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SIGMODON HISPIDUS (RODENTIA) IN LOBLOLLY PINE

SUCCESSION AS INFLUENCED BY SUPPLEMENTAL FOOD

presented by

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has been accepted towards fulfillment of the requirements for

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SIGMODON HISPIDUS (RODENTIA) IN LOBLOLLY PINE SUCCESSION AS INFLUENCED BY SUPPLEMENTAL FOOD

by

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ABSTRACT

SIGMODON HISPIDUS (RODENTIA) IN LOBLOLLY PINE SUCCESSION AS INFLUENCED BY SUPPLEMENTAL FOOD

by

William Reinhold Teska

An experiment was designed to evaluate the following hypothesis: Food is a critical factor in the dynamics of Sigmodon hispidus populations particularly during the winter and in suboptimal habitats. Populations of Sigmodon were studied in six South Carolina loblolly pine plantations of two ages. Initially, the two-year-old plantations (planted in 1973) were characterized by optimal habitat and peak densities of Sigmodon. The three-year-old plantations (planted in 1972) were characterized by suboptimal habitat and declining densities. Populations on the three plantations of each age were live trapped from April 1975 through June Each plantation had two, 1-hectare, live-trapping 1976. grids, one to sample a Sigmodon population which received supplemental food, the other to sample a control population. A mixture of sunflower seeds and oats was provided to each food-supplemented population by maintaining 20 feeding stations and by broadcasting 17 kg of mixed seed weekly from 2 May 1975 through June 1976.

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During the experiment densities of the 1973 control populations were higher, and the breeding seasons were longer than for the 1972 control populations. Populations from the control grids on both plantation ages, however, exemplified demographic patterns typical for <u>Sigmodon</u> in South Carolina.

For both plantation ages supplemental food increased population density, lengthened the breeding season, increased average litter size, increased average growth rate, and improved the physical condition of <u>Sigmodon</u> during the winter. Supplemental food decreased trappable longevity. Decreased survivorship on the food-supplemented grids may have been due to an increased emigration rate in addition to low trappability of Sigmodon on the food grids.

The food treatment had a greater effect on <u>Sigmodon</u> populations in the 1972 than in the 1973 plantations. Population densities were higher on the 1972 food grids than on the 1973 food grids especially during the early summer and the winter. In addition, growth rates for a fall cohort were higher on the 1972 than on the 1973 food grids.

Natality rates rather than mortality rates appeared to be the primary determinant of <u>Sigmodon</u> densities. Changes in density were closely associated with the rates of reproduction. Natality rates were dependent on the food supply. Reduced breeding during the winter was accompanied by and may have been caused by poor body conditions. The

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supplemental food maintained the body condition of the cotton rats during the winter, and a significant number of food-supplemented <u>Sigmodon</u> bred during the late winter.

Food appears to be limiting for <u>Sigmodon</u> populations, especially in suboptimal habitat and during unfavorable seasons. The food supply, as distinct from cover, is important in determining the <u>Sigmodon</u> densities in older pine plantations. The distribution and abundance of <u>Sigmodon</u> in areas undergoing rapid succession are strongly influenced by the available food.

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INTRODUCTION

The mechanisms which regulate the densities of rodent populations remain uncertain despite years of research on this subject. This is probably due at least in part to a complicated multitude of interacting factors which may regulate populations (Lidicker, 1973). A multiple-factor approach to the study of population regulation, although ideal, generally is not feasible because multiple factors can seldom be tested experimentally (Krebs and Myers, 1974). An alternate approach, as used in the present study, is to delineate one or two factors, and to investigate these by designing experiments to test their roles in population regulation (see review in Krebs and Myers, 1974).

The food supply of rodents is one factor considered by some not to regulate the densities of natural populations (Chitty, 1960; Krebs and DeLong, 1965; Krebs and Myers, 1974). Fleharty and Olson (1969), for example, investigated the food habits of two rodents and reported that food did not limit the number of these rodents because there was no indication of an over utilization of the food resource. Hairston, Smith and Slobodkin (1960) argued that since herbivores rarely have any detrimental effect on the standing crop, they could not be food limited. Measurements

of primary productivity support this belief since herbivorous rodents usually consume less than 5 per cent of the annual production (Golley, 1960; Drozdz, 1966). Grodzinski (1971), however, calculated that rodents could consume up to 47 per cent of the food supply during certain years. Under normal conditions <u>Microtus</u> can significantly affect the standing crop and seed crop of preferred grasses (Batzli and Pitelka, 1970). Recent estimates of the metabolic requirements of some rodents indicate that the available food during the winter may be insufficient to meet the energetic demands of reproducing females (Sadleir, Casperson, and Harling, 1973; Collier et al., 1975).

Chitty, Pimentel and Krebs (1968) found that herbivorous rodents had an abundant food supply throughout the year, and that declines in population numbers were not correlated with changes in the food resource. Other field studies have indicated a positive correlation between the food supply and the rodent population densities and reproductive rates (\underline{e} . \underline{g} ., Linduska, 1942; Myllymaki, 1969; Smirin, 1970; Hansson, 1972). Ferns (1976) noted that an optimal quality forage for <u>Microtus agrestis</u> was not necessarily as abundant as a cursory examination of the habitat might indicate.

Many studies, which mostly have been conducted in the laboratory, demonstrate that the quantity and quality of an animal's diet can significantly affect the vigor of the animal. Dietary alterations primarily change an animal's body condition and subsequently alter the growth rate (Millar, 1975; Glass, Harrison, and Swerdoff, 1976),

reproductive performance (Gunn and Doney, 1973) and behavior (Frankova, 1973) of the animal. Laboratory studies cannot indicate that the natural food resources are limiting (Ashby and Vincent, 1976); instead, these studies clarify the consequences of an insufficient level of nutrition. The exact role of the food supply is not easily determined since energetic demands are difficult to estimate in the field, and the quantity and quality of the actual food supply are unknown for the typically opportunistic rodent (Batzli and Pitelka, 1971).

To test the necessity of a quality food supply for growth and maintenance of free-living populations, experimental manipulations of the food supply are required. Typically, supplemental food, usually a grain, has been supplied in feeding stations to a population of rodents. Data collected from live trapping such populations have been compared with the data collected from similar populations which have not received supplemental food. Although not all researchers have examined the same species or the same aspects of the populations, several consistencies resulting from the supplemental food have been noted. With supplemental food the breeding seasons of Clethrionomys glareolus were extended from a few weeks to an entire winter (Watts, 1970; Bujalska, 1975; Andrzejewski, 1975). The breeding season was also extended or began earlier for Apodemus sylvaticus (Flowerdew, 1972; Watts, 1970), Peromyscus maniculatus (Fordham, 1971), P. leucopus in

Michigan (Lackey, 1974), <u>M</u>. <u>ochrogaster</u> (Cole, 1977), and <u>Mus musculus</u> (DeLong, 1967). Bendell (1959), who examined the effects of supplementary food on <u>P</u>. <u>leucopus</u> in Ontario, failed to note any changes in the breeding season.

Supplemental food has particularly enhanced the survivorship of juvenile animals; for example, in <u>C. glareolus</u> (Bujalska, 1975), <u>A. sylvaticus</u> (Flowerdew, 1972), <u>M. ochrogaster</u> (Cole, 1977), and <u>P. leucopus</u> (Bendell, 1959; Lackey, 1974). Supplemental feeding lowered the survival rates for <u>M. californicus</u> (Krebs and DeLong, 1965) but did not change the winter survivorship of <u>C. glareolus</u> (Andrzejewski, 1975).

A parameter which has been reported to be influenced by supplementary food and which in turn affects reproductive potential is the growth or maturation rate. Growth rates increased when supplementary food was supplied for <u>C. glareolus</u> (Andrzejewski, 1975; Bujalska, 1975), <u>P. leucopus</u> (Bendell, 1959), <u>P. maniculatus</u> (Fordham, 1971), <u>M. musculus</u> (DeLong, 1967), and <u>M. californicus</u> (Krebs and DeLong, 1965).

The increased reproductive performance of the foodsupplemented populations generally increased the densities of rodents. Densities of the food-supplemented populations were increased for <u>A</u>. <u>sylvaticus</u> (Flowerdew, 1972; Watts, 1970), <u>P</u>. <u>leucopus</u> (Bendell, 1959; Lackey, 1974), <u>P</u>. <u>maniculatus</u> (Fordham, 1971), <u>P</u>. <u>polionotus</u> (Smith, 1971), <u>M</u>. <u>musculus</u> (DeLong, 1967), <u>C</u>. <u>glareolus</u> (Bujalska, 1975;

Andrzejewski, 1975), and <u>M</u>. <u>ochrogaster</u> (Cole, 1977). Watts (1970) studying <u>C</u>. <u>glareolus</u> and Krebs and DeLong (1965) studying <u>M</u>. <u>californicus</u> reported reverse density trends.

The trends from these supplemental food studies vary in degree, and simple statement of trends can therefore be somewhat misleading. For example, Watts (1970) reported a longer breeding season for a food-supplemented population of C. glareolus than for a control population. This increase, however, was only 2 to 3 weeks, and the biological significance of such an increase is questionable. Other problems compound the drawing of conclusions from such data. Most of the studies have had no replications; and when different researchers have repeated the experiment with the same species at different localities, results have not always been consistent. The inconsistent results partly may have been due to differences in the type of supplemental food and in the size of the study area. Also, many experiments have been short term, some have been coupled to the study of cycles, and most have utilized feeding stations which may alter the movements and social structure of the populations.

The present experiment was designed to ascertain the relationships of the food supply and the population dynamics of the hispid cotton rat (<u>Sigmodon hispidus</u>). The role of the food supply in determining the distribution and abundance of <u>Sigmodon</u> in areas undergoing rapid succession was also investigated. Supplemental food was used as the experimental treatment.

Fundamental differences exist between the nutritional strategies of herbivorous and granivorous rodents (Baker, 1971). Granivores are thought to experience food shortages more commonly than herbivores, partly because of the seasonal production of seeds (Hansson, 1971a). Also, estimates of primary production indicate that more biomass is available as food for herbivores than for granivores (Odum, Connell and Davenport, 1962; Zemanek, 1972). Not all rodents are easily categorized as herbivores or granivores. A large number of rodents eat a variety of foods and should be classified as omnivores (Landry, 1970).

Although usually considered to be primarily herbivorous (Fleharty and Olson, 1969; Baker, 1971), <u>S</u>. <u>hispidus</u> may consume substantial amounts of insects and seeds during the fall and winter (Gaertner, 1968; Briese, 1973). <u>Sigmodon</u> <u>hispidus</u> probably should be regarded as an omnivorous rodent. Rodents considered to be largely herbivorous, such as <u>M</u>. <u>ochrogaster</u> (Zimmerman, 1965), <u>M</u>. <u>agrestis</u> (Hansson, 1971b), and <u>C</u>. <u>glareolus</u> (Holisova, 1975), also eat insects or seeds during certain seasons. It is not known if such seasonal shifts in diet are purely due to phenological conditions. Rodents can have very selective food habits (Gill, 1977) and do not necessarily eat the most abundant food in the habitat (Zemanek, 1972).

To examine the importance of the food supply in determining successional patterns of <u>S</u>. <u>hispidus</u>, young loblolly pine (<u>Pinus taeda</u>) plantations were selected as study sites. The characteristic forest succession

following the planting of trees affects the density and species composition of the small mammal fauna. For example, a shift in the mammalian species composition following logging has been documented in Oregon (Hooven, 1972), New Hampshire (Lovejoy, 1975), and Ontario (Martell and Radvanyi, 1977). A similar change in species composition occurs in old-field succession in the upper coastal plains of South Carolina (Golley <u>et al.</u>, 1965). The planting of pine trees in plantations affects the understory species composition and greatly accelerates succession (Spurr and Barnes, 1973). The latter effect permits major successional events to be observed within a limited time span.

<u>Sigmodon hispidus</u> is a common rodent in the dense grass cover of the early stages of succession (Goertz, 1964). During forest succession, once the understory progresses beyond the grass-forb stage and becomes shaded by shrubs and trees, <u>Sigmodon</u> populations decline sharply in density and vigor (Perkins, 1973). For example, in pine plantations on the Georgia piedmont, this decline occurs after the fourth year following planting (Atkeson, 1974).

Much of the research on population regulation has been oriented toward population fluctuations and cycles (Krebs and Myers, 1974). Fluctuations and cycles can be difficult to study because fluctuations can be hard to predict, and cycles require long periods of examination. In the present study, I tried to alleviate the problem of studying unexpectedly fluctuating populations by utilizing the

predictability of known successional trends. Populations of <u>Sigmodon</u> were studied in pine plantations of two ages, the younger age characterized by optimal habitat and peak densities of <u>Sigmodon</u>, the older age characterized by suboptimal habitat and declining densities.

This experiment, therefore examined the effects of supplemental food on populations of <u>S</u>. <u>hispidus</u> occurring in successionally optimal and suboptimal habitats. Because habitat quality was defined by the stage of forest succession, an insight was also gained into the relationships of the food supply, forest succession, and patterns of mammalian succession. The exact causes of the shifts in the mammalian species composition due to vegetative succession have never been tested by critical experimentation and remain poorly understood.

In summary, it was the purpose of the present experiment to test the following hypotheses:

Central Hypothesis:

Food is a critical factor in the dynamics of <u>Sigmodon hispidus</u> populations particularly during the winter and in suboptimal habitats. Null Hypotheses Which Were Tested:

- Population densities of <u>Sigmodon</u> are not affected by the presence of supplemental food.
- Survival rates for the control and foodsupplemented <u>Sigmodon</u> populations are the same.

- 3. The length of the <u>Sigmodon</u> breeding season and the reproductive effort are the same for the control and food-supplemented populations.
- 4. On food-supplemented grids the average litter size of female <u>Sigmodon</u> is the same as on control grids.
- 5. Growth rates of a <u>Sigmodon</u> cohort are not changed by the addition of supplemental food.
- During late winter the body condition of adult and subadult <u>Sigmodon</u> is the same for control and food-supplemented populations.

All null hypotheses were tested for populations in successionally optimal and suboptimal habitats. In this way the interaction between successionally determined habitat quality and food supplementation was examined.

MATERIALS AND METHODS

Selection of Study Sites

This study was conducted on the U. S. Department of Energy Savannah River Plant (SRP) in Barnwell and Aiken Counties, South Carolina. The habitat on the SRP is typical of the sandhill and upper coastal plain regions of the southeastern U. S. During the study, temperature and rainfall were average.

In the spring of 1975 six loblolly pine plantations on the SRP were selected for study; three each had been planted in 1972 and 1973. Each plantation had been prepared for planting by K-G blading (bulldozing), root-raking, and windrowing (piling the logging debris into long rows about two meters high and several meters wide). All of the areas had been logged during the summer and planted with one-yearold seedlings the following spring. The seedlings were spaced every 2.0 m in rows 3.5 m apart. The rows were parallel to the windrows.

Initially, to establish the patterns of mammalian succession, the densities of small mammals were determined on loblolly pine plantations planted from 1 to 5 years earlier. On each plantation, live traps were set in the most suitable habitat for S. hispidus until an index of the

<u>Sigmodon</u> populations was determined. From two to six plantations of each age were sampled. Trapping was concentrated in the two-, three-, and four-year-old plantations because these were the only ages characterized by a grassforb understory.

The trapping results (Table 1) indicate that on the SRP <u>S. hispidus</u> populations attained peak densities 2 years following planting and afterwards sharply decreased in density. Because of the low number of cotton rats caught in the fouryear-old plantations, the two- (1973) and three-year-old (1972) plantations were selected for intensive study. Naturally occurring densities during the late winter of 1975 were the criteria for establishing two-year-old plantations as optimal <u>Sigmodon</u> habitat and three-year-old plantations as suboptimal habitat.

Potentially, six 1972 and ten 1973 plantations were available for study. Of these, three of each age were eventually selected. With one type of exception, explained below, the individual plantations were selected independently of the <u>Sigmodon</u> densities. Instead, the plantations were chosen using physical and habitat criteria.

The plantations had to be large enough to establish two l-hectare (150 x 65 m) trapping grids at least 150 m apart and at least 15 m from the edge of the plantation. The selection of the plantations was further limited since each grid was to be divided lengthwise by a windrow. The windrow had to be at least 150 m long and separated at least 45 m from a parallel windrow. In addition, all-weather

Table l.	Summary of a pine plantati	<u>Sigmodon</u> trappi ons planted fro	ng survey (1 m 1970 to 19	.6 January to 2 174.	March 1975) on loblolly
Year Planted	Number of Plantations	Trap Nights	<mark>Sigmodon</mark> Captures	Captures/100 Trap Nights	Adjusted * Captures/100 Trap Nights
1970	۰ ۲	06	0	0.0	
1971	Ŋ	590	12	2.0	2.0
1972	9	4T0	30	7.3	5.1
1973	Ŋ	354	53	15.0	0.0
1974	N	. 20	0	0.0	-
	•				

*The adjusted number corrects for the different number of trap nights on each age of plantation by dividing the largest number of trap nights (590) into the total number of <u>Sigmodon</u> caught on plantations of each age, then multiplying by 100.

vehicular access to the plantations was necessary. Four plantations of each age met these criteria. During March 1975 the small mammals on each plantation were live trapped. The plantation of each age which had the lowest density of <u>Sigmodon</u> was dropped from the study because logistical limitations dictated that only three plantations of each age could be examined.

Description of Study Sites and the Experimental Design

The location of each plantation is identified by a U. S. Forest Service timber compartment and stand number. This number, my area code, the year of planting, the size, the elevation, and the soil type for each plantation are listed in Table 2. Figure 1 shows the location of each plantation on the SRP. The species of understory vegetation and of shrubs and trees on these plantations are listed in Tables 3 and 4, respectively.

Even though the 1973 and 1972 plantations differed in age by only one year, the densities of <u>Sigmodon</u> were greater on the 1973 plantations. The unequal densities were correlated with the appearance of the plantations. At the start of the experiment, the two-year-old plantations (planted in 1973) resembled typical old-fields; the planted pines had not grown taller than the grass and forbs (Figure 2). By the third year after planting (planted in 1972), the pine seedlings dominated the grass-forb layer and had begun rapid growth. The three-year-old plantations could be characterized as young pine stands rather than as old-fields (Figure 3).

Soil Type*	Orangeburg & Troup Sand	Orangeburg & Troup Sand	Gunter Sand	Wagram & Fuquay Sand	Wagram & Fuquay Sand	Wagram & Fuquay Sand
Elevation (m)	55	75	60	105	55	105
Size (ha)	35	34	23	32	15	20
Year of Planting	1973	1972	1973	1972	1973	1972
Area Code	73-1	72-1	73-2	72-2	73-3	72-3
Timber Stand	10	20	7	ħ	10	Ŋ
Timber Compartment	13	16	11	17	60	16

Table 2. General information about study sites.

*Aydelott, 1971.

Note: The timber compartment and stand numbers refer to a specific U. S. Forest Service management unit. The area code is the designation for each of these units in the present study. Figure 1. Location of the loblolly pine plantations studied; those with the same number (1, 2 or 3) were paired and trapped simultaneously (a trapping set).



Figure 1.

Table 3. Major understory vegetation on study sites.

Dyschoriste oblongifolia Opuntia sp. Cassia fasciculata Lonicera sp. Stipulicida setacea Helianthemum sp. Lechea sp. Aster paternus Aster sp. Carduus sp. Erigeron canadensis Erigeron strigosus Eupatorium capillifolium Eupatorium compositifolium Eupatorium recurvans Gnaphalium obtusifolium Haplopappus divaricatus Heterotheca gossypina Heterotheca graminifolia Heterotheca subaxillaris Senecio sp. Solidago odora Solidago sp. Carex sp. Cnidoscolus stimulosus Baptisia perfoliata Clitoria mariana Lespedeza angustifolia Lespedeza cuneata Lespedeza hirta

Lespedeza repens Lespedeza sp. Rhynchosia reniformis Tephrosia sp. Hypericum gentianoides Salvia lyrata Smilax sp. Yucca sp. Polypremum procumbens Passiflora incarnata Phytolacca americana Erigonum tomentosum Rubus betulifolius Diodia teres Galium pilosum Agalinis fasciculata Aureolaria pectinata Vitis rotundifolia

Andropogon spp. Aristida sp. Cenchrus echinatus Gymnopogon ambiguus Leptoloma cognatum Panicum sp. Paspalum sp. Pteridium aquilinum Sorghastrum nutans Triplasis americana Table 4. Major trees and shrubs on study sites.

Carya tomentosa	mockernut (hickory)
Crataegus flava	hawthorn
Diospyros virginiana	persimmon
<u>llex</u> sp.	holly
<u>Pinus palustris</u>	longleaf pine
<u>Pinus taeda</u>	loblolly pine
Prunus angustifolia	plum
Prunus serotina	black cherry
Quercus falcata	southern red oak
Quercus laevis	turkey oak
Quercus marilandica	blackjack oak
Quercus stellata	post oak
Rhus copallina	winged sumac
Rhus radicans	poison oak

Figure 2. A 1973 loblolly pine plantation (area: 73-1) photographed winter, 1975.

Figure 3. A 1972 loblolly pine plantation (area: 72-2) photographed winter, 1975.



Figure 2.



Figure 3.

Figures 4 and 5 further illustrate the rapid growth of the pine trees. Figure 4 shows a 1973 plantation during the winter of 1976 when the pines were three years old. Figure 5 shows the same area during the summer of 1976.

A paired design was used to test the effects of the food treatment. Each plantation had two live-trapping grids, one to sample a population which received supplemental food the other to sample a control population. The experimental and control grids were randomly designated within each plantation.

Previous studies have shown that <u>S</u>. <u>hispidus</u> requires areas of dense ground cover (Goertz, 1964; Wiegert and Mayenschein, 1966). In loblolly pine plantations the piles of logging debris, the windrows, are an important source of cover, particularly during winter when the vegetation dies back. M. H. Smith and L. A. Briese (unpublished) have noted that in the winter, <u>Sigmodon</u> activity is concentrated in the windrows. As mentioned above, each grid was divided lengthwise by a windrow. Because the windrows were stable and were similar on all plantations, winter cover was held relatively constant within and between grids throughout the experiment.

On each plantation the two grids were carefully selected so that soil type, the slope, the aspect, and the structure of the vegetation were as similar as possible. The habitat structure reflects the site quality, an important variable, influencing both the naturally occurring food and

Figure 4. A 1973 loblolly pine plantation (area: 73-3) photographed winter, 1976.

Figure 5. A 1973 loblolly pine plantation (area: 73-3) photographed summer, 1976.

•



Figure 4.



cover. Within practical limits, the paired design controlled for this variable in the tests for effects of supplemental food.

A comparative index of the canopy cover and of the quality of growing conditions was obtained by measuring the heights of 56 loblolly pines on each grid. The trees were selected by the point-centered quarter method (Cottam and Curtis, 1956) in which 14 points were used. The pines were measured with a 2.5 m pole in February 1976 and 1977. The same points and the same trees, unless a tree died, were measured each time. The mean heights of the trees for each grid and year are listed in Table 5. Despite the basic similarity in heights between the two grids on each plantation, the heights on such pairs of grids were generally significantly different (P < 0.05; "t" test). There were three exceptions (73-1, 1976; 72-3, 1976 and 1977). The tree heights for the two ages were also significantly different. In 1976, for example, the mean tree heights for the 1973 and 1972 plantations were 1.51 and 2.29 m, respectively.

Predation was another important independent variable. Since the control and food populations were generally a few hundred meters apart, a predator seemingly had an equal opportunity to encounter either population first. The presence of mammalian, avian, and reptilian predators was monitored. Mammalian predators were removed since they disturbed the small mammal traps.

Plantations planted in 1972 and 1973 were paired, a priori, for purposes of experimental logistics and
6 m c c	Cartala	Average He	ight (m)
Area	Grid	1976	1977
73-1	C	1.61 <u>+</u> 0.53 ^b	2.37 <u>+</u> 0.79
73-1	F	1.71 <u>+</u> 0.63	2.61 <u>+</u> 0.79
72-1	С	20.1 <u>+</u> 0.69	3.05 <u>+</u> 0.84
72-1	F	2.29 <u>+</u> 0.66	3.23 <u>+</u> 0.87
73-2	С	1.47 <u>+</u> 0.47	2.24 <u>+</u> 0.58
73-2	F	1.21 <u>+</u> 0.31	1.86 <u>+</u> 0.40
72-2	С	2.08 <u>+</u> 0.58	3.02 <u>+</u> 0.65
72-2	F	1.76 <u>+</u> 0.59	2.63 <u>+</u> 0.76
13-3	C	1.04 ± 0.47	2.50 + 0.60

1.41 <u>+</u> 0.37 2.31 <u>+</u> 0.48

2.81 + 0.81 3.86 + 1.08

2.77 ± 0.66 3.74 ± 1.09

Table 5. Average loblolly pine heights, February 1976, 1977.

^a Symbols: C = Control Grid; F = Food Grid

F

С

F

b + one standard deviation

73-3

72-3

72-3

Note: On each grid, 56 trees were measured.

subsequent statistical analysis; the pairings are indicated by area code (see Table 2) as follows: 73-1 with 72-1, 73-2 with 72-2, and 73-3 with 72-3. The first number of the code is the year of planting, and the second indicates the trapping set. The trapping set denotes which plantations were trapped simultaneously and received the supplemental food treatment on the same day. This pairing was based partly on the soil type (Table 2) and partly on a growing quality index as determined by loblolly pine heights. As shown in Table 5, set 2 had the lowest growing quality index, set 3 had the highest, and set 1 was intermediate. The pairing, in part, controlled for the effects of site quality upon the treatment. It also helped to control for the effects of daily weather upon the trappability of the rodents.

Supplemental Food Treatment

A mixture by weight of 1/3 unshelled sunflower seeds and 2/3 clipped oats was used as the supplemental food. Commercial laboratory pellets were not used because they are enriched with vitamins and dietary supplements, and any subsequent response of the rodents might have been due solely to these enrichments. The mixed seed was roughly equivalent to food which a cotton rat normally might consume. Freeliving <u>Sigmodon</u> have been reported to eat the seeds of wheat (Fleharty and Olson, 1969) and sunflowers (Goertz, 1964). During the present study, seed preference tests were conducted in the laboratory and small field enclosures to determine the most suitable supplemental food. When tested with whole

corn, wheat, cracked corn, milo, red millet, white millet, oats, and sunflower seeds, <u>Sigmodon</u> showed a strong preference for sunflower seeds and oats.

The experimental populations received two types of supplemental food applications from 2 May 1975 through June 1976, the last month of live trapping. First, to assure an even distribution of supplemental food and to reduce the possible effect of the food on Sigmodon movement patterns and social structure, the mixed seed was broadcast. At weekly intervals, 17 kg of seed was thrown evenly over each experimental grid and along a 5 m buffer strip surrounding each such grid. Prior to broadcasting, the seed was heated at 69° C in wire mesh containers for 1 week to prevent germination. In addition, mixed seed was provided ad libitum in 20 feeding stations on each experimental grid. The stations were positioned in between trap sites and at least 15 m from the edge of the grid. At monthly intervals each station was moved to a new location at least 10 m from the previous one. The second type of food application guaranteed that supplemental food was always available.

Trapping Methods

The small mammals on each study area were sampled with 128 galvanized steel drop-door live traps (6.5 x 9 x 28 cm) arranged in a one-hectare grid (150 x 65 m). A large windrow (average width 5 m) divided each grid lengthwise. On both sides of the windrow, in 16 lines oriented perpendicular to the windrow and spaced 10 m apart, the traps were set 0, 5, 15, and 30 m from the windrow. At monthly intervals

from April 1975 through June 1976, each population was trapped for three consecutive nights. The food and control grids on the 1972 and 1973 plantations of each trapping set were sampled simultaneously.

Each month the captured mammals were weighed, examined for sexual condition and, if not previously captured, marked by toe clipping. In addition, each month all captured <u>Sigmodon</u> were anesthetized with Metofane (methoxyflurane) for close examination. For <u>Sigmodon</u> males position of the testes and color of the cremaster were recorded. Condition of the vulva, size and color of the nipples, number of palpable embryos, and evidence of lactation were noted for each female. All animals were released at the point of capture as soon as possible.

Traps were baited with sunflower seeds. Between trapping periods all traps were locked open. After each <u>Sigmodon</u> capture, a clean, newly baited trap was placed at the capture site to reduce the role of social rank in a heterogeneous trap response by cotton rats (Summerlin and Wolfe, 1973). Because of strong odors remaining in the traps after each <u>Neotoma</u>, <u>Blarina</u> and <u>Cryptotis</u> capture, these traps were also replaced. With a few exceptions, such as June 1975, the supplemental food was broadcast 5 days prior to the first day of trapping each month. While trapping, the food stations were not accessible to rodents.

Trapping methods varied slightly with the season. From May to September 10 per cent chlorodane powder was sprayed around each trap to protect trapped rodents from ants.

During the winter (November through February) cotton was placed in the traps to provide nesting material. While trapping from May through September, the traps were closed during the day and re-opened in the evening to prevent heat mortalities. During the rest of the year, the traps remained set during the day while trapping.

To obtain an index of <u>Sigmodon</u> body condition during parts of February and March 1976, the thickness of four skin folds was measured on each <u>Sigmodon</u> weighing over 50 g. The four measurement locations were the stomach, right shoulder, and right and left hip. In February a Mitutoyo dial caliper (model 505-633) was used. In March a Lange skin-fold caliper set to a constant tension of 10 g was used.

The effects of the food treatment on the trap response of <u>Sigmodon</u> were tested on areas 73-3 and 72-3, which were trapped for nine consecutive nights in late October 1975. Supplemental food was broadcast 5 days prior to trapping and again midway through the trapping period.

At the conclusion of the study, the rodents on each grid were trapped for seven consecutive nights to remove as many resident animals as possible. After the third night of trapping, all captured animals were brought into the laboratory and killed.

RESULTS

Population Numbers

When permanent trap stations are used, direct enumeration yields the best estimate of relative density (Krebs and Myers, 1974). Densities in the present study are expressed as relative densities rather than as absolute densities since no adjustments for possible edge effects have been made (Smith et al., 1975). If these adjustments were made, the densities would be lowered. For each month the minimum number of small mammals which were known to be alive (MNKA; Krebs, 1966) was calculated. The present report concerns the dynamics of only the Sigmodon populations, and Table 6 details the monthly MNKA for the cotton rats on each Tables 17, 18, and 19 in the appendix show the monthly grid. MNKA on each grid for P. polionotus, for P. gossypinus, and for all the other small mammals, respectively. In addition, for P. gossypinus the monthly MNKA on the three control and the three food grids for each plantation age have been combined in Table 20 of the appendix. The effects of the food treatment and succession on the dynamics of the Peromyscus populations and on rodent diversity will be discussed in a subsequent paper.

Table 6.	Minim 1975	um ni to Ji	umber ane 19	of <u>Sig</u> 76.	nopou	1 hispic	dus kı	umou	to be	alive	on e	ach grl	d from	Apri	ц.
Area	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
73-1-C* 73-1-F	14 8	20 3	23 7	18	11 8	10	15 15	13 22	17 34	23 35	20 30	17 29	14 62	19 24	21 54
73-2-с 73-2-F	mm	0 0		10 10	9 17	7 10	7 14	10 13	2 S 2 S	12 27	8 20	9 17	11 31	13 22	14 23
73-3-С 73-3-F	15 3	15 3	22 15	27 27	26 22	27 30	57 46	452 48	42 60	37 60	30 54	27 52	19 72	19 91	39 146
72-1-F	2 11	7 2	Чœ	40	17	20	527	ц 34	7 55	8 77	68 8	59	4 6 6	42 42	4 7 4
72-2-C 72-2-F	ЧЮ	om	12	6 22	19 19	8 15	16 22	12 30	12 31	36 36	34	10 28	7 25	23 23	40 41
72-3-C 72-3-F	2 10	13	28 21	4 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	36 30	35 27	3 9 69	85 85	27 92	23 84	20 72	19 70	18 65	12 61	20 141
* The fir trappin simulta	st num g set neousl	ber j (thos y), s	ls the se with and the	year h the e lett	the r same er de	olantat number signate	lon wa indic	as pl cate	anted, which trol (the s populs C) and	secon ation 1 food	d number s were d (F) g	r is tl trapped rids.	d b	

The MNKA of Sigmodon for the combined food and control grids from both plantation ages is shown in Figure 6. During April 1975, the month before food supplementation began. relative densities were almost the same, about 38 Sigmodon for both the combined food and combined control populations (Table 7). The relative densities of these populations followed roughly similar trends until September and increased to about 100 animals. From September to January the density of the combined food populations increased to 319 Sigmodon. After January the density of the food populations declined until April at which time sufficient juvenile cotton rats entered the populations to increase the density. The density of the food populations dropped in May but increased by June when 484 cotton rats were captured. The control populations reached a peak density of 139 Sigmodon in October, declined in November, and after a small increase in December continued to decline through May. In June, 110 cotton rats were captured on the control grids. From November 1975 to June 1976, the relative densities of the food populations were significantly larger than those of the control populations (see food treatment analysis, Table 8). Although data from successive months were not independent, the analysis is helpful in evaluating the effects of the food treatment on the populations. The monthly changes in the significance levels were due to variability among the food and control populations.

Figure 6. The MNKA of <u>Sigmodon</u> <u>hispidus</u> for the combined food and control grids from both the 1973 and 1972 plantations.



Figure 6.

Table	7. MJ 15	Inim 975	um n to J	umber une 19	of <u>S1</u> 76.	gmode	on knov	vn to	be alj	ive on	the the	combi	ned gri	ds fro	tdA mo	11.
Area	Apr	11	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
73-C*		32	34	56	55	46	44	62	75	81	72	58	53	44	51	74
73 - F	П	14	9	23	43	47	50	65	83	711	122	104	98	165	137	223
72-C		Ъ	15	30	38	50	45	60	45	911	40	37	37	30	22	36
72 - F		56	20	4 J	76	66	62	113	149	178	197	174	157	136	126	261
Total	en en	37	49	86	93	96	89	139	120	127	112	95	06	74	73	110
Total	7 Н	01	26	64	119	113	112	178	232	295	319	278	255	301	263	484
* The	numher.	1 3	the	vear	the n	lante	tton v	la sev	anted.	and	the l	etter	design	atest	the co	ontrol

j. • 2, 2, (C) and food (F) grids.

able 8.	F values a minimum nu to June 19	und the lev umber of <u>Si</u> 76.	els of a <u>gmodon</u> 1	significance known to be	e from t alive f	che ana. Cor eacl	lysis of var n month from	iance for April 19	the 175
Source	đf	April	May	June	July	Aug.	Sept.	Oct.	Nov.
Age of lantation Factor A		3.57	0.07	0.08	0.26	2.20	12.92 ^a	6.79	6.45
rood Trmt Factor B	1	0.07	2.39	1.46	3.73	0.68	1.02	2.06	9.96 ^a
interacti x B	on 1	d67.11	4.93 ^a	5.85ª	13.81 ^b	0.53	0.23	6.07 ^b	7.32 ^b

ç ¢, ç 9 ç β α Tabl

Source	đſ	Dec.	Jan.	Feb.	March	April	May	June
Age of Plantation (Factor A)	г	2.39	4.96	9.72 ^a	17.94 ^a	7.14	1.26	0.0
Food Trmt. (Factor B)	Ч	14.89b	26.97c	28.36c	20.53b	31.190	6.88a	10.31 ^b
Interaction A x B	Ч	4.86 ^b	7.20 ^b	4.01 ^b	4.24	0.14	0.06	0.43
					•			

Table 8 (cont'd.).

Superscripts designate: df = 4;Split Plot Design; Error (A) df = 2; Error (B)
a = P < 0.10, b = P < 0.05, c = P < 0.01.</pre>

If the MNKA for the 1973 and 1972 plantations are separated (Figures 7 and 8, respectively), the population response on each plantation age can be tested. Utilizing a split plot design, two periods (April 1975 to July 1975 and October to February) had a significant interaction between plantation age effect and food treatment effect (Table 8). This indicates that when compared with the comparable control populations, the food-supplemented populations for each plantation age responded differently to the food treatment. During both of these periods, the 1972 food populations had higher relative densities than the 1973 food populations.

On the 1973 plantations (Table 7; Figure 7) the combined control populations initially had 18 more animals than the combined food populations, but by August both had increased to almost the same density. By November there were more animals on the food grids than on the control grids, and the food populations continued to increase in density until January. The food and control populations decreased in density during the late winter. This decline stopped in April for the food populations and in May for the control populations. In June, 223 and 74 <u>Sigmodon</u> were removed from the food and control grids, respectively.

A different pattern occurred on the 1972 plantations (Table 7; Figure 8). Initially there were 21 more animals on the combined food grids than on the combined control grids. The density of the food populations increased to a summer peak in July, decreased during late summer and then

Figure 7. The MNKA of <u>Sigmodon hispidus</u> for the combined food and control grids from the 1973 plantations.



Figure 7.

Figure 8. The MNKA of <u>Sigmodon hispidus</u> for the combined food and control grids from the 1972 plantations.



Figure 8.

increased steadily until January. A continuous winter decline in density ended in June when 261 <u>Sigmodon</u> were captured on the food grids. The control populations essentially increased in density until October. From October until June, these populations decreased in density. In June, 36 Sigmodon were removed from the control grids.

The ability to estimate population size by direct enumeration depends on the trap response of the mammals (Hilborn, Redfield and Krebs, 1976). The food treatment affected the trappability of <u>Sigmodon</u> on each of the foodsupplemented grids as evidenced by a reduced trap response. In late October the populations on areas 73-3 and 72-3 were trapped for nine consecutive nights with supplemental food broadcast on the food grids five days prior to trapping and again midway through the trapping period. While trapping, the food stations were not accessible to rodents.

Food availability had both a short and long term effect on the trappability of <u>S</u>. <u>hispidus</u>. Figure 9 illustrates the short term or immediate effect of the presence of abundant food on trap response. The ratio of the number of captures on food grids over the number of captures on all of the grids of areas 73-3 and 72-3 combined (N_F / N_T) for the days 5 through 9 was averaged to obtain an expected ratio of 0.31. The trapping ratio for each of the next four days was compared with the expected ratio. The drop in trappability occurring on the food grids was significant

 $(\underline{x}^2 (day_1) = 20.77, \underline{x}^2 (day_2) = 11.49, \underline{x}^2 (day_3) = 8.44, \underline{x}^2 (day_4) = 8.67; df = 1; P < 0.005).$

Figure 9. Ratio of the number of captures on the food grids (N_F) to the total number of captures on all grids (N_T) for nine consecutive days in late October 1975 on areas 73-3 and 72-3. Note: The means of the ratios for each set of grids are indicated by solid circles and the range by the vertical lines.



Figure 9.

On areas 73-3 and 72-3 the MNKA of <u>Sigmodon</u> during October was 114 and 97 on the food and control grids, respectively. For days 5 through 9, an average of 24 per cent of the known population on the food grids was captured, whereas an average of 64 per cent of the control populations was captured. The continued low trap response five days after the immediately preceding food application is noteworthy. Most of the broadcast seeds should have disappeared from the ground since rodents, birds, and insects also compete for the grain (Smith and Blessing, 1969). Because cotton rats do not hoard food (Dewsbury, 1970), the long term effect of the supplemental food on the trap response probably was due to other factors such as a change in body condition of the rats.

Monthly differences in the trappability of the known population further indicate a reduced trap response for supplementally fed animals. The percentage of <u>Sigmodon</u> captured relative to the number of <u>Sigmodon</u> known to be alive each month was calculated (Table 9). The first and last months of the study were dropped since calculations of trappability are valid only from the second to the penultimate trapping sessions. With the exception of the 1972 grids in May 1975, animals in the control populations were more trappable than those in the populations receiving supplemental food. The high capture rate during October partly was due to trapping areas 73-3 and 72-3 for nine days rather than the usual three days.

Month	73-C	73-F*	72-C	72 - F	Total C	Total F
May	91	33	0	35	63	35
June	80	43	93	80	85	67
July	89	37	100	88	94	70
Aug.	87	32	100	45	94	40
Sept.	91	46	91	66	91	57
Oct.	95	83	88	77	92	79
Nov.	81	66	91	54	85	59
Dec.	91	59	89	60	91	59
Jan.	92	65	85	69	89	67
Feb.	88	71	89	61	88	65
March	94	70	95	73	94	72
April	86	84	87	64	86	75
May	84	73	100	52	89	63

Table 9. The percentage of <u>Sigmodon</u> captured relative to the number of <u>Sigmodon</u> known to be alive on the combined grids from May 1975 to May 1976.

* The number is the year the plantation was planted, and the letter designates the control (C) and food (F) grids.

The reduced trappability of food-supplemented animals is important since it affected the ability to census these populations. The MNKA for the food populations is likely to be a more conservative estimate of the true number of <u>Sigmodon</u> present than the MNKA for the control populations. Because the differences in the trappability would tend to reduce differences measured between the food and control grids, the data are sufficient to reject the null hypothesis that population densities of <u>Sigmodon</u> are not affected by the presence of supplemental food. Supplemental food increased the densities of S. hispidus.

Survivorship

Minimal calculated survival rates indicate the proportions of the trappable population which when first captured will still be on the trapping grid during the next trapping session (Krebs, 1966). The minimal survival rates for <u>Sigmodon</u> were calculated for each trapping interval of one month (Table 10). Survival rates for the food and control populations were greatest in the winter. For all months except November, the combined control populations had greater survival rates than the combined food populations. The consistency of this trend was significant (Sign test; P < 0.01). There were no significant differences among the control populations or among the food populations within each plantation age. The degree to which the altered trappability of the food populations affected these rates is unknown. The

	68 (50) .72 (74) .76 (34) .53 (116) .71 (64) .01 (190)	84 (51) •74 (77) • •85 (33) •65 (11) (21) • •85 (33)	.58 (50) .21 (38) .55 (38) .21 (75) .57 (88) .21 (113)	.52(54) .30(20) .54(28) .18(40) .52(82) .22(60)	.50 (32) .60 (5) .33 (12) .19 (16) .45 (44) .29 (21)	.42 (31) .15 (13) .20 (5) .26 (23) .39 (36) .22 (36)	a1 Food Food Food 22 62 22 62 75 75 71 72 71 72 73 740 75 75 70 71 72 73 740 75 75 70 71 72 71 72 73 73	Control .39 (36) .45 (444) .52 (88) .57 (88) .65 (88) .74 (105) .74 (105) .71 (125) .71 (125) .71 (125) .71 (125) .71 (125) .71 (125) .71 (125) .71 (125) .71 (84)	Food Food 19 (16) 19 (16) 19 (16) 19 (16) 19 (16) 110 1110 1115 1115 1115 1115 1115 1115	Control 20 55 55 55 55 55 55 55 55 55 55 55 55 55	Food Food 15 (13) 60 (5) .30 (20) .21 (38) .22 (38) .29 (39) .77 (59) .77 (59) .72 (92) .72 (92) .72 (92) .72 (92) .72 (92) .72 (92) .72 (74)	Control 50 50 50 50 50 50 50 50 50 50
34 (51) .74 (77) .85 (33) .65 (115) .85 (84) .69 (192 58 (50) .72 (74) .76 (34) .53 (116) .71 (84) .61 (190 2.2.2.2.2.2.2.2.2.2.2.2.2.2.2.2.2.2.2.	84 (51) .74 (77) .85 (33) .65 (115) .85 (84) .69 (192)		63 (38) .29 (38) .66 (50) .24 (59) .65 (88) .26 (97) 70 (40) .46 (39) .67 (42) .51 (55) .68 (82) .49 (94) 79 (71) .54 (59) .77 (125) .58 (162) 69 (64) .77 (66) .83 (41) .74 (114) .76 (180) 77 (77) .72 (92) .80 (44) .70 (131) .78 (121) .71 (223)	58 (50) .21 (38) .55 (38) .21 (75) .57 (88) .21 (113) 63 (38) .29 (38) .66 (50) .24 (59) .65 (88) .26 (97) 70 (40) .46 (39) .67 (42) .51 (55) .68 (82) .49 (94) 79 (71) .54 (59) .74 (54) .60 (103) .77 (125) .58 (162) 69 (64) .77 (66) .80 (44) .70 (131) .74 (105) .71 (223)	52 (54) .30 (20) .54 (28) .18 (40) .52 (82) .22 (60) 58 (50) .21 (38) .21 (75) .57 (88) .21 (113) 63 (38) .29 (38) .26 (97) .65 (88) .26 (97) 70 (40) .46 (39) .67 (42) .51 (55) .66 (97) 79 (71) .54 (59) .83 .41) .74 (114) .77 (125) .75 (180) 77 (77) .72 (92) .80 (44) .70 (131) .74 (125) .71 (223)	50 (32) .60 (5) .33 (12) .19 (16) .45 (44) .29 (21) 52 (54) .30 (20) .54 (28) .18 (40) .52 (82) .22 (60) 58 (50) .21 (38) .55 (38) .21 (75) .57 (88) .21 (113) 63 (38) .29 (38) .55 (38) .21 (75) .57 (88) .26 (97) 70 (40) .46 (39) .67 (42) .51 (55) .68 (82) .49 (94) 79 (71) .72 (92) .80 (44) .70 (131) .78 (121) .71 (223)	.70 (244	.82 (101)	.71 (153)	.89 (35)	(16) (20)	79 (66)
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Minimum survival rates per one month for <u>Sigmodon hispidus</u> on the combined grids from April 1975 to May 1976. Table 10.

Note: The number captured and released each month is in parentheses.

null hypothesis that the survival rates for the control and food-supplemented <u>Sigmodon</u> populations are the same is rejected. The data indicate that the supplemental food lowered the survival rate of S. hispidus.

Reproduction

To compare the breeding intensity of the populations, the percentages of males with scrotal testes and of pregnant females were examined. The average litter sizes determined by palpation were also compared.

At least 50 per cent of all the subadult (weighing 60 to 99 g) and adult (weighing at least 100 g) males had scrotal testes except during the colder months, October through March (Table 11). During December and January few cotton rats with scrotal testes were captured, indicating reduced breeding. The combined control populations had a higher percentage of scrotal males than the food populations, except during the winter. This difference was significant during three months (\underline{X}^2 (October 1975) = 6.56, \underline{X}^2 (June 1976) = 7.03; df = 1; P < 0.01 and \underline{X}^2 (May 1976) = 5.97; df = 1; P < 0.05). During two winter months the combined food populations had a significantly higher proportion of scrotal males than the control populations (\underline{X}^2 (February 1976) = 7.11, \underline{X}^2 (March 1976) = 8.02; df = 1; P < 0.01).

The percentage of pregnant females (Table 12) is the definitive indicator of breeding intensity. From December

	on the	combinec	gri(is from Api	711 I	975 to	June	1976.				
		1973				1972				Tota	al	
Month	Contr	ol F	lood		Cont	rol	Food	5	Cont	trol	Рос	q
April May June July Aug. Sept. Jan. Feb. March May June	H H H H H H H H H H H H H H H H H H H	80000700000000000000000000000000000000			000011401400000	1000 800 800 800 70 70 70 70 70 70 70 70 70 70 70 70 7	5001001001001001001001001000100010000000	1000 000 000 000 00 00 00 00 00 00 00 00	のもらてらのされるとことです。	өлшршол±996906 8998 27499806 1	00000000000000000000000000000000000000	00000000000000000000000000000000000000
Note:	Under each caught, and	heading the sec	the tond o	first colur column is 1	nn is che p	the n ercent	umber age of	of subadult f those with	and scro	adult r otal te:	nales stes.	

Note:

Monthly percentage of subadult and adult Sigmodon hispidus with scrotal testes Table 11.

	on the	e combj	ined gr	ids from Ap	r11 1	975 to	June	1976.				
		1973				1972				Tota	al	
Month	Cont	rol	Food		Cont	rol	Food		Cont	rol	Н 00	ъ
April May June July Aug. Sept. Sept. Jan. Feb. March May June	20000000000000000000000000000000000000	544 144000000000000000000000000000000000	+W&460605701958	10300000000000000000000000000000000000		9000000000 900000000000000000000000000	28469922999200400 824666974889700440	40080000000000000000000000000000000000	00000000000000000000000000000000000000	98000000000000000000000000000000000000	р 1 200 1 200 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	7270404040408408 400020 44040
Note:	Under each caught, an	n head1 1d the	ng the second	first colu column is	mn is the p	the ni ercenta	umber age of	of subadult those preg	and nant.	adult 1	female:	10

Monthly percentage of subadult and adult Sigmodon hispidus which were pregnant Table 12.

through March, no pregnant cotton rats were found on any of the control grids. During the fall, the <u>Sigmodon</u> in the 1973 control populations bred longer than those in the 1972 control populations. Breeding in the control populations was restricted to the spring, summer, and early fall.

The food populations, especially on the 1972 plantations, had a high percentage of pregnant cotton rats during the early summer, 1975. Breeding continued on the food grids for most of the year but at low levels from November to January. Although no pregnant cotton rats were captured in January, two lactating females were captured on a 1972 food grid in February. On the food grids breeding increased during February when 27 per cent of the subadult and adult females captured on the combined food grids were pregnant. <u>Sigmodon</u> embryos could be palpated only after about the fourteenth day of gestation. Therefore, since some pregnant individuals may not have been counted, these figures are only an index of the reproductive condition and not the absolute number pregnant.

Except for the first month of food supplementation and in January when no pregnant cotton rats were captured, the combined food populations always had a higher percentage of pregnant subadult and adult females than the combined control populations. The differences for the combined populations were significant in four months (\underline{X}^2 (June 1975) = 7.51, \underline{X}^2 (February 1976) = 10.99, \underline{X}^2 (March 1976) = 15.21, X^2 (May 1976) = 8.57; df = 1; P < 0.01).

The breeding season was longer, and the reproductive effort was higher on the food-supplemented grids than on the control grids. The null hypothesis that the length of the <u>Sigmodon</u> breeding season and the reproductive effort are the same for control and food-supplemented populations is rejected.

The average Sigmodon litter sizes from the control and food grids were compared for two periods, the fall, September-October 1975, and the spring, May-June 1976 (Table 13). These periods were selected because they are the times of high reproductive activity for Sigmodon (O'Farrell et al., 1977). During the fall the average litter sizes for the Sigmodon on the combined control and the combined food grids were 4.2 and 4.8, respectively. In the spring the average litter sizes were less, 4.1 and 4.7 for the combined control and food grids, respectively. For both periods the average litter sizes on the food-supplemented grids were significantly larger than on the control grids (F (spring) = 5.74, df = 1, 123, P < 0.02; andF(fall) = 6.80, df = 1, 67, P < 0.02). There was not a significant interaction between the treatment and the plantation age which indicates that the food treatment had the same effect on the populations of both plantation ages. The null hypothesis that on the food-supplemented grids the average litter size of female Sigmodon is the same as on the control grids is rejected.

Season	Area	Ν.	Average Size	S. D.
September- October 1975	73-C*	15	4.20	1.32
	73-F	18	5.00	0.77
	72-C	13	4.23	0.83
	72-F	25	4.72	1.02
May-				
June 1976	73-C	16	4.19	0.98
	73-F	60	4.73	1.09
	72-C	5	4.00	1.00
	72-F	46	4.70	0.92

Table 13. The number of <u>Sigmodon hispidus</u> litters and the average size as determined by palpation during two seasons.

* The number indicates the year the plantation was planted, the letter designates the control (C) and food (F) grids.

Note: N. = number of litters; S. D. = one standard deviation.

Growth Rates and Body Condition

The rate of weight gain has been used as an index of the general condition of a population (Goertz, 1965a; Krebs, Keller, and Tamarin, 1969). In the present study the rate of growth was expressed as the weight gain of a cohort of cotton rats. The weight of each <u>Sigmodon</u> weighing less than 43 g in October was compared to the weight of the same individual if it was still present in January (Table 14). This metric was chosen because it distinguishes all of the cotton rats which were not yet born or were too small to have been captured during the preceding trapping session. It includes only those individuals born between 8 September and 17 October, a period of high reproductive activity.

Sexes were considered separately in the analysis. The males gained an average of 42 and 74 g on the combined control and food grids, respectively. The females gained an average of 33 and 56 g on the combined control and food grids, respectively. For either sex the differences in the weight gains by the food and control animals were highly significant (F (males) = 71.87, df = 1, 21, P < 0.0001; andF (females) = 33.42, df = 1, 24, P < 0.0001). In addition, there was a significant interaction between plantation age and the treatment indicating that the food treatment had a greater effect on animals in the 1972 populations than on those in the 1973 populations (F (males) = 11.00, df = 1, 21 P < 0.01; and F (females) = 8.73, df = 1, 24, P < 0.01).

Sex	Area	N .	Average Weight Gain (g)	S. D.
Males	73-C*	10	44.4	3.69
	73 - F	6	67.5	10.56
	72 - C	6	37.3	5.05
	72 - F	3	87.0	21.79
Females	73-C	7	34.0	6.45
	73 - F	6	44.2	9.91
	72-C	5	31.4	8.08
	72 - F	10	63.2	11.09

Table 14. Weight gains of a <u>Sigmodon hispidus</u> cohort from October 1975 to January 1976.

* The number indicates the year the plantation was planted, the letter designates the control (C) and food (F) grids.

Note: N. = sample size; S. D. = one standard deviation.

Growth rates were higher on the food grids than on the control grids. The null hypothesis that growth rates of a <u>Sigmodon</u> cohort are not changed by the addition of supplemental food is rejected.

An indicator of an animal's condition is the amount of subcutaneous fat (Kolodziej-Banach, 1976). An index to the amount of this fat can be obtained by measuring the thickness of a fold of skin (Sloan, 1967). The four skin folds which were measured on each cotton rat weighing over 50 g in February and March were averaged. Data were analyzed separately for each sex and month of sampling. During both months (Tables 15 and 16) the average skin folds for either sex were significantly thicker on the combined food grids than on the combined control grids (F (February males) = 36.78, df = 1, 78, P < 0.0001; F (February females) = 52.63,df = 1, 95, P < 0.0001; F (March males) = 36.95, df = 1, 111,P < 0.0001; F (March females) = 38.95, df = 1, 137, P < 0.0001). For example, in February the average thicknesses of the male skin folds were 1.12 and 1.37 mm on the control and food grids, respectively. There were no significant interactions between the food treatment and the age of the plantations for either February or March. This indicates that the food treatment had the same effect on the populations of both plantation ages.

The body conditions of <u>Sigmodon</u>, as determined by skin-fold measurements, were better on the food grids than on the control grids. The null hypothesis that during late

Sex	Area	N .	Average Thickness (mm)	S. D.
Males	73-C *	21	1.14	0.15
	73-F	28	1.31	0.20
	72 - C	10	1.07	0.13
	72 - F	23	1.45	0.18
Females	73 - C	13	1.09	0.15
	73-F	26	1.34	0.26
	72-C	16	1.07	0.17
	72 - F	44	1.44	0.19

Table 15. Average skin-fold thickness of <u>Sigmodon</u> <u>hispidus</u> caught in February 1976.

* The number indicates the year the plantation was planted, the letter designates the control (C) and food (F) grids.

Note: N. = sample size; S. D. = one standard deviation.

Sex	Area	Ν.	Average Thickness (mm)	S. D.
Males	73-C*	30	1.13	0.16
	73-F	27	1.31	0.16
	72-C	15	1.06	0.17
	72 - F	43	1.28	0.17
Females	73-C	21	1.07	0.18
	73-F	36	1.32	0.16
	72-C	20	1.07	0.15
	72 - F	64	1.24	0.19

Table 16. Average skin-fold thickness of <u>Sigmodon</u> <u>hispidus</u> caught in March 1976.

* The number indicates the year the plantation was planted, the letter designates the control (C) and food (F) grids.

Note: N. = sample size; S. D. = one standard deviation.
winter the body condition of adult and subadult <u>Sigmodon</u> is the same for control and food-supplemented populations is rejected.

DISCUSSION

Populations of rodents vary in density through time and space. The densities of rodent populations probably are regulated by a multitude of interacting factors (Lidicker, 1973). The availability of food is just one of the suggested factors (e.g., Kalela, 1962; Schultz, 1964), but there is little experimental data with which to evaluate any of the proposed factors. Because rodents rarely consume more than a small per cent of the annual primary production (e.g., Golley, 1960), they are not thought to be limited by food (Hairston, et al., 1960). These rates of consumption, however, do not take into account that food availability varies with the season and the habitat. During unfavorable seasons and in unfavorable habitats, food is more likely to become limiting. Furthermore, the actual food supply may be less than estimates of primary productivity indicate since rodents can be very selective in food habits (Gill, 1977). The productivity estimates also do not account for seasonal variations in food quality.

The importance of habitat quality and of seasonal changes in the food supply for the hispid cotton rat was

investigated in the present study. The central hypothesis was that food is a critical factor in the population dynamics of <u>S</u>. <u>hispidus</u> populations particularly during the winter and in suboptimal habitat. To evaluate the central hypothesis, six null hypotheses were tested. Each of these will be discussed with respect to the general population dynamics of <u>S</u>. <u>hispidus</u> and other rodents. The role of the food supply in determining habitat quality also will be discussed.

Of the six testable hypotheses, the first concerns the effects of food on population numbers. The data clearly establish that food limited <u>Sigmodon</u> densities. The maximum densities of <u>Sigmodon</u> previously reported for populations on the SRP ranged from 10 to 37 per hectare (Golley <u>et al</u>., 1965; Schnell, 1968; Gardner, 1975). The highest MNKA for the 1973 and 1972 combined control grids were within this range, 27 and 20 per hectare, respectively. The highest MNKA for the 1973 and 1972 combined food grids were 74 and 87 per hectare, respectively. The densities on the combined food grids are greater than any densities reported for the SRP.

The supplemental food altered the timing of the seasonal population fluctuations. The combined control grids exemplified patterns typical for <u>Sigmodon</u> in the southeastern U. S. (Layne, 1974) and in South Carolina (Gardner, 1975). When compared with the control populations, the densities of the food populations continued to increase longer in the fall and began to increase earlier in the spring.

The increase in density due to the supplemental food was predicted, but not altogether expected since supplemental food experiments with similar rodents have produced equivocal results. For example, Krebs and DeLong (1965) failed to obtain high densities of Microtus with supplemental food. In another supplemental food study (Cole, 1977), the addition of food increased Microtus densities but failed to prevent a general population decline. In both of these experiments the factors which caused the low densities were not determined. The experimental design may have influenced the conclusions since neither study had any replicates, and the foodsupplemented areas were less than 1 hectare in size and were smaller than the control areas. In addition, the study areas of Krebs and DeLong were 9 km apart. To account for the natural variability within and between small mammal populations, it is essential to replicate experiments.

In the present study, the increased densities with food supplementation indicate that food was limiting, but density changes alone cannot clarify the mechanisms which cause the changes in population size. Fluctuations of population density are due to the effects of one or a combination of three factors, emigration-immigration, natality, and mortality. The following discussion and the rest of the null hypotheses concern these factors and their relative influence on <u>Sigmodon</u> densities.

Schnell (1968) and Fleharty, Choate, and Mares (1972) concluded that densities of <u>Sigmodon</u> are determined primarily by the mortality rates, especially from predation. Few

studies, however, have documented the mortality rates of Sigmodon. Data from enclosed populations led Wiegert (1972) to suggest that avian predators had a larger effect on Sigmodon populations than mammalian predators. In the present study few avian predators were seen, and there was little evidence to suggest that mammalian predators concentrated on the high density populations. In late April 1976, however, someone accidently released a number of raccoons (Procyon lotor) near two of the study sites. While trapping the food grids on area 72-3 in April and on areas 72-3 and 72-2 in May, the traps were heavily disturbed by raccoons. Density estimates for these months were lowered because of the trap disturbances and perhaps because of predation. Whether the raccoons were attracted to the food grids by the high rodent densities or by the food readily available in feeding stations is not known.

Although no one has studied the impact of snakes on <u>Sigmodon</u> populations, snakes may have been an important cause of mortality, especially on the food grids. Relatively few snakes were seen during the study, but most were located on the food grids. Twice during June 1976, when <u>Sigmodon</u> were at their highest densities, two snakes (<u>Pituophis melanoleucus</u> and <u>Coluber constrictor</u>) were observed in the afternoon killing <u>Sigmodon</u>. Perhaps related to the predation by snakes, trappable longevity was greatest during the winter when the snakes were not active. Predation certainly is capable of lowering population densities. But, since densities on the food-supplemented grids were twice as high as the "predator limited" densities suggested by Schnell (1968), it can be concluded that other agents were more important in determining <u>Sigmodon</u> densities in the present study.

From the second hypothesis, the data tend to indicate that supplemental food lowered the survival rates of Sigmodon. Several factors probably were responsible for the apparent low survival rates of Sigmodon on the food grids, but the major reason may have been the reduced trappability of the Sigmodon on those grids. Hilborn et al. (1976) established that low trappability impairs the ability to census populations and to obtain an accurate measure of survivorship. This impairment would be particularly significant with an animal, such as Sigmodon, which has a high turnover rate. Goertz (1964), for example, reported that of the Sigmodon which he trapped, about 50 per cent had disappeared by the second month and 98 per cent by the sixth month. Chances are that if a marked individual was not captured during a particular trapping session, it would disappear before the next trapping session. Survival rates would therefore appear artificially low.

Although difficult to distinguish, mortality and emigration are the primary factors responsible for reducing survival rates. The main causes of mortality would have been predation and starvation. Data to be discussed later about

<u>Sigmodon</u> body condition suggest that starvation was not the cause of the low survival rates on the food grids. Predation, which has been discussed, also was probably not a significant factor. Increased snake predation on the food grids may have contributed somewhat to the reduced survival rates.

During the present study emigration and immigration were not studied intently, but there was no evidence to suggest that large numbers of Sigmodon moved into the food grids from surrounding areas due to the availability of The net movement of cotton rats may have been in the food. opposite direction. Of the 2093 Sigmodon marked during the study, 50 switched grids, a distance of at least 150 m. 0f these Sigmodon a significant number, 39, were first marked on a food grid and later caught on a control grid ($X^2 = 7.84$; df = 1; P < 0.01). Increasing densities, such as those which occurred on the food grids, have commonly been associated with rodent dispersal (Lidicker, 1975; Krebs et al., 1976). The emigration from the food grids, compounded by the low trappability of Sigmodon on those grids, was most likely responsible for the low survival rates on the food grids.

Because the survival rates were influenced by rodent trappability, dispersal, and the food treatment, it may be unwise to draw conclusions about the actual survival rates from these data. Similarly, previously reported effects of supplemental food on rodent survivorship are difficult to evaluate. Each supplemental food study has used different methods of trapping; for example, in several studies the

traps were placed within the feeding stations. Their placement probably increased rodent trappability and hence survival rates.

The third hypothesis deals with the effects of supplemental food on natality, specifically on the breeding intensity and the length of the breeding season. The conclusion from these data is that the level of the food supply, particularly during the winter, controlled breeding. Typically Sigmodon in the southern U. S. have a bimodal reproductive cycle with peaks of activity in the spring and fall (Layne, 1974; Bigler and Jenkins, 1975; O'Farrell et al., 1977). During the winter on the SRP, pregnant females rarely have been caught; and males have reduced testicular size (Briese, 1973; O'Farrell et al., 1977). Similar seasonal trends occurred on the control grids in the present study. On the other hand, the food populations bred throughout most of the year, including the winter when a few pregnant females were captured. The percentage of females which were pregnant when captured indicates that breeding began two months earlier on the food grids than on the control grids in the spring of 1976.

From correlative data others have concluded that for <u>Sigmodon</u> the cessation of breeding during the winter was due to unfavorable weather conditions (Goertz, 1965b; Cameron, 1977) along with a decline in the quantity or quality of the food supply (Negus, Gould, and Chipman, 1961; Layne, 1974).

The present study provides the first experimental data to substantiate the effects of food on the breeding intensity of Sigmodon.

An important aspect of natality is the litter size. Cole (1977) noted that supplemental food increased the litter size of M. ochrogaster, and a similar trend was expected in the present study. The effects of nutrition on the average litter size during two seasons were investigated with the fourth hypothesis. For both seasons the average size of palapable litters was significantly greater on the food grids than on the control grids. It should be noted that the average litter sizes obtained during the present study are not directly comparable with other reported litter sizes, since those sizes generally have been determined by dissecting the animals. For example, O'Farrell et al. (1977) found an average litter size of 4.66 for Sigmodon on the SRP. This is larger than the average litter sizes for the control populations, and therefore, it appears that palpations underestimate the actual litter size.

<u>Sigmodon</u> litter size varies throughout its geographical range. Data presented here support the probable explanation that this variability represents a response of <u>Sigmodon</u> to local conditions. The litter size of cotton rats is positively correlated with female age (Layne, 1974) and body size (Goertz, 1965b). As will be discussed below, the supplemental food increased growth rates and hence affected the ageweight distribution of the populations. Therefore, it is not possible to state conclusively from these data if the

increased litter size was directly due to the improved food resource or indirectly to the altered age-weight distribution of the females. In either case, however, the increased litter size on the food-supplemented areas represents an increase in the natality rate, an important factor in population growth.

In most previous studies, supplemental food has been reported to increase individual growth rates (\underline{e} . \underline{g} ., Krebs and DeLong, 1965; Andrzejewski, 1975; Cole, 1977). Findings in the present study were consistent with those reported for other rodents. Data from the test of the fifth hypothesis indicate that growth rates from October to January of a fall-born cohort were significantly greater on the food grids than on the control grids.

The age to sexual maturity of rodents is determined in part by individual growth rates (Cole, 1954). In addition, litter size is correlated with female body size, therefore faster growing females may produce larger litters (Goertz, 1965b). In such ways, increased individual growth rates can cause an increase in the population growth rate which subsequently may result in an increase in density.

Individuals usually have been reported either to lose weight or at least to gain very little weight during the winter (Goertz, 1965a; Fleharty and Choate, 1973; Layne, 1974). During the late winter of the present study, <u>Sigmodon</u> on the control grids appeared thin and emaciated, especially when compared with robust Sigmodon on the food

grids. With the sixth hypothesis, the body conditions during the winter were investigated.

One recurrent problem in population biology is to accurately quantify changing body conditions of living rodents. Fleharty, Krause, and Stinnett (1973) found that lipid reserves in cotton rats were depleted during the winter, but this determination required killing the animals. In the present study measurements of the skin-fold thickness on living animals were utilized. These measurements can be used to obtain a reliable index of body fat and condition of living rodents. The average skin-fold thickness was significantly greater on the food grids than on the control grids.

The present data suggest that nutrition may have controlled the breeding intensity by affecting the total body condition of the rodents. These data are not sufficient to establish a causal relationship between body condition and reproductive performance, however, such a relationship exists for laboratory rodents (Millar, 1975). Similarly, the body condition may have affected the reproductive rates in other supplemental food studies in which a grain was supplied. Negus and Berger (1977) recently reported that limited supplements of green forage can start reproduction in nonbreeding winter populations of M. montanus. Chemical stimulants were thought to be the factors which increased breeding intensity. These studies suggest that the role of nutrition in determining reproductive output is complex and can be influenced in a number of different ways. Additional studies need to be conducted to clarify the role of the

quantity and quality of the food supply in determining body condition and reproductive output.

Throughout the U. S., winter appears to be the critical season for cotton rats. As previously noted, population numbers decline, breeding rates decrease, and body conditions deteriorate during the winter. Particularly for northern populations, poor body conditions (Dunaway and Kaye, 1964; Fleharty et al., 1972) and population declines (Goertz, 1964) during the winter have been associated with cold temperatures. Although difficult to document in the field, Sigmodon mortality was attributed directly to cold temperatures combined with starvation in at least one case (Dunaway and Kaye, 1961). Since Sigmodon populations decline in vigor during the winter in southern as well as northern populations, the simplest explanation for the seasonal decline is shortages of food and not cold temperatures per se. Similar conclusions from previous studies on Sigmodon populations were based on correlative information (Layne, 1974; Fleharty et al., 1973). The present study provides experimental data which clearly indicate that the winter decline was due to an insufficient supply of food.

All six of the null hypotheses were tested for populations of <u>S</u>. <u>hispidus</u> in successionally optimal and suboptimal habitats. Habitat quality was defined by the stage of forest succession. Previous comparisons of logged areas with mature forests suggested that the shift in species composition of small mammals which accompanies forest succession may be caused by differences in cover and food

(Lovejoy, 1975; Martell and Radvanyi, 1977). In addition to the obvious changes in plant life forms, succession affects the nutritive content of the plants. Klein (1965) reported that the nutritive content of shaded plants growing on the forest floor was less than that of plants growing in open areas.

The present study is the first experimental manipulation of the food supply of rodents in areas undergoing rapid succession. The evidence suggests that low densities of Sigmodon in older pine plantations were primarily due to inadequate food resources. In comparison with the populations on the 1972 control grids, higher densities and longer breeding seasons observed for those on the 1973 control grids indicated that the Sigmodon habitat was more favorable on the 1973 plantations. Yet, the 1972 food grids generally had higher densities of Sigmodon than the 1973 food grids. The significant interaction between the effects of the food treatment and the plantation age on density support the importance of the food supply. The significant interaction during the early summer of 1975, partly a function of the sharp increase in densities on the 1972 food grids, is noteworthy. It may indicate that food was more limiting on the 1972 grids than on the 1973 grids even during the summer. The significant interaction between the effects of the food treatment and the plantation age on growth rates also demonstrates that food is more limiting on the older plantations. Higher densities on the combined control grids at the end of the study than at the start, despite unfavorable

succession of the vegetation, may have been due to the dispersal of individuals from the food grids.

The above discussion regarding forest succession is applicable to a discussion of habitat quality since at the start of the experiment, the 1973 and 1972 plantations were designated optimal and suboptimal habitat, respectively. Habitat quality for rodents is determined by a number of interrelated characteristics, but cover and food are two of the primary components. A common difficulty in evaluating these two factors is that for many rodents the source of cover also provides the source of food. Because of this, only a few researchers have been able to separate the effects of cover and food. For example, food may be more important than cover in determining the distribution of M. californicus populations (Batzli and Pitelka, 1970). Batzli (1974) and Cole (1977) showed strong positive correlations between habitats with an optimal, quality forage and the demographic characteristics of Microtus populations. When supplemental food was provided to M. ochrogaster in a suboptimal habitat (Cole, 1977), the food population increased in density and showed higher reproductive rates and higher average growth rates than the control population. The supplemental food, however, did not prevent declining densities which occurred on the study site. Regretfully, Cole did not simultaneously feed populations living in optimal habitat.

For Sigmodon populations adequate cover is a recognized feature of optimal habitat (Goertz, 1964). In the present experiment the windrows were an excellent source of cover. During the winter virtually all Sigmodon captures occurred within about five meters of the windrows. An unique aspect of this experiment was that although the windrows provided abundant winter cover, the windrows did not also represent a food supply. Because of the association of each grid with a windrow, it was assumed that cover was held relatively constant between the grids. The differences noticed between the food and control grids on the two plantation ages, therefore should have been due to the level of the food resource and not to cover. The experimental manipulation of the food supply indicates that food, as distinct from cover, was an integral, important component of a quality habitat and important in determining Sigmodon densities.

In addition to the windrows, vegetation throughout the grids also provided some cover and food. Due to succession, vegetation shifted from predominately grass and forbs to woody species. These changes undoubtedly affected both the quality and quantity of cover and food. Whereas the above discussion suggested that food became limiting with succession, field observations seemed to indicate that the vegetative cover increased with succession and was not a limiting factor. These impressions were based on an increase during the study in the size and density of woody vegetation, including briars, shrubs, and pines. The grass-forb component of the habitat decreased in response

to the woody growth; but when the grass and forbs died, the dead stalks still contributed to the total cover. The dead grass and forbs and the woody vegetation were not utilized for food.

<u>Sigmodon</u> densities lend some support to these observations. As previously noted, the 1972 combined food grids had higher densities than the 1973 combined food grids; yet the reverse was true for the combined control grids. This suggests that the major factor which kept the 1972 plantations from being optimal habitat was the food supply, and not cover.

The high densities of <u>Sigmodon</u> on the food supplemented areas support the central hypothesis that food is a critical factor in the dynamics of <u>S</u>. <u>hispidus</u> during the winter and in suboptimal habitat. Mortality rates previously have been suggested to be the primary determinant of <u>Sigmodon</u> densities (<u>e</u>. <u>g</u>., Schnell, 1968). The present experiment indicates that changes in the natality rates rather than mortality rates may best explain the observed population fluctuations. A general relationship between reproductive activity and population density has been observed before (Goertz, 1965b; Fleharty <u>et al</u>., 1972; Layne, 1974; Cameron, 1977). In addition, the present study provides experimental data which establish that <u>Sigmodon</u> natality rates are dependent on the food supply.

As previously noted, granivorous rodents are thought to be limited by food more frequently than herbivorous

rodents. In part, the supplemental food studies of Krebs and DeLong (1965) and Cole (1977) support this statement. The present study documents that food can limit populations of <u>S</u>. <u>hispidus</u>, an omnivorous rodent. The contrasting conclusions from the various supplemental food studies may be due to different nutritional requirements and to the feeding strategies of the rodents. The design of the experiment may also be an important factor. Unlike most previous studies on rodent population dynamics, the present experiment was replicated which allowed the data to be analyzed statistically. Also, populations were simultaneously studied in habitats of different quality. As illustrated here, habitat quality can affect the results and the subsequent conclusions.

Before population regulation can be fully understood, additional experimental manipulations of rodent populations are required. Also, the nutritional requirements and the availability of a quality food for rodents in the field need to be studied further.

SUMMARY

An experiment was designed to evaluate the following hypothesis: Food is a critical factor in the dynamics of <u>S. hispidus</u> populations particularly during the winter and in suboptimal habitats. Data from experimental supplementation of the food supply of <u>Sigmodon</u> populations on six young loblolly pine plantations support this hypothesis.

Data collected at the start of the experiment were used to predict that pine plantations planted in 1973 and 1972 represented optimal and suboptimal <u>Sigmodon</u> habitat, respectively. Population data gathered during the experiment substantiated this prediction. Densities of the 1973 control <u>Sigmodon</u> populations were higher, and the breeding seasons were longer than for the 1972 control populations. Populations from the control grids on both plantation ages exemplified demographic patterns typical for <u>Sigmodon</u> in South Carolina.

For both plantation ages the addition of supplemental food increased population density, lengthened the breeding season, increased average litter size, increased average growth rates, and improved the physical condition of <u>Sigmodon</u> during the winter. Supplemental food decreased trappable longevity. Decreased survivorship on the

food-supplemented grids may have been due to an increased emigration rate in addition to low trappability of <u>Sigmodon</u> on the food grids.

The food treatment had a greater effect on Sigmodon populations in the 1972 plantations than in the 1973 plantations. Population densities were higher on the 1972 food grids than on the 1973 food grids especially during early summer and winter. The effects of the supplemental food were most noticeable during the winter when the natural food supply is believed to be at a low level and when cold temperatures increase the energetic demands. In addition, growth rates for a fall cohort were higher on the 1972 food grids than on the 1973 food grids. Comparisons of the demographic data from all of the food and control populations indicate that Sigmodon populations were limited by inadequate food resources, particularly in suboptimal habitat. The data also suggest that the food supply, as distinct from cover, was important in determining the densities in the older pine plantations. It can be concluded that food strongly influences the distribution and abundance of Sigmodon in areas undergoing rapid succession.

Natality rates rather than mortality rates appeared to be the primary determinant of <u>Sigmodon</u> densities. Changes in density were closely associated with the rates of reproduction. Natality rates were dependent on the food supply. Reduced breeding during the winter was accompanied by and may have been caused by poor body conditions. The

supplemental food maintained the body condition of the animals during the winter, and a significant number of food-supplemented <u>Sigmodon</u> bred during the late winter.

Contrasting conclusions between the present study and previous supplemental food studies may be due to different nutritional requirements and feeding strategies of the rodents. The levels of the food resource are important in the population dynamics of <u>Sigmodon hispidus</u>, an omnivorous rodent.

APPENDIX

Minimum number of <u>Peromyscus</u> polionotus known to be alive on each grid from April 1975 to June <u>1976.</u> Table 17.

Area	Apr	il May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
73-1-C 73-1-F	* 12 21	13 11	60	7 19	8 21	7-8	~~	7	ωσ	13	8 17	12 13	12	10 25	12 47
73-2-C 73-2-F	6 12	Ωω	2	94	$\omega \varphi$	4 17	10	10 18	11 17	10 22	10 25	12 30	12 29	17 36	17 42
73-3-C 73-3-F	01	00	00	10	40	0 0	οIJ	om	07	0 0	0 0	07	0 M	47	ο'n
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72-3-C 72-3-F	00	00	00	00	00	00	Р О	00	00	ЧО	00	00	00	00	10
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The first number is the year the plantation was planted, the second number is the trapping set (those with the same number indicates which populations were trapped simultaneously), and the letter designates the control (C) and food (F) grids.

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Table 18.	-

Area	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
73-1-С * 73-1-F	18 3	13 9	11 17	12 23	28 28	26 26	14 16	13 22	4 4 7	17 53	26 40	33 37	40 35	34 48	0 0 80
73-2-C 73-2-F	00	Ч 0	N ⇒	C 7	4 4	N M	89	9 4	7	6 14	190	19 19	7 22	25	9 31
73-3-C 73-3-F	M 4	ς Υ	NΜ	н 0	н н	0 0	οſΛ	40	ဝထ	11	4 21	2 6 2 3	4 17	27	38
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72-2-C 72-2-F	00	чω	cy m	NΓ	44	мп	73	ЧГ	Н 6	11	н б	0	00	0 11	06
72-3-C 72-3-F	om	4 11	16 16	21 21	183	18	23 7	20	31 31	0 40	38 38	4 3 4	4 6 4	61	327

* The first number is the year the plantation was planted, the second number is the trapping set (those with the same number indicate which populations were trapped simultaneously), and the letter designates the control (C) and food (F) grids.

Minimum number of small mammals known to be alive on each grid from April 1975 to June 1976. Table 19.

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Table 19. (cont'd.).

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Table 19. (cont'd.).

Area	Species	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June
73-1-F	MOGEZOAR	н				0 0	7 5		6 7	N 0124	ич м юл			m m=≠ N	ന ഗവ ന	4 4 10 7
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Area	73-1-C	73-2-C	73-3-C

first number is the year the plantation was planted, the second number is the trapping (those with the same number indicate which populations were trapped simultaneously), the letter designates the control (C) and food (F) grids. arne / set and

- асохоочко Ф
- <u>Blarina brevicauda</u> <u>Cryptotis parva</u>
- n n

- Ochrotomys nuttall1 Neotoma floridana Oryzomys palustris Pitymys pinetorum Reithrodontomys humulis Sorex logirostris

Minimum number of Peromyscus gossypinus known to be alive on the combined grids from April 1975 to June 1976. Table 20.

Area	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
73-C* 73-F	22 6	17 14	15 24	15 29	14 33	10 31	22 27	20 29	22 58	24 78	35 805	47 79	51 74	47 100	45 149
72-C 72-F	0 M	1 1 8 1	29 29	31	27	9 0 8	368	ς γ	533	75	7 80	15 96	12 92	12 112	54 13
Total C Total F	22 9	32	21 49	24 60	53 60	19 61	30 63	23	25 111	29 153	42 160	62 175	63 166	59 212	58 203
* The n	umber 1	s the	e year	the p	lante	ation w	as pla	anted	, and	the l	etter	design	ates t	the co	

(C) and food (F) grids.

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