959b). Consequently, with an increase in the level of ACTH, these cells become more active (Deane, Shaw, and Greep, 1948). Other effects of ACTH are: decrease in sudanophilic substance, decrease in concentration of cholesterol, and increase in glandular weight (Sayers, 1950). After a stressful situation, which has the same effect as ACTH (Sayers, 1950), the sudanophilic substance of the gland re-accumulates (Sayers and Sayers, 1949). Of the several glucocorticoids produced by the zona fasciculata (Christian, 1960), the laboratory rat secretes primarily corticosterone (Hofmann, 1957). These steroids are concerned with gluconeogenesis, resistance to stress, and antibody production (Sayers, 1950; Thomas, 1953; McMaster and Edwards, 1957). Therefore, the width of this zone should be a reasonably good indicator of the amount of stress to which an animal is subjected.

There was also a wide variation in the number of vacuoles within the zona fasciculata, but the variation was to be found within each monthly sample as well as between months and between populations. Some of the sections have an almost foamy appearance, for which reason this zone is sometimes referred to as the zona spongiosa. These vacuoles contain lipid materials, most of the lipid being cholesterol (Glick and Ochs, 1955). Following ACTH stimulation or stress, there is a depletion of the lipid content of the cells (Bergner and Deane, 1948; Sayers and Sayers, 1949; Sayers, 1950). During the "resistance" phase of the stress syndrome,

however, the steroid content increases above normal, then later declines and disappears (Greep and Deane, 1949).

If a low number of vacuoles is indicative of a stressed condition, the animals on the grid appeared to be subject to stress during the month of June and later in the following spring (Tables XV, XVI, and XVIII). The greatest number of vacuoles is found from September to January, and after this month there is a gradual decrease in number.

In summarizing the data obtained from measurements of the width of the zona fasciculata and the number of lipid vacuoles within this zone, the results are not as clear-cut as those obtained from the zona glomerulosa. The width of this zone does not appear to change seasonally, or with changes in population; this fact indicates that there is no measurable change in ACTH production, stress, or consequent production of glucocorticoids. There is some suggested relationship between seasonal changes and the number of lipid vacuoles in the zona fasciculata, but insufficient data from the population at the farm does not permit a comparison between the two populations. If there is a positive correlation between stress due to density and the width of the zona fasciculata in a wild population, it is not evident from this research.

It cannot be stated definitely, however, that no such correlation exists. More than at any other point in this research, it is necessary to employ highly refined techniques and to possess a more thorough knowledge of the social structure of the population before any conclusive statement can be made. Often the zona fasciculata would appear to blend into the zona reticularis, with the result that the exact point of separation could not be determined. This zone, moreover, frequently varied in width from one part of the section to another. A more unequivocal measurement of the width of this zone is need.

In addition, social relationships between adult male rats have not been taken into consideration, because it was impossible to tell which animals were dominant and which were subdominant in a sample taken at random from a wild population. Because of the expected social interactions, as well as individual temperaments, there were doubtless some males that were subject to stress in the most favorable environment and others that were relatively tranquil in the most unfavorable environment. There was, consequently, little uniformity in the monthly sample and small likelihood that there would be measurable difference between samples. Not until these two problems are solved, that of measuring the zona fasciculata more accurately and that of determining the social structure of the wild population, can anything conclusive be asserted about the relationship between adrenocortical changes and the density of population.

Accessory Reproductive Organs. A study of Tables XIX, XX, and XXI reveals that there are two factors which lead to changes in the weight of the accessory reproductive organs, namely that which is concerned with climate and that which is concerned with density. Each of these factors will be discussed respectively, using the weights of the glands in milligrams, although the adjusted weight or the weight of the largest sample could just as well be used.

In the population on the grid, the preputial glands attained their greatest weight in September (294.60 mg.), then declined to 48.55 mg. in October, and to 33.70 mg. in November; they remained at approximately this weight for the remainder of the non-breeding season. It should be recalled that the ascent of the testes had occurred in 99.40% of the population by the time of the trapping period in September. One of the sequelae of this ascent into the abdominal cavity was the decrease in

in weight of the preputial glands. This phenomenon is also shown in the monthly changes of the farm population.

The seminal vesicles of the animals from the grid showed even greater changes in weight. From September to October the glands decreased in weight from 1497 mg. to 43.1 mg. on the grid (Table XX). The decline was not quite as sudden in the population at the farm: from 1016.6 mg. in September to 506.5 mg. in October. Between the months of September and October the ventral prostates of the animals on the grid also declined from 269.8 mg. to 28.0 mg. As can be seen from Table XXI, the population on the farm paralleled this decrease.

If one views either of these populations separately, not making any comparison between them, this fact becomes clear: the seasonal defects which are associated with the ascent of the testes are of some consequence relative to the weights of the accessory organs. Since the androgens produced by the testes bring about an enlargement and an increase of secretory activity of the accessory organs (Burrows, 1949), these reductions in weight appear to be a direct consequence of testicular ascent. Moreover, the size of these glands, especially the preputial, has been used as a bioassay for sterioids with androgenic effects (Huggins, Parsons, and Jansens, 1955). The androgens apparently have a direct effect on the accessory organs, since hypertrophy of the preputial glands can be produced with testosterone propionate in either the intact or the hypophysectomized rat (Rennels, Hess, and Finerty, 1953). ACTH, however, is also known to stimulate growth of the preputial glands in female white rats (Jacot and Selye, 1951).

Of this much one can be quite sure in the case of sigmodon males: when they enter the non-breeding season, the accessory reproductive organs involute and become rudimentary; this state follows ascent of the testes

into the abdominal cavity. After all such has taken place, the animals are incapable of reproducing themselves.

It should be noted that the changes of the population on the grid took place earlier than those at the farm, as can be seen in Tables XIX, XX, and XXI. For example, in October the paired preputials of the animals on the grid weighed only 48.55 mg.; those at the farm weighed 112.75 mg. (Table XIX). Table XXI shows the same effect in the weights of the ventral prostates. Again, for the month of October, the ventral prostates of the animals on the grid had a mean weight of 28.8 mg., while those taken from the sample on the farm was 150.1 mg. It appears from these data that the more dense population terminated its reproductive period at an earlier date than did the less dense one.

It also appears that the more dense population began its breeding season in the spring at a later date. The first indication of this is the difference in the weights of the seminal vesicles for the month of February (Table XX). The animals samples from the grid had seminal vesicles with a mean weight of 4.8 mg.; those from the farm had a mean weight of 23.8 mg. During this month, success in trapping on the grid was 41.1%, as compared to 8.0% at the farm (Table XI).

Metabolism of the testes. Two antecedent events appear to be responsible for the changes in metabolism of the testes: seasonal changes in weather (having the same effect in both populations) and density changes (resulting from a difference between populations). Such, at least, is the working postulate in the light of which the data will be interpreted. These data are found in Tables XXII to XXXI.

The climate was constant for both populations. Changes in testicular metabolism due to weather changes should have occurred simultaneously and should have been of the same magnitude in both populations. Differences

due to density of population, when combined with those resulting from weather differences, showed one population to rise higher or fall lower than the other; they also showed a change in the time at which the effect was produced. These differences, treated below, which appear as a difference in magnitude of response, or as a difference in the time at which the response took place, are here attributed to differences in the density of each population.

a. Weight of the testes. The weight of the testes (Tables XXII, XXIII, and XXVI) in both populations had reached their maxima in September, when the mean on the grid was 2318.42 mg.%, and that on the farm was 2245.75 mg.%. During the non-breeding season the weights were quite similar for both populations. In January, for instance, the mean on the grid was 125.81 mg.%, and that on the farm was 102.42 mg.%. The first suggestion of the onset of the breeding season was found on the farm in February, when the weight of the testes had risen to 444.36 mg.%. The weight of the testes from the sample on the grid in March was still less than this (146.85 mg.%). It seems not unreasonable, therefore, to suggest these conclusions from the data: first, both populations terminated their breeding season at approximately the same time; second, that the less dense population was prepared for breeding earlier in the spring.

b. Percent dry weight of the testes. In November and January the size of the sample made it impossible to obtain measurements from the animals on the grid; in January and February the samples from the farm were too small to make any kind of measurement (Tables XXII, XXIII, and XXVI). From June, when the dry weight was 14.31%, to September, when the dry weight was 14.04%, there appears to be little change. In March, the dry weight of the testes from the grid sample was 17.03%. From the small amount of data available, this seems to be the only variation, and it may be related

to seasonal conditions or to conditions of density. Since only one animal comprised the size of the sample in both October and February, no conclusions are warranted for these two months. There was apparently no difference between these populations for this parameter, either in magnitude or in time.

c. Uptake of oxygen by the testes. The rate of the uptake of oxygen was measured with and without a nutrient. The uptake of oxygen without a nutrient does not show any consistency of pattern either on the grid or at the farm, and the effects of differences of season and density are not evident. On the other hand, the uptake of oxygen with a nutrient does seem to reflect both these factors (Tables XXII, XXIII, and XXVII). The rate of testicular uptake of oxygen for the grid animals during June and September was high (8.70 ul/mg/hr and 8.44 ul/mg/hr respectively), followed by a decline during October, November, and January (5.06 ul/mg/hr, 5.51 ul/mg/hr, and 5.61 ul/mg/hr again respectively). In February the rate returned to that of the breeding season. On the farm during September the rate was high (10.54 ul/mg/hr), decreased in October (7.81 ul/mg/hr), then remained at this level for January and February (7.55 ul/mg/hr and 7.42 ul/mg/hr).

The effects were parallel at two levels, there being some difference in time. At both places the rate was high in September (the farm higher than the grid) and at both the rate decreased in October and remained low for the winter months (the level on the farm still higher than that of the grid). As may have been anticipated, the rate of uptake of oxygen in both populations was higher during the breeding season than during the non-breeding season. In addition to this, however, it is also evident that the more dense population has a slower rate of uptake of oxygen by the testes than does the less dense population. If one may assume that a decreased metabolic rate is associated with a decreased

function of the tissue, the testes of animals in the more dense population are not as functionally active.

c. Metabolism of glucose. Tables XXIV, XXV, and XXVIII show that the metabolism of glucose was high in October for both populations: 136.96 ug/mg/hr on the grid and 124.98 ug/mg/hr at the farm. It then declined for the following month; the level for the farm population was quite far below that of the grid. In January, for example, the sample from the grid was 83.48 ug/mg/hr, whereas that from the farm was only 48.5 ug/mg/hr.

Again in summary: at the end of the breeding season, after the testes had ascended into the body cavity, there was an increase in the metabolism of glucose by the testes, with the grid reaching a higher level than the farm. For every month of the study, the level of metabolism of glucose was higher in the more dense population than in that which was less dense. This observation gains more significance when it is related to the production of lactic acid.

d. The production of lactic acid. The production of lactic acid by the testes showed the very same patterns of change that were evident in the metabolism of glucose. Both populations reached a high in October (62.28 ul/mg/hr on the grid and 49.78 ul/mg/hr at the farm), as is shown in Tables XXIV, XXV, and XXIX. Again, for every month of the study, the level of production of lactic acid by the testes was higher in the more dense population. Seasonal effects were most evident in the month of October in both populations, but the effect of density of population is evident throughout the year.

October, as has been mentioned, was the month in which changes occurred in both populations. Approximately one month after the ascent of the testes, both the metabolism of glucose and the production of

lactic acid reached a maximum; these maxima were followed by minima which were lower than those of the breeding season.

The data relative to uptake of oxygen, metabolism of glucose, and production of lactic acid may now be summarized and related to density of population. Recall that the testes of animals in the dense population are using less oxygen, presumably because of its inaccessibility due to constriction of blood vessels. Anaerobic metabolism, or glycolysis, would then be the norm, and this was verified by the greater production of lactic acid. More glucose was being utilized by the testicular tissue because glycolysis is not as efficient, in terms of energy produced, as is aerobic respiration. Therefore, the testes of animals in the more dense population are using a greater amount of glucose and are not metabolizing it as efficiently as are the animals in the less dense population.

e. Protein content. The protein content of the testes appeared to change with the changes of the seasons. There was, however, no noticeable difference between the populations other than a time lag in the month of February for the animals on the grid (Tables XXIV, XXV, and XXX.) In January, for example, the grid sample value was 69.92 mg./gm., and in February 9.62 mg./gm. This seasonal decrease in protein content had taken place one month earlier at the farm. The significance of this mid-winter decrease in protein content is not clear as yet.

f. RNA and DNA content. The RNA content in both populations increased in February, the increase being greater at the farm than on the grid. In September, for example, the RNA content of the testes was slightly higher in both the breeding and non-breeding season in the instance of the less dense population. Using the amount of RNA as a measurement of the ability of cells to synthesize protein, it appears that the testicular cells of animals in a more dense population were more quiescent than

were those of animals in population of less density.

The DNA content of the testes was lowest in October for both populations, with the animals from the grid having a lower DNA content than those from the farm (1.10 mg./gm. and 5.66 mg./gm.), as is found in Tables XXIV, XXV and XXI. For every month that a comparison between population could be made, the DNA content of the testes of animals in the more dense population was lower than that of the animals in the less dense population. Since the amount of DNA is a measurement of the number of cells (Barrows, C. H., M. J. Yiengst, and N. W. Shock, 1958; Falzone, J. A., C. H. Barrows, and N. W. Shock, 1959), it would appear that the animals in the more dense population have fewer cells.

Summation

The introduction to this report suggested several possible processes by which a population might be able to regulate its own rate of reproduction. Only one of these homeostatic processes was singled out as the proper object of this research: the early termination or prolonged continuance of the breeding season in the fall of the year and time of its commencement in the spring.

To reduce vegetational and nutritional differences to a minimum, one population of sigmodon, living in its natural habitat (the grid), was studied for one year and field data sheets of three previous years were also used. From this it became quite evident that the fall breeding season was extended into November, or even continued all winter if the late summer population was low, and terminated in August if the late summer population was high.

In order to limit the effect of climatic differences, two populations

of different densities were compared for one year. From this comparison it can be stated that the adult males terminated the breeding season earlier in the fall and commenced later in the spring if the population was more dense, as is evidenced by the weights of the accessory reproductive organs and the testes. In addition to this, the testes of animals in the more dense population had a less efficient metabolism, both during the breeding and during the non-breeding season. The rate of oxygen uptake was less, the metabolism of glucose and production of lactic acid was greater than in animals from a less dense population. The testes of animals in a more dense population also were found to contain less DNA and less RNA, suggesting that there are fewer cells, and that ability to synthesize proteins is not as great as in animals from a less dense population.

That there are measurable anatomical and physiological differences between adult males from populations of different densities is evident. Such differences have been reported for other organs, but this is, to my knowledge, the first report of changes in the metabolism of the testes. A study of the adrenal weights and of adrenal sections did not result in a clarification of the processes by which these are effected.

CHAPTER V

SUMMARY AND CONCLUSIONS

The purpose of this study has been to determine whether a population of small mammals, living in natural habitat, is able to regulate its own rate of natality, and adjust this to the optimum level which the environment can support. Briefly, the question is whether there are homeostatic, negative feedback processes, similar to those described in the Introduction to this research, which operate to control population size. Possible physiological processes by which this might be effected, if it were found to be present, were also investigated. The cotton rat, Sigmodon hispidus, was selected as the experimental animal because of its local abundance and because of the dramatic fluctuations in numbers this species sometimes experiences. Data were collected from two populations, one in which the animals were marked and released, and the other in which the animals were removed upon capture. The actual comparison between these populations was carried out for one year; however, trapping records for three previous also were available for one of the two populations.

Although Sigmodon hispidus is a seasonal breeder in its natural habitat, the summer breeding season may vary in length as it extends into the fall months. With a high summer density, breeding activity terminates in late August, while such activity may continue all winter if the density is low. There is a high negative coefficient of correlation between breeding activity and density of population during the months of the fall, both in males and in females.

Attrition to the more dense population during the fall months was heavy, and not selective for sex, although summer-like conditions extended into November. The attrition which began in January appeared to have affected males more than females.

The male, to some extent, determines the length of the breeding season in this species. Females with open vulvae were captured after males had become sterile in the fall and before they had become sexually competent in the early spring.

Juvenile members of the population showed a retarded growth rate until April. Winter attrition was greatest among animals weighing more than 90 grams; there were no survivors in these weight classes.

Associated with an unexplained decrease in the population during the early fall, immigrants from peripheral areas presumably moved onto the grid. It appeared that animals in the center of a dense population were being lost to the population, and that the area was re-populated by immigrants.

No definite correlation could be established between the weights of the adrenal glands and seasonal weather changes or between these weights and density of the population.

The zona glomerulosa of the adrenal cortex was wider during the winter months in animals from both populations. Since this zone is that portion of the gland where the mineral regulating hormones are synthesized, and varies in width with shifts in the sodium-potassium balance, it is here suggested that there is a lower sodium level in the winter diet of the animal.

The zona fasciculata of the adrenal cortex was not found to vary in width with either the changes in weather or with density of population. Therefore, using the width of this zone as an indicator of stress, it cannot be established that the animals were under greater stress at any particular season of the year or that the degree of stress increased with an increase in population density.

The accessory reproductive organs of the male sigmodon decreased greatly in size after the ascent of the testes into the body cavity at the termination of the breeding season. This occurred earlier in the more dense population. In the spring of the year, the increase in size of the seminal vesicles occurred later in the more dense population. The general conclusion, arrived at from a study of the ventral prostate, seminal vesicles, and preputial glands, is that in the more dense population the breeding season ended earlier in the fall of the year and was initiated later in the spring than in the less dense population.

The testes became rudimentary after ascent into the body cavity, rendering the animals seasonally sterile. On the basis of the weight of the testes, it can be asserted that the more dense population began preparation for the spring breeding season later than did the less dense population.

There was a measurable difference between the two populations in the rate of uptake of oxygen by the testes. The more dense population had a slower rate both during the breeding and during the non-breeding season.

The amount of glucose metabolized by the testes was greater in the more dense population, both during the breeding and during the non-breeding season.

The production of lactic acid by the testes was greater in the more dense population, both during the breeding and during the non-breeding season.

The amount of RNA in the cells of the testes was less in the more dense population, both during the breeding and during the non-breeding season.

The amount of DNA in the cells of the testes was less in the more dense population, both during the breeding and during the non-breeding season.

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APPENDIX

Estimate of Population Density using the
Simple Capture-recapture Method

Data from the January, 1964
Trapping Period

- Day 1. Trapped, marked, and released 124 animals.
 Day 2. Trapped and released 138 animals.
 40 were previously marked
 98 were marked on Day 2
 There are now 222 marked animals in the population.
 Day 3. Trapped and released 138 animals.
 53 were previously marked
 85 were marked on Day 3
 There are now 307 marked animals in the population.
 Day 4. Trapped and released 148 animals.
 103 were previously marked
 45 were marked on Day 4
 There are now 352 marked animals in the population.
 Day 5. Trapped and released 137 animals.
 106 were previously marked.
 31 were marked on Day 5
 There are now 383 marked animals in the population.

| Day | Trapped | Previously marked (r) | Total marked (a) |
|-----|---------|-----------------------|------------------|
| 1 | 124 | --- | 124 |
| 2 | 138 | 40 | 222 |
| 3 | 138 | 53 | 307 |
| 4 | 148 | 103 | 352 |
| 5 | 137 | 106 | 383 |

- Population Estimate, $X_4 = \frac{a(n-1)}{(r-1)} = \frac{(352)(138)}{(107)} = 454.$
- Variance, $T = \frac{a^2(n-1)(n-r)}{(r-1)^2(r-2)} = \frac{(352)^2(138)(137-106)}{(107)^2(108)} = 428.65$
- Standard Error, $\hat{S}_{x_4} = \sqrt{T} = 20.70.$
- Coefficient of variation, $CV = 100 \frac{\hat{S}_{x_4}}{X_4} = \frac{(100)(20.70)}{454} = 4.83\%$

ADDENDUM

Management Implications

This research was made possible through the use of facilities provided by the Oklahoma Cooperative Wildlife Research Unit, and was directed by the leader of this Unit. For this reason, practical application of the results to the control of sigmodon and the management of other species of mammals has been a frequent subject of conversation and a motive for the research. In addition to this, the majority of the readers of this report, because of the mode of its distribution, will be concerned with conservation practices and management techniques -- further reason for this addendum. The following comments fall quite naturally into two sections: the control of sigmodon when it does reach peak levels of density, and the application of general principles of population dynamics to other species of mammals.

Since it is evident that there are measurable differences in the anatomy and physiology of sigmodon as the population changes in size, it appears quite feasible that an increase in population could be predicted several months in advance. Any number of parameters could be used: the relative number of young in the population, the reproductive competence of the males, the time at which the breeding season terminates, or the rate of turnover in the population. The point I wish to make is that a continued study of one population of sigmodon may well lead to a clarification of the process by which this species does occasionally reach

peaks of density, and that the application of this knowledge to the control of the population before the actual increase would be less costly and more effective than a sudden "crash" program on the eve of the actual irruption. A continued study of sigmodon, exploring other facets of population interactions and regulation, would not fail to contribute to this fund of knowledge and result in a more effective and less costly rodent control program.

That there are homeostatic processes by which a population regulates its own rate of expansion is a general principle which should have application to species of mammals and suggest more effective management of these species. In other words, sigmodon is an excellent experimental animal for the clarification of these processes, and the knowledge obtained about the structuring of its population may well be transferred to the conservation of game species. For instance, the concept of social interactions adds a new dimension to the often-heard expression "carrying capacity".

Often a game species cannot be studied directly because of scarcity of numbers and also because of public opinion against taking the animals outside of the hunting season. On the other hand, it has been found that farmers, quite understandably, encourage the trapping of sigmodon on their property. Moreover, the greater number of sampled animals can lead to more valid conclusions. It does appear eminently practical to formulate general principles from a study of sigmodon, and use these principles, as applicable, in the management of game species of mammals.

VITA

Peter Mathias Green

Candidate for the Degree of

Doctor of Philosophy

Thesis: DENSITY OF POPULATION AS A REGULATING FACTOR IN THE
REPRODUCTIVE POTENTIAL OF SIGMODON HISPIDUS.

Major Field: Zoology

Biographical:

Personal Data: Born in Minneapolis, Minnesota, January 10, 1926,
the son of Waldon J. and Regina H. Green.

Education: Attended grade school in Minneapolis, Minnesota; graduated from Southwest Minneapolis High School in 1943; attended St. John's University from 1946 to 1949; received a Bachelor of Science degree from St. Benedict's College in 1952; studied theology at St. Gregory's Seminary from 1952 to 1956; attended summer sessions at Oklahoma University from 1956 to 1958; attended summer sessions at Oklahoma State University from 1959 to 1961; received the Master of Natural Science degree in August, 1961; completed requirements for the Doctor of Philosophy in August, 1964.

Professional Experience: Entered the United States Navy in 1943, and was honorably discharged in 1946; is a Roman Catholic priest and a member of the Order of St. Benedict; has served as an Auxiliary Chaplain at Fort Sill from 1956 to 1960; has taught high school science courses from 1952 to 1960 and a college science course from 1960 to 1961; is a member of the American Association for the Advancement of Science, the American Institute of Biological Sciences, the Ecological Society of America, the National Association of Biology Teachers, and the Oklahoma Academy of Sciences; has obtained three summer grants and one full-year grant from the National Science Foundation.