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SMALL MAMMAL STUDIES IN NATURAL AND MANIPULATED SHORTGRASS PRAIRIE

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ABSTRACT

The structure of small mammal communities was studied in six 1-ha plots of shortgrass prairie manipulated for 5 years previously through the application of water, nitrogen, or both. Two additional 1-ha plots served as controls. The stress treatments have caused a differential response of vegetation growth, being maximal on the water + nitrogen treatment, intermediate on the water only and the nitrogen only treatments, and minimal on the control treatments. The five small mammal species present on the plots (*Peromyscus maniculatus*, *Microtus ochrogaster*, *Reithrodontomys megalotis*, *Spermophilus tridecemlineatus*, and *Onychomys leucogaster*) have responded to the differences in the vegetation structure and biomass. A negative linear correlation was found between foliage height diversity and species diversity in the stress treatment plots. This result, which is different from that found in natural habitats, is interpreted in terms of colonization rates of the small mammals. The difference between the small mammal communities found on the four treatments is suggested to be the result of differences in habitat priorities and competitive ability.

On a ninth 1-ha plot food in the form of oats and alfalfa pellets was added on a 2-week schedule. A new small mammal species (*Dipodomys ordii*) not usually found in most types of the shortgrass prairie habitats, invaded the area. The fact that this species was captured only in this plot and not around or in the nearby control plots was interpreted as a response of the species to the seed supplement. It is suggested that seed availability limits its distribution in the study area.

Microtus ochrogaster invaded the nitrogen + water treatment in 1971 and showed a unique population behavior. Unlike most populations of this species and other microtines, this population has not exhibited a

2- to 4-year cycle. Instead the population has simply exhibited a seasonal fluctuation in abundance. The summer peak population sizes progressively increased from 1971 to 1976. Only small differences were found between the demographic parameters of this annually fluctuating population and cyclic populations of the same species reported in the literature. Because the nitrogen + water treatment was located in the middle of a "sea of shortgrass prairie habitat," the *Microtus* population that invaded the area was semi-isolated. Hence, one can question Chitty's and Krebs' theory of population regulation in microtines. I have concluded that their theory that certain genotypes emigrate from the population causing the 2- to 4-year cycle holds only if immigrants play an important role in determining the rate by which the population genetic structure changes.

Based on the field study a population dynamics simulation model was put forth. Time-dependent coefficients were advanced to account for reproduction and mortality. Inter- and intraspecific competition undergone by a species was utilized to model emigration. On the other hand, the immigration was described in terms of the size of the habitat, its distance and habitat priority index. Good agreement was found between the model results and the field data with regard to community composition and species changes in density. The sensitivity analyses and the experimental runs indicated that dispersal of individuals plays an important role in population dynamics.

GENERAL INTRODUCTION

Many agents have been hypothesized to account for population regulations. These agents include resources (Lack 1954a, Pitelka 1964, MacArthur 1972), predators (Elton 1929, Pearson 1966, Pain 1966), dispersal (Lidicker 1962, 1975; Healey 1967; Myers and Krebs 1971a), weather (Andrewartha and Birch 1954), self-regulation (Wynne-Edwards 1962), and genetic feedback (Chitty 1967, Pimentel 1968). In addition, interspecific competition has also been suggested as a determinate of species abundance, at equilibrium. In spite of the vast amount of work and theories developed, the population regulation problem has not been solved and a comprehensive approach in which more than one factor is considered seems to be more appropriate (Wilson 1975).

Most species and individual organisms, however, do not live in a biotic vacuum but usually in assemblages of species, with some degree of organization or structure (i.e., communities). Patterns of community structure and organization have been hypothesized to evolve as a result of intensive interspecific competition between the species involved (Levins 1968, MacArthur 1972). Recently, predation and the weather were also suggested to account for observed community structure (Pain 1966, Ehrlich and Birch 1967, Connell 1975, Hutchinson 1975).

These two main problems, population regulation and community structure in small mammal species, were studied in three habitats created by enrichment of a shortgrass prairie with water, nitrogen, or both. The enrichment which caused a differential response of plant growth has resulted in creating habitat patches which offered a unique opportunity for studying species interactions and regulation.

The first section of this dissertation investigates the potential causes for the small mammal community structures formed in these habitats, while the second section analyzes the population dynamics and regulation of *M. ochrogaster*. In the third section, the results of the field experiment and current theory in the literature are applied to construct a population dynamics simulation model.

SITE DESCRIPTION

These studies were conducted at the Pawnee Site of the US/IBP Grassland Biome study in northeastern Colorado. The site is located within the Central Plains Experimental Range unit of the USDA Agricultural Research Service, about 40 km south of Cheyenne and approximately 61 km northeast of Fort Collins (40°49'N latitude, 104°46'W longitude). The topography of the area consists of gently rolling hills with broad tops separated by wide ephemeral stream courses. The elevation is 1650 m.

Vegetation at the Pawnee Site and in adjacent areas is classified as shortgrass prairie and has been described by Klipple and Costello (1960). Hyder et al. (1975) have given a more detailed description of the vegetation within few kilometers of my study site. The principal perennial species on the site are blue grama grass (*Bouteloua gracilis*) fringed sagewort (*Artemisia frigida*), plains pricklypear (*Opuntia polyacantha*), and scarlet globemallow (*Sphaeralcea coccinea*). The most commonly encountered annual species are lambsquarter (*Chenopodium album*), Redowski's stickseed (*Lappula redowskii*), prairie pepperweed (*Lepidium densiflorum*), woolly Indian wheat (*Plantago patagonica gnaphaloides*), six-weeks fescue (*Festuca octoflora*), Russian thistle (*Salsola kali*), and Canadian thistle (*Cirsium arvense*).

The climate of the Pawnee Site is typical of mid-continental areas except for the strong influence of the Rocky Mountains approximately 60 km to the west. Mean annual precipitation is 311 mm with a range of 110 to 580 mm recorded over the past 31 years at the Central Plains Experimental Range. Approximately 70% of the mean annual precipitation occurs during the April-to-September growing season. Mean monthly

temperatures range from below 0°C in December and January to 22°C in July (Hyder et al. 1975). During the study period the amount of precipitation was similar to the long-term average while the average monthly temperatures were slightly higher than the long-term average (Fig. 1). The soil is Ascalon sandy loam (Grant et al. 1976).

Within this area, six 1-ha stress plots, ungrazed by large mammals, have been treated since 1971 by additions of water, nitrogen, or both. Two 1-ha plots, which are undisturbed prairie, served as control (Fig. 2). In the water treatment the soil matric potential at a depth of 10 cm was maintained between 0 and -0.8 bars from 1 May to 1 September in the last 5 years (Lauenroth and Dodd 1976). The nitrogen treatment consisted of maintaining a difference of at least 50 kg/ha of soil mineral nitrogen (NO_3 + NH_4) between the nitrogen treated and control plots (Lauenroth and Dodd 1976). The nitrogen + water treatment was maintained as above with both water and nitrogen.

The herbage biomass responded differently to the four treatments (Fig. 3). The water and the nitrogen treatments had more herbage biomass than did the control treatment. The water treatment had more herbage biomass than did the nitrogen treatment in 1972 and 1973 and similar biomass in 1974 and 1975. In the nitrogen + water treatment the amount of herbage biomass reached a peak of 1100 g/m^2 in 1972. The total biomass on the nitrogen + water treatment has decreased since 1972, though in 1975 it was three times that of the control treatment and twice that of either the water or the nitrogen treatments. Further information on the response of the plant community on the different treatments is discussed by Lauenroth and Dodd (1976).

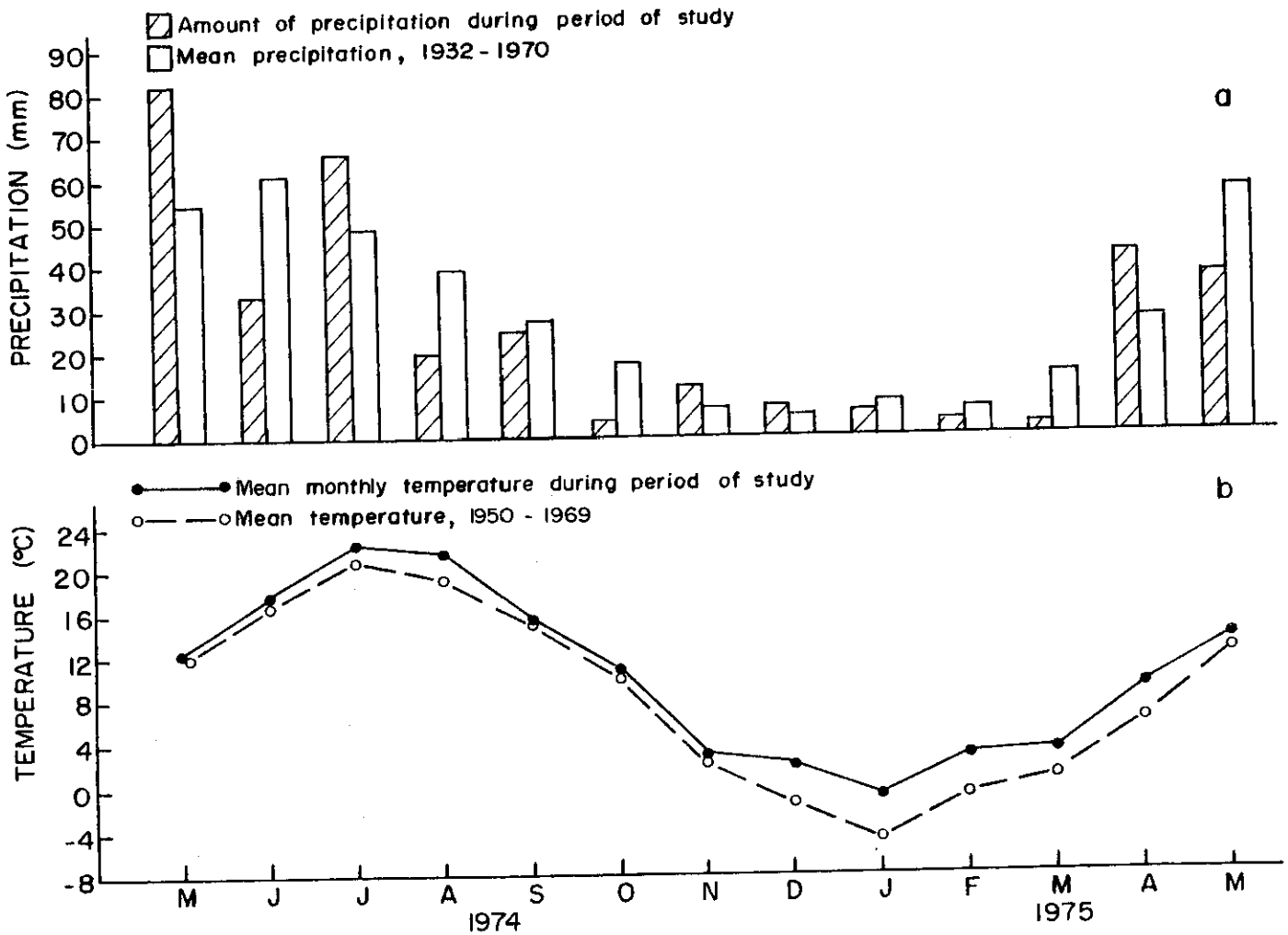
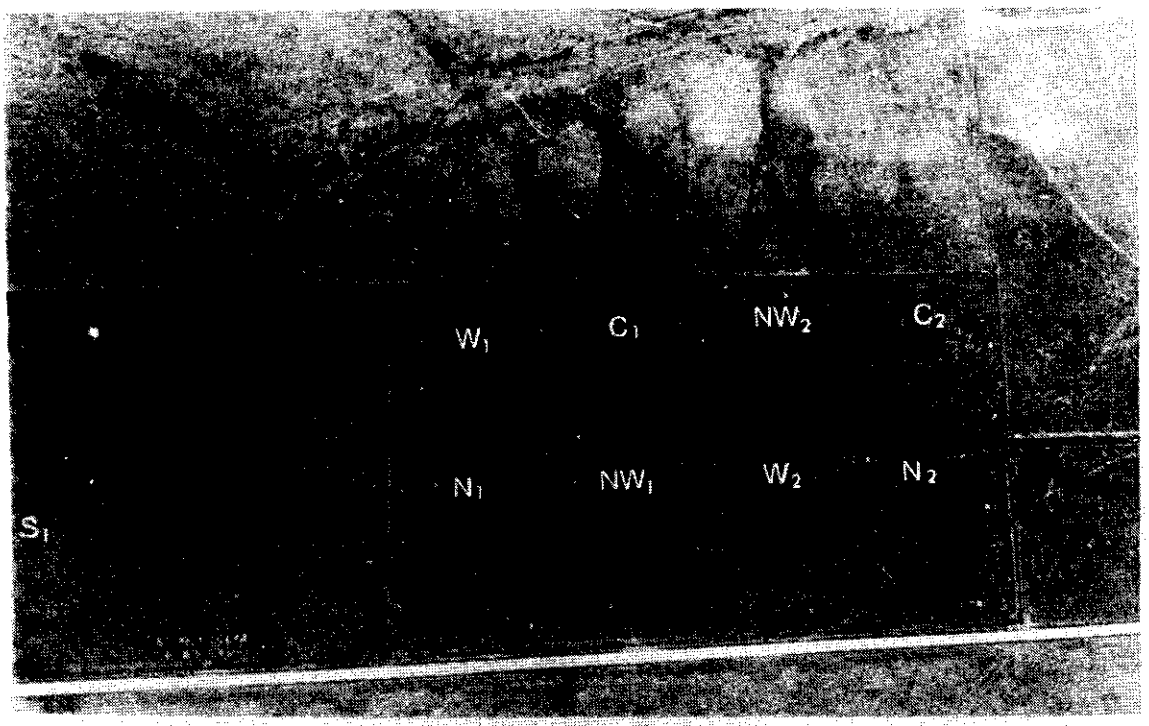


Fig. 1. Mean monthly temperatures and amount of precipitation during the period of study.



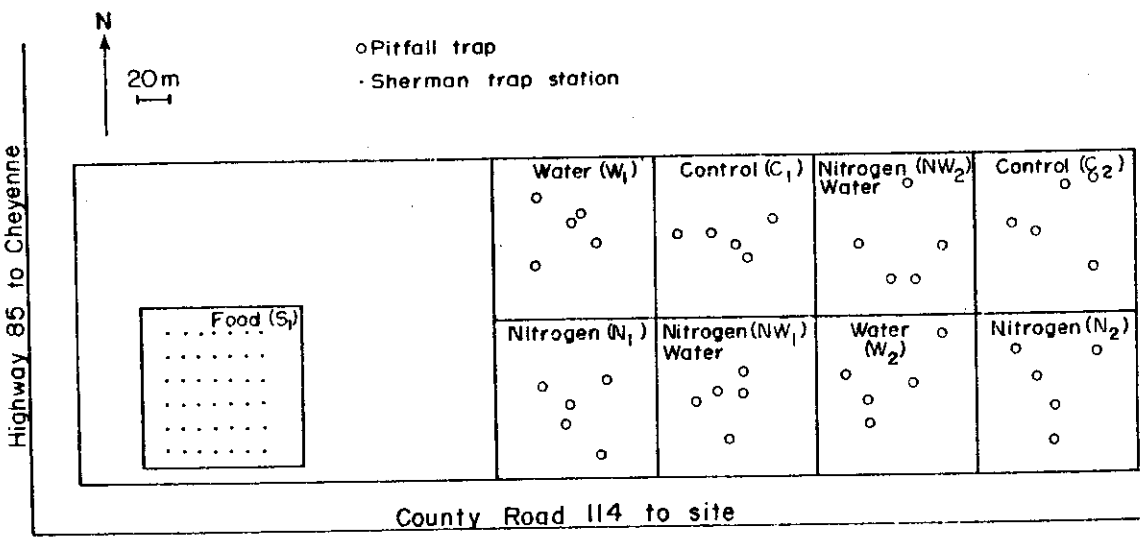


Fig. 2. The study site: An aerial photograph and a map of the study area.

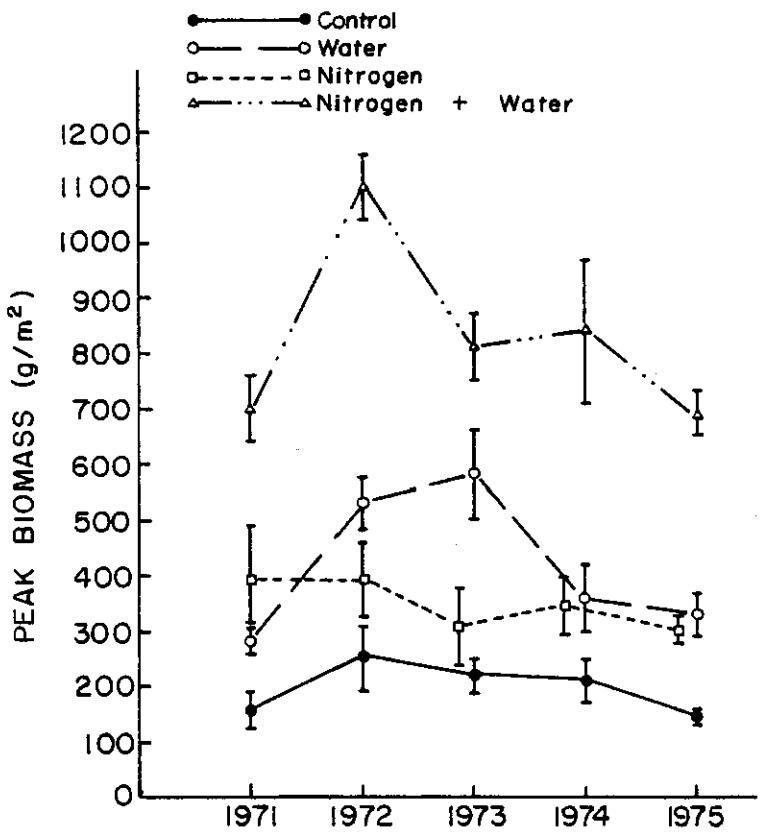


Fig. 3. Mean and standard error of peak herbage biomass in the four stress plots.

FIELD METHODS

Species Identification

Species identification of small mammals in the field followed the procedures of Grant et al. (1976). However, in June 1976 I discovered that individuals that were classified as juveniles of *Peromyscus maniculatus* during this study (and previous studies) were adults and subadults of *Reithrodontomys megalotis*. Fortunately, it was possible to trace back and correct the identification of all but five individuals (these individuals were captured only once and were not weighed), and thus distinguish between the two species. This was done by three methods: (a) reexamination of dead individuals stored frozen, (b) recapturing marked individuals and reexamination after the mistake was detected, and (c) use of weight categories. Adult *P. maniculatus* weights range between 19 and 22 g. Adult *R. megalotis* weights range between 10 and 13 g, pregnant females weigh about 15 g. Thus, any individual with a body weight lower than 14 g (except pregnant females) could have been either *R. megalotis* or juveniles of *P. maniculatus*. By examining the weight data of individuals initially classified as *P. maniculatus*, it was apparent that most of the individuals with body weight lower than 14 g were captured in the nitrogen + water treatment. Only six individuals with body weight lower than 14 g were caught on the other treatments, three each in the nitrogen and the water treatments. All these individuals were caught in the column of traps next to the nitrogen + water treatment. These individuals could be identified accurately as *R. megalotis* because they were recaptured a few months later and had body weights lower than 14 g. No individual with body weight lower than 14 g was caught on the control or the food treatments.

The fact that all the individuals captured outside the nitrogen + water treatment with a body weight lower than 14 g could be accurately identified as *R. megalotis* suggests that juveniles of *P. maniculatus* did not enter the traps before reaching body weight of 17 g or higher. This conclusion was supported by following the weights of marked individuals that were recaptured several times. Individuals that were initially lower than 14 g did not exceed this weight when recaptured.

The data of June to December 1976 sampling periods could be used to further demonstrate the fact that juveniles of *P. maniculatus* did not enter traps. About 80 individuals caught in the nitrogen + water treatment on these dates had body weights lower than 14 g and all were identified as *R. megalotis*. Individuals of *P. maniculatus* which were caught on these dates in the nitrogen + water treatment weighed more than 19 g. In the other treatments trapped on these dates only adult *P. maniculatus* were caught. Because reproduction in *P. maniculatus* in this area starts in February and continues through November (Flake 1974), it is reasonabl to assume that juveniles existed in the area but were not trapped. Thus, it was concluded that all individuals caught with body weight lower than 16 g on the water and the nitrogen treatments, and which could not be identified by the other methods mentioned above, were *R. megalotis*.

In summary, individuals of *R. megalotis* were initially misidentified as juveniles of *P. maniculatus*; however, all but five individuals were subsequently correctly identified.

Small Mammal Trapping

On each of eight 1-ha plots, a 1-year live-trapping program for small mammals was initiated in May 1975. Each plot consisted of 6 rows by 7 columns of trap stations spaced at intervals of 15 and 9 m, respectively (Fig. 2). The stations were marked with numbered stakes. Initially one Sherman live trap (13 × 13 × 38 cm) was set in each station. In July 1975 the number of rodents in the nitrogen + water treatment exceeded the number of traps. The number of traps was then doubled in this treatment by placing additional traps in each station to ensure the number of traps was not a limiting factor for trapping success.

A ninth 1-ha plot (Fig. 2) was established in 1975 to investigate the possibility that the rodents are food limited. The populations on this plot were sampled for four consecutive months before the food was supplied. About 11 kg of whole oats and 11 kg of alfalfa pellets were evenly spread between the six trap rows at 10- to 14-day intervals starting in August 1975.

Small mammals were trapped for five consecutive nights on a monthly schedule during the spring, summer, and fall of 1975, and on a bimonthly schedule during the winter of 1975 and early spring of 1976. In May 1975 and March 1976 severe weather prohibited continuous 5-night sampling. This sampling was reinitiated on these dates after the weather calmed until five nights were accumulated. In December 1975 and May 1976 the small mammals were sampled for only four consecutive nights because of severe weather.

Live trapping was continued after May 1976 on the nitrogen + water treatment, one replicate of the control treatment (C1, Fig. 2),

and the food plot for two consecutive nights on a 2- to 3-week schedule between late May 1976 and December 1976. The trap number was increased to 118 per plot on the nitrogen + water treatment and to 78 traps on the control and food plots. This was done by placing additional traps between each of the original trap stations along the rows. Only part of the results obtained in this additional study is discussed in this report.

Before each sampling period the traps were cleaned and baited with whole oats. Additional baiting during the sampling period was done when necessary. In the summer, traps were routinely set in late afternoon and checked in the early morning of the following day. During the fall, winter, and early spring, traps were left open throughout the sampling period. In these periods, traps were checked three times a day: early morning, noon, and midnight.

Because of relatively high trap mortality on the nitrogen + water treatment, in July 1975 bedding material (cotton) was added to the traps of this treatment. Cotton was added to the traps of the other treatments in September 1975. The cotton was replaced when necessary.

Every new individual trapped was marked by toe clipping and the following data were recorded at each capture: species, individual number, location on grid, age, sex, weight to the nearest 0.5 g, position of testes for males, and size of nipples and pregnancy status for females. In September 1975 the marking technique was changed and upon first capture each individual was tagged with a numbered fish tag in the right ear. Fresh pellets were collected from each captured individual, when available, and frozen for later microscopic examination.

Herbage Sampling

Herbage biomass was determined by choosing sites randomly within each plot and clipping the samples at ground level. Six 0.5 m^2 circular quadrats were collected by the Grassland Biome study personnel in each of the plots. These samples were collected several times during the growing seasons since 1971. The material was separated by species, oven dried, and weighed. In each treatment, the herbage biomass was also estimated in 80 quadrats each 0.5 m^2. For further information see Swift and French (1972).

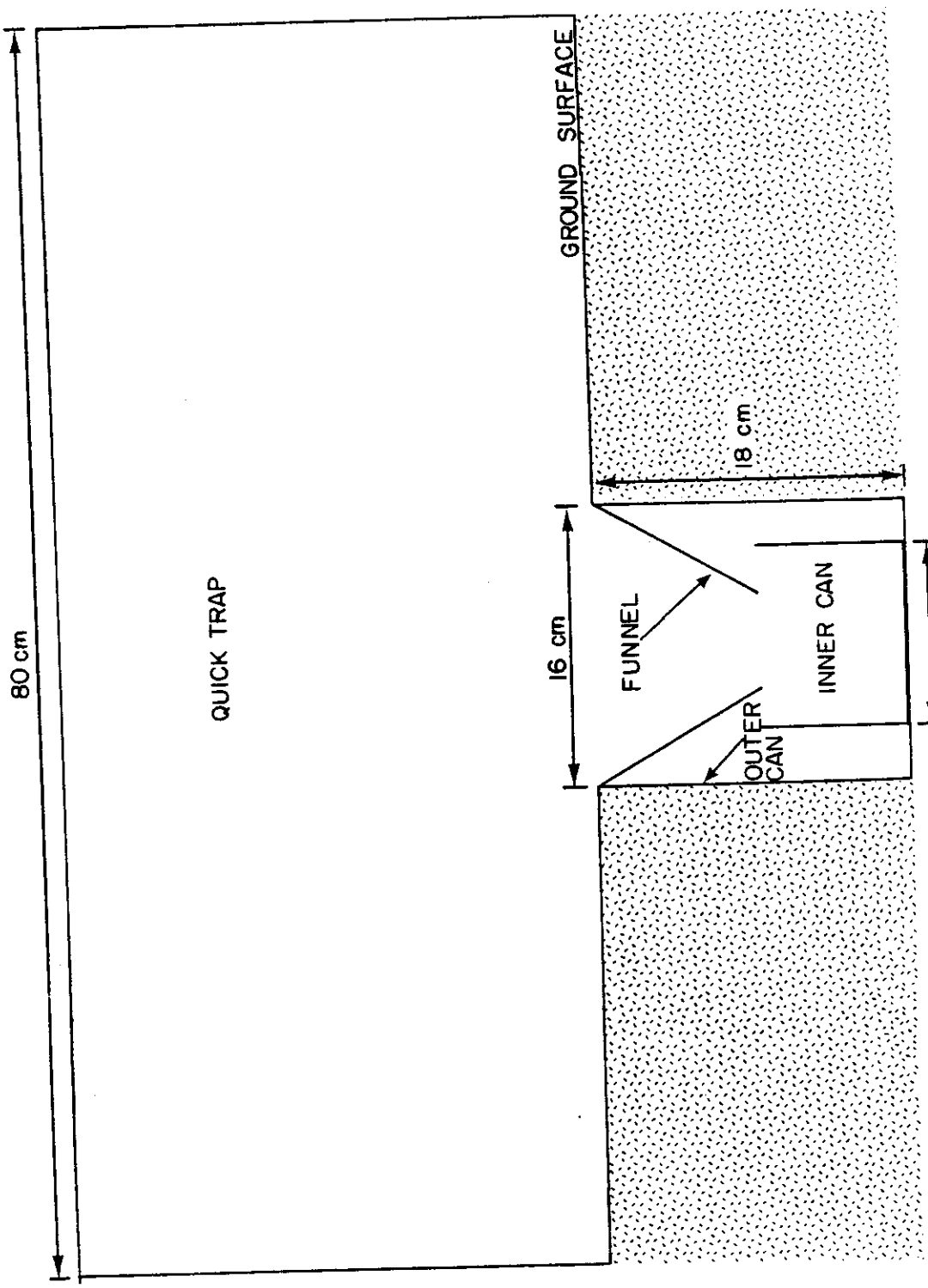
Foliage Vertical Density

Vertical density of foliage, defined as the number of leaves or stems of the vegetation vertically above a point (Cody 1968), was measured at 20 randomly chosen points. At each selected point a thin steel rod was dropped to the ground at four places each 30 cm along axes at right angles to each other through the reference point. The orientation of the axes was chosen with regard to the four major compass directions. The number of contacts of the vegetation with the rod was recorded in 5-cm height increments from ground level. Thus the vertical density was sampled in 20 × 4 = 80 different samples.

At each reference point litter depth was measured, and litter and herbage cover were estimated.

Arthropod Trapping

Arthropods were sampled in June, August, September, and December of 1975 using a combination of pitfall traps and quick traps (Fig. 4). The pitfall trap consisted of two cans and a funnel. Commercial ethylene



[illegible] schematic illustration of the pitfall-quick trap combination.

glycol antifreeze diluted 50% was used as preservative. The quick trap (Fig. 4) consisted of a 0.5 m^2 circular trap with a 16-mesh screen. The quick trap was placed on top of the pitfall trap. Thus, the quick trap bordered an area from which insects were sampled by the pitfall trap. When not in use the quick traps were removed from the area and the pitfall traps were covered with plastic lids.

Five pitfall-quick trap combinations were randomly placed on each of the eight stress plots (Fig. 2). On each sample date the traps were allowed to catch arthropods for 10 consecutive days. Because only 20 quick traps were available, the traps were first set for 10 days on four plots (one replicate of each treatment), and then were moved to the other four plots. The arthropods trapped were stored in jars containing 70% isopropyl alcohol.

Radiotelemetry Equipment

AVM SM1 "mouse style" transmitters manufactured with RM 312 batteries were used to track individuals. The transmitter and the battery were insulated with Deep Flex Rub-M-Mold, a rubber latex compound which cures in air at room temperature. Initially, the transmitters were glued directly to the animal's nape using Eastman 9-10 compound. However, several voles lost their transmitter. Consequently, the transmitter was first glued to a nylon self-locking tie which was mounted around the neck with transmitter in a dorsal position. A Dav Tron receiver and hand-held directional antenna were used to locate the voles.

LABORATORY TECHNIQUES

Fecal Analysis

The feces were prepared for the microtechnique analysis by the method of Flinders and Hansen (1972). All the feces collected from individuals belonging to a given species on each of the treatment replicates were combined, and washed over a 200-mesh screen to remove dirt. The washed samples were spread evenly and mounted on microscope slides, using Hertwig's solution and Hoyer' solution. Two slides were made from each sample.

Forty nonoverlapping, randomly chosen microscopic fields were then read from each slide under low-power (20X) compound binocular microscope to determine the relative frequency of arthropods. Twenty nonoverlapping, randomly chosen microscopic fields were then read from each slide under high-power (100X) magnification to determine the relative frequency of the plant species. Arthropods were identified at least to order. Percent frequency was then converted to particle density per field, and relative density (the number of particles of a plant species or arthropod order expressed as a percent of the total number of particles of all plant species and arthropod order) was calculated for each food category (Appendix I). The relative densities of the food categories in each of the treatments were averaged, when possible, over the two replicates. The analysis of the feces was done by the CSU Range Science Department Diet Laboratory.

Correct species identification could not be done for the feces collected from what was initially classified as *P. maniculatus*. This is because the feces of all individuals of the same species were lumped together for each of the treatment replicates. Nevertheless, it was

shown above that in the control treatment only individuals of *P. maniculatus* were trapped through the study. Thus, diet analysis data in the control treatment are available. On the other treatments it was assumed that the individuals of *P. maniculatus* ate the same type of food in the same proportions as in the control treatment.

The arthropods collected by the pitfall-quick trap combination were sorted to order. The body length of each individual was also recorded.

Small Mammal Populations Size

The intensive live-trapping program was aimed at obtaining accurate information about changes in population size, as well as death and dilution rates, through the use of capture-recapture analysis (Leslie et al. 1953, Jolly 1965). A basic assumption of this estimation procedure is that all animals in the population are at equal risk of capture, and consequently that there is no differential trap response between marked and unmarked animals. Only after this assumption is tested and realized, can capture-recapture analysis be applied, and conversely, if the basic assumption is not realized, then no valid estimates can be made of the parameters one may wish to determine (Leslie et al. 1953).

The assumption of randomness in sampling the marked vs. the unmarked segments of the population can be tested only in a nonbreeding population in which no immigration is occurring (Leslie et al. 1953). In this study only one species, *M. ochrogaster*, was represented in sufficient numbers to test this hypothesis. However, the *M. ochrogaster* population was in breeding condition throughout the study period, and thus the basic assumption cannot be tested. Nevertheless, this test was done for populations of *M. agrestis* (Leslie et al. 1953), *M. californicus*

(Krebs 1966), and *M. ochrogaster* and *M. pennsylvanicus* (Krebs et al. 1969). For all these species the assumption of random capture of the marked and unmarked segments of the population was violated.

It was assumed that the individuals of *M. ochrogaster* in my area behaved similarly to the other microtine species and thus the hypothesis that the marked and unmarked segments of the population were trapped randomly was rejected.

If the marked and unmarked segments of the population are sampled nonrandomly, total population size and dilution rates cannot be estimated validly. Nevertheless, if sampling within the marked population is random, valid inferences may still be made about death rates, which are estimated only from marked animals. Leslie et al. (1953) discussed one method for testing the marked animals for randomness of capture. Unmarked animals can be ignored at each sampling, and the subpopulation of marked animals can be considered in exactly the same way as the whole population is normally considered. Animals caught only once previously are then considered as new members of this subpopulation of marked animals. Instead of compiling a table of recaptures according to the interval since last capture, one compiles a table of re-recaptures (Leslie et al. 1953, their Table 6). From these data we can calculate a parameter (Z) which estimates the number of animals marked for the first time and released at each trapping. Since this parameter is known from our original data, estimates of Z can be compared with the true value. This calculation was made for the most abundant species (*M. ochrogaster*) on the nitrogen + water treatment. The estimated number (Z) of individuals marked and released is 1562, while the known number is 591.

This resulted in a percent difference of -62% (100 (observed - estimated)/estimated, Krebs 1966) which means that a valid inference cannot be made about the mortality rates.

The conclusion is that the marked and the unmarked segments of *M. ochrogaster* population did not show random capture, and thus, the population size could not be estimated by the conventional capture-recapture type of analysis. Similarly, it was shown that within the marked population the capture was also nonrandom and thus the death rate could not be estimated by capture-recapture type of analysis. The other species caught in this study were not numerous enough to test any of the above assumptions or to be used in a conventional capture-recapture type of analysis.

Enumeration Technique

The only alternative method of population estimation is direct enumeration (Krebs 1966). The minimum number of mice alive at time t on each treatment is obtained by summing two counts: (1) the actual number caught at time t and (2) the number of previously marked individuals caught after time t, but not at that time.

Although there is no way of determining the accuracy of these enumerations (Krebs 1966), we can examine the efficiency with which the trapable population was sampled. This can be done by estimating "trapability" (Krebs et al. 1969), by comparing the actual catch in each trapping period of 5 days with the number of mice known to be alive on each of the treatments (Table 1). To increase the sample size, the individuals caught on the replicates of each treatment were combined. Only on two occasions was the trapability under 50% (*M. ochrogaster* in the nitrogen + water treatment in May 1975 and *P. maniculatus* in the

Table 1. Trapability of *M. ochrogaster*, *P. maniculatus*, *O. leucogaster*, *S tridecemlineatus*, and *R. megalotis* on the four treatments.[a/] Trapability is measured by the percentage of mice known to be alive which were actually caught.

Period	*M. ochrogaster*				*P. maniculatus*							
	Nitrogen + Water		Water		Control		Nitrogen		Nitrogen + Water		Water	
	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability
May 1975	22	40	0	--	6	100	4	100	2	100	2	100
June 1975	41	95	0	-	2	50	2	100	1	100	5	100
July 1975	135	95	5	100	4	75	1	100	0	--	1	100
Aug. 1975	161	96	13	100	4	100	0	--	0	--	0	--
Sept. 1975	148	91	3	77	7	29	0	--	4	100	1	100
Dec. 1975	150	91	3	100	10	90	9	100	1	100	8	100
March 1976	117	95	0	--	10	100	8	100	3	100	6	100

Period	*O. leucogaster*				*S. tridecemlineatus*						*R. megalotis*	
	Control		Nitrogen		Control		Nitrogen		Water		Nitrogen + Water	
	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability	N[b/]	Trap-ability
May 1975	0	--	0	--	5	100	6	83	10	70	20	--
June 1975	3	100	3	100	4	75	4	50	10	90	10	90
July 1975	1	100	2	100	10	90	6	67	8	100	2	100
Aug. 1975	2	100	3	100	10	80	11	91	7	86	1	100
Sept. 1975	2	50	2	100	8	--	6	--	0	--	1	100
Dec. 1975	3	--	0	--	--	--	--	--	--	--	11	100
March 1976	2	--	0	--	9	56	5	60	1	75	11	100

[a/] NW = nitrogen + water; W = water; N = nitrogen; C = control.

[b/] Number of mice known to be alive on the area at the time sampled.

control treatment in September 1975). All other trapability estimates were usually above 80%. This means that the trapping was efficient in most of the species/treatment/date categories and thus by repeating this enumeration, I can obtain a reasonably precise description of demographic trends (Krebs et al. 1969).

Arthropods

The objective of the arthropod sampling was to devise a method which would sample coleoptera accurately. The reason for concentrating on beetles was that this group of insects was shown to comprise a large percent of the small mammals' animal diet (Flake 1973).

Pitfall traps have been used successfully in the study of various ground-dwelling organisms such as Coleoptera (Doane 1961, Meijer 1971). However, pitfall traps cannot be used as a quantitative sampling device (Southwood 1966). This is because the activity of the arthropods, and thus the efficiency of the traps, changes with the weather conditions, habitat type, and the amount of moisture in the soil (Southwood 1966). Because of these limitations the pitfall-quick trap combination was used. In this way the area from which the arthropods were trapped was restricted by the quick trap. Also, by letting the traps operate for 10 consecutive days it was hoped that the differences in activity due to severe weather would be overcome. The efficiency of the pitfall-quick trap combination was tested in June 1975. After the regular 10-day sampling period, insects caught were collected and the traps were then reset and operated for another five consecutive days. Negligible numbers of arthropods were caught in the second period; thus, it was

concluded that the pitfall-quick trap combination operated as an efficient sampling device.

The standard error associated with the mean density of the insects was very high, and in most cases the 10 samples taken were not sufficient to obtain a moderate goal (20% of the mean 80% of the time).

Foliage

Pielou's (1966) procedure was used to test the adequacy of the sample size of the foliage height density. As can be seen from Fig. 5, changes in cumulative diversity with increasing sample size became very slight, usually within the range of 20 to 30 samples; thus, the number of samples was more than enough and additional samples would not have improved the sample. I also checked sample size according to the procedure suggested by Snedecor and Cochran (1973:516). I found that in the worst case the variance was large enough to be within 10% of the mean 95% of the time.

Similarity Index and Competition Coefficient

Whittaker's (1952) similarity index was used as an indication of overlap between the frequencies of food categories found in the feces of a given species on the different habitats. It is calculated* as:

$$SI = 2 \sum_{i=1}^{n} w_i / \sum_{i=1}^{n} (a_i + b_i)$$

*Examples of calculations used in data analysis appear in Appendix II.

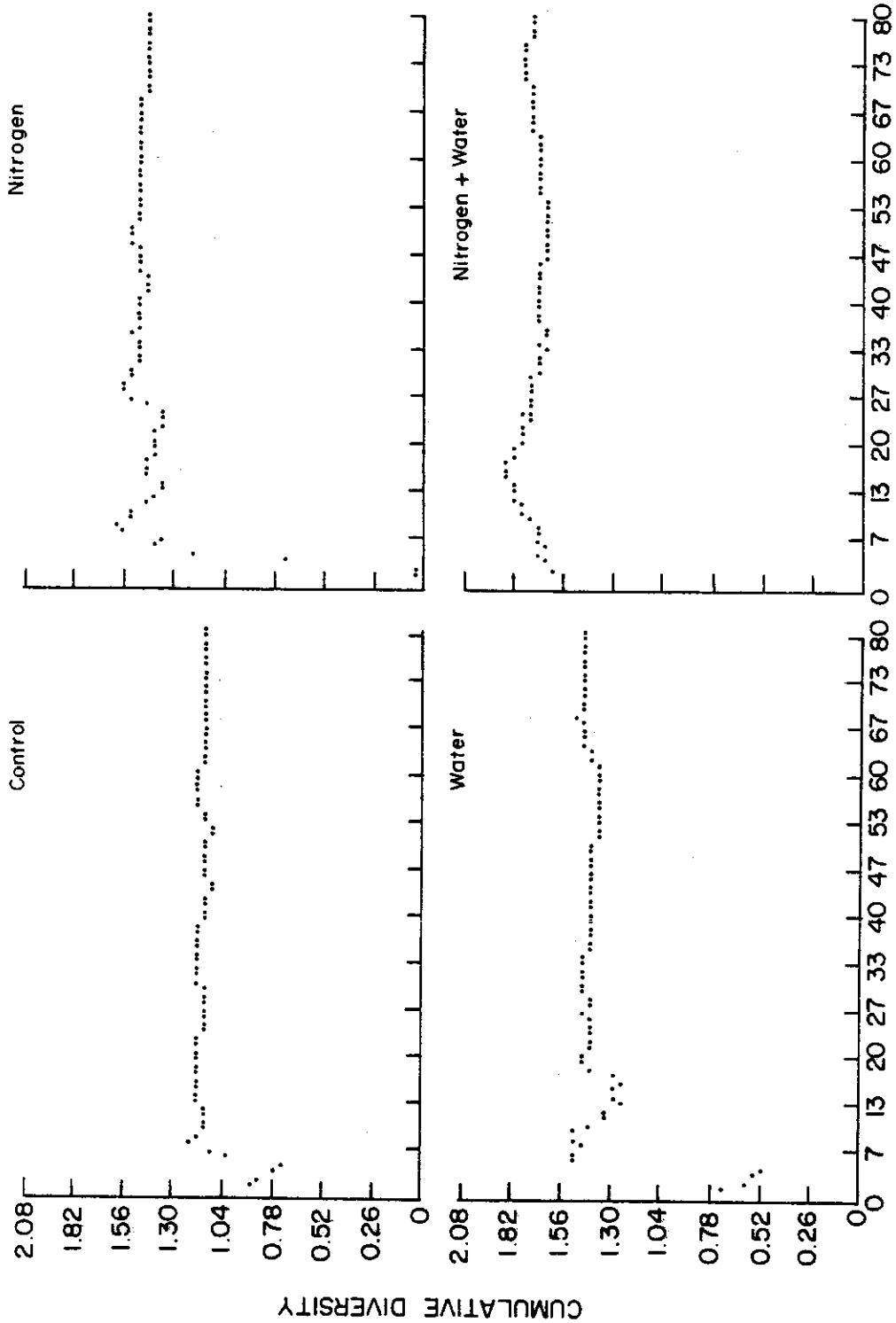


Fig. 5. Cumulative foliage diversity as a function of sample size.

where a_i represents the mean percentage of food category i in a given rodent species on habitat one, b_i represents the mean percentage of food category i in the same rodent species in habitat two, w_i represents a_i if $a_i \leq b_i$ and b_i if $b_i \leq a_i$, and n is the number of categories. The value of SI ranges between 0 for no similarity and 1 for complete similarity.

The competition coefficients for the habitat and the food dimensions of the ecological niche were calculated using Levins' (1968) approximation equation. This competition coefficient is based on the probability of the co-occurrence of individuals of two populations over a range of habitats when the competition for habitats was considered, and the probability of co-occurrence of the same food category in the diet of two rodent species when the competition for food was considered.

Levins (1968) used the following expression for the effect of species j on species i:

$$\alpha_{ij} = \sum_{h=1}^{n} P_{ih} P_{jh} / \sum_{h=1}^{n} P_{ih}^2$$

where h is a habitat type (or food category) and P_{ih} and P_{jh} are the proportions of species i and j occurring in the same habitat, respectively, and the summation is over all habitats n. If two species are separated in spatial-temporal positioning, then their probability of co-occurrence will be small and vice versa.

Niche breadth was calculated after Levins (1968):

$$\ln B = - \sum_{i=1}^{n} P_i \ln P_i$$

where P_i is the proportion of the species individuals found in habitat i (or the proportion of food category i in the diet of a given species), B is the niche breadth, and n is the number of categories. B equals n when all n resources are being used equally and equals 1 when only one resource category is utilized.

Simulation Model

Data from this study and the literature were used to construct a small mammal population dynamics compartment model. The model was coded in SIMCOMP 3.0 (Gustafson and Innis 1972) simulation language. The model uses difference equations and runs on 2-week time step.

COMMUNITY STRUCTURE

The concept of competitive interaction between similar species has been introduced by Grinnell (1917), Volterra (1926), and Lotka (1932). According to this concept two species cannot occupy the same ecological niche (Vandermeer 1972) for a long time. Because of competitive interactions for limiting and common resources, either competitive exclusion or niche shift will result. Gause (1934) has shown experimentally that the process of competition does exist. Few direct studies have provided evidence for the importance of inter- and intraspecific competition (Connell 1961, 1975; Pain 1966; P. R. Grant 1972). Evidence has also been reported for laboratory experiments (Park 1948, 1954; Slobodkin 1961). However, many studies have provided indirect evidence for the occurrence of this process in natural communities of various organisms (MacArthur 1972, Cody 1974, Rosenzweig et al. 1975, Brown 1975; review papers by Miller 1967, P. R. Grant 1972, Schoener 1974a, Connell 1975). In spite of the fact that only a few direct field experiments support this concept, and that the concept has been criticized (Andrewartha and Birch 1954, Murdoch 1966, Ehrlich and Birch 1967), the importance of interspecific competition as a mechanism that has determined the distribution and abundance of species is given considerable importance today (Miller 1967, MacArthur 1972, Cody and Diamond 1975, Hutchinson 1975).

One of the suggested means for avoiding competition in small mammals is differential habitat utilization (P. R. Grant 1972, Rosenzweig et al. 1975, Brown 1975). This concept suggests that closely related species have reduced competition between themselves by utilizing different habitats or habitat patches.

However, very little is known about the impact of habitat manipulation on animal communities that inhabit them, and about the influence of species that have invaded the manipulated habitats on the original community. Such perturbation experiments which result in the formation of new habitat types offer a unique opportunity to study the relation between habitat structure and between the distribution and abundance of species. Species that occupy a certain habitat type have reduced the competition between them in a certain way. However, the same species communities when faced with different habitat patches are probably forced to resort themselves. This is because a given species which may be competitively inferior in one habitat type can be competitively superior in a different habitat type (P. R. Grant 1972).

This study reports on the response of a small mammal community previously inhabiting shortgrass prairie, to habitat manipulation induced through the application of water, nitrogen, or both. Factors that may have been responsible for the response are analyzed.

Results and Discussion

Small Mammal Populations

Five small mammal species were regularly captured in the four stress treatments (*Peromyscus maniculatus*, *Spermophilus tridecemlineatus*, *Onychomys leucogaster*, *Microtus ochrogaster*, and *Reithrodontomys megaloti*. A sixth species, *Dipodomys ordii*, was caught only in the food treatment and it will be discussed later. *P. maniculatus*, *S. tridecemlineatus*, and *O. leucogaster* are common species of the shortgrass prairie and can be found there in variety of habitats within this ecosystem (Flake 1971, W. E. Grant 1972). *M. ochrogaster* and *R. megalotis* are rare in most

habitats of the shortgrass prairie, but, infrequently, transient individuals may be found (W. E. Grant and D. S. Dobkin, pers. comm.).

M. ochrogaster invaded the nitrogen and water treatment when the treatment was initiated in 1971 (W. E. Grant 1972) and persisted in the area until the termination of this study in 1976. Unfortunately, I don't know when *R. megalotis* invaded the nitrogen + water treatment. *R. megalotis* was trapped consistently in 1975 and 1976. One individual which was marked and identified in late 1974 (by an I.B.P. Grassland Biome study field technician) as a juvenile *P. maniculatus* was recaptured in 1975 and reclassified as *R. megalotis*. Thus, it is safe to assume that *R. megalotis* invaded the nitrogen + water area in 1974, though it is probable that the invasion occurred earlier, but was not detected by the field technicians. Because in an earlier study during 1971 to 1974 (Grant et al. 1976) weights of individuals were not taken, it is impossible to determine when the invasion of *R. megalotis* occurred (see Methods).

The nitrogen + water treatment, which carried the highest herbage biomass relative to the other plots, was also inhabited by the highest number of small mammals (Fig. 6). The differences between the total number of individuals which inhabit the water, nitrogen, and control treatments from 1975 to 1976 is relatively small (Fig. 6). A similar pattern was also observed (Grant et al. 1976) between 1971 and 1974 (Fig. 6).

Although the four treatments were adjacent to each other (Fig. 2), and in spite of the fact that the total area of the stressed plots was only 6 ha, differences between compositions of the small mammal communities were observed in the four treatments (Table 2).

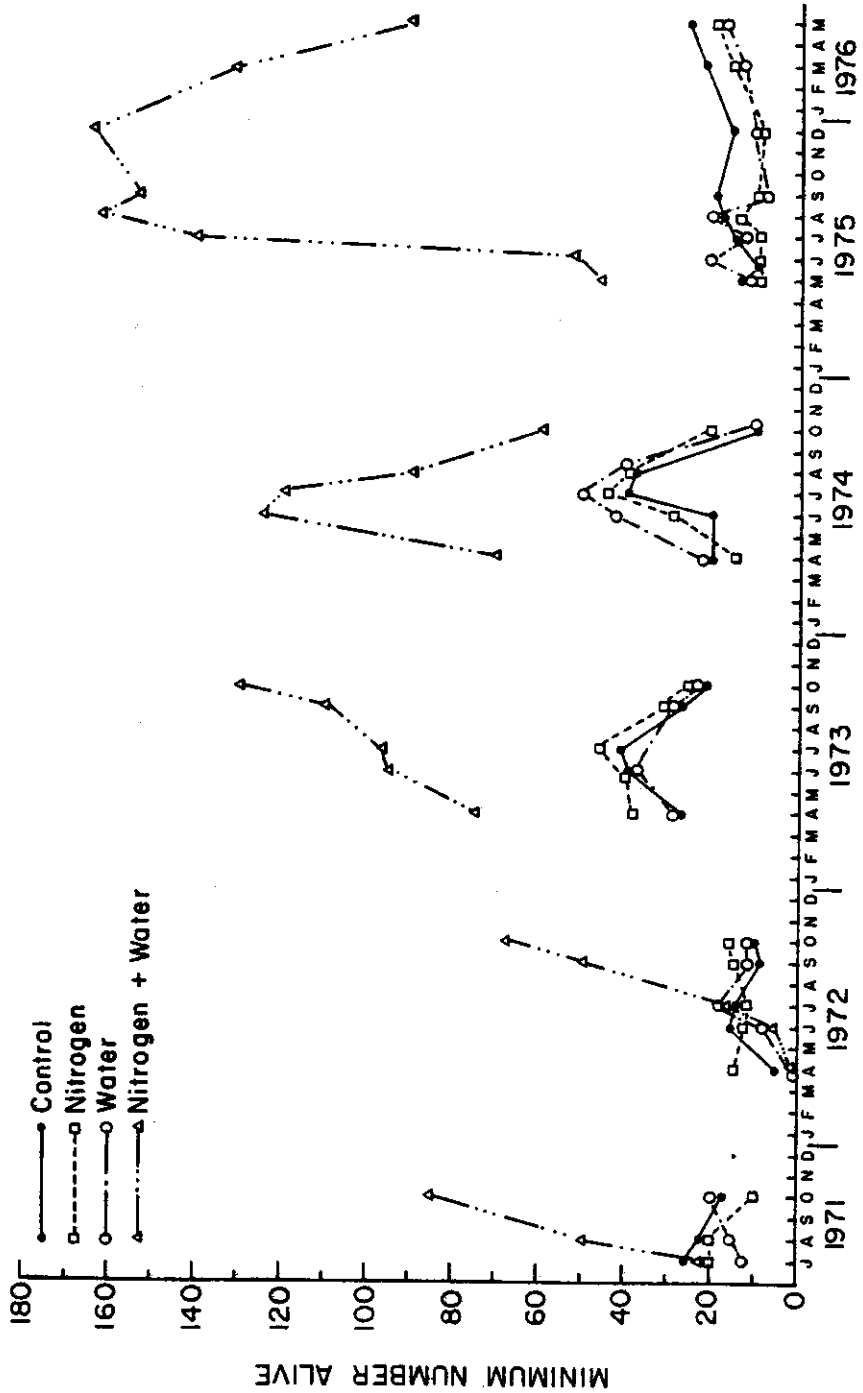


Fig. 6. Total number of individuals known to be alive in the four stress plots from 1971 to 1976. (The data collected by Grant et al. (1976) were used to calculate the population densities between 1971 and 1974.)

Table 2. Number of individuals known to be alive on the treatments during 1975 and 1976.

Treatment	Species	May	June	July	Aug.	Sept.	Dec.	March	May	Total
Control	*Microtus ochrogaster*	--	--	--	--	--	--	--	--	--
	Peromyscus maniculatus	9	2	4	4	7	10	10	8	54
	Spermophilus tridecemlineatus	5	4	11	10	8	2	9	15	64
	Onychomys leucogaster	--	3	1	2	2	3	2	2	15
	Reithrodontomys megalotis	--	--	--	--	--	--	--	--	--
Total		14	9	16	16	17	15	21	25	133
Nitrogen	*Microtus ochrogaster*	--	--	--	--	--	--	--	--	--
	Peromyscus maniculatus	5	2	--	--	--	9	7	4	27
	Spermophilus tridecemlineatus	7	4	6	11	6	--	5	13	52
	Onychomys leucogaster	--	3	2	3	2	--	--	--	10
	Reithrodontomys megalotis	--	--	1	--	--	--	1	1	3
Total		12	9	9	14	8	9	13	18	92
Water	*Microtus ochrogaster*	1	5	5	13	3	3	0	1	31
	Peromyscus maniculatus	2	5	--	--	1	7	5	1	21
	Spermophilus tridecemlineatus	10	11	11	7	5	--	8	16	68
	Onychomys leucogaster	--	--	--	--	--	--	--	--	--
	Reithrodontomys megalotis	--	--	1	--	--	1	1	--	3
Total		13	21	17	20	9	11	14	18	123
Nitrogen + water	*Microtus ochrogaster*	22	41	135	161	148	150	117	69	843
	Peromyscus maniculatus	2	1	--	--	4	1	3	--	11
	Spermophilus tridecemlineatus	3	2	1	--	--	1	1	2	10
	Onychomys leucogaster	--	--	--	--	--	--	--	--	--
	Reithrodontomys megalotis	20	10	2	1	1	11	11	19	75
Total		47	54	138	162	153	163	132	90	1062

Individuals of *M. ochrogaster* were trapped only in the nitrogen + water and the water treatments. Individuals of *R. megalotis* were trapped only in the nitrogen + water, the water, and the nitrogen treatments. Individuals of *O. leucogaster* were trapped only in the control and the nitrogen treatments (Table 2). The difference between the habitat utilization exhibited by the small mammal species was also reflected through their density. It seems that each species had an "optimal" habitat in which its density was relatively high, "suboptimal" habitats in which its densities were relatively low, and habitats where the species was completely absent. *M. ochrogaster* and *R. megalotis* were most "abundant" in the nitrogen + water treatment, *O. leucogaster* and *P. maniculatus* were most abundant in the control treatment, and *S. tridecemlineatus* was most abundant in the water treatment (Table 2).

Although some species were never caught in some of the treatments, they may have utilized them to a limited degree. Grant et al. (1976) report an occasional trapping of *M. ochrogaster* in the control and nitrogen treatments and of *O. leucogaster* in the water treatment. These few individuals that were trapped outside their "optimal" habitats probably represent transient individuals. Thus, I concluded that the data collected in 1975 and 1976 represent the species habitat utilization accurately.

The described pattern of differential habitat utilization by the small mammal species may result from differences in habitat priorities exhibited by the species, interspecific competition, or a combination of both factors (Wecker 1963, Rosenzweig and Winakur 1969, P. R. Grant 1972, Schroder and Rosenzweig 1975).

Treatments

The measured habitat variables exhibited a similar pattern. All the variables increased over the three stress treatments, showing the highest increase in the nitrogen + water treatment, intermediate increase in the water treatment, and the smallest increase in the nitrogen treatment relative to the control treatment (Table 3). Thus, a series of habitats were formed ranging from the control plots of shortgrass prairie habitat (where the herbage biomass was the lowest) to the extreme habitat in the nitrogen + water treatment plots (where the herbage biomass was the highest).

A similar trend was also observed in the arthropod biomass (Appendix III). Although high variance was associated with the means of Coleoptera density in the four treatments, a comparison between their abundances can still be made. It was found that in the two wet treatments the number of Coleoptera was significantly higher than in the two dry treatments ($P < 0.001$). Similar results were found for trapped Orthoptera, Araneida, and Hemiptera individuals. Individuals of Hymenoptera were more abundant in the dry treatments relative to the wet trea ments. It should be noted that the pitfall-quick trap combination was designed and usually efficient in catching only ground-dwelling arthropods (Southwood 1966). The variation in the density of arthropods was lower in the sampling conducted from 1971 to 1973 by the Grassland Biome staff (Lavigne et al. 1972, Lavigne and Kumar 1974, Andrews 1976). In these samples the quick trap was dropped at a selected random point and the arthropods were collected by vacuuming. The results of the arthropod sampling from 1971 to 1973 also showed that arthropods were usually more abundant in the wet treatments relative to the dry treatments.

Table 3. Main variables of the habitat.

Habitat variable	Control	Nitrogen	Water	Nitrogen + water
Foliage height diversity	1.12	1.46	1.47	1.77
Litter cover (%)	0.16	0.25	0.41	0.24
Litter depth (cm)	0.17	0.21	0.55	2.62
Vegetation cover (%)	0.20	0.28	0.32	0.84
Mean herbage biomass (g/m^2)	125	189	242	365

It follows that the two wet treatments carried more food (in terms of arthropods and herbage) to the small mammals than did the dry treatments.

The structure and the amount of plant biomass in the nitrogen + water treatment is similar to those found in a tallgrass prairie habitat (Grant et al. 1976). The structure and the amount of plant biomass in the water treatments, and to a lesser degree in the nitrogen treatment, is similar to that found in a midgrass prairie (R. G. Woodmansee, pers. comm.). The vegetational structure and biomass in the control plots were typical of the natural ungrazed shortgrass prairie. Thus, the series of habitat types formed by the application of the stress treatments was similar to the habitats found within the gradient betweer shortgrass and tallgrass prairie habitats. However, while the natural gradient of habitats covers large geographical area, the habitat formed by the application of the stress treatments is limited to an area of 8 ha in size.

Foliage height diversity (FHD) across habitat gradients has been used extensively to predict species diversity of birds (MacArthur and MacArthur 1961, Karr and Roth 1971, Cody 1974), lizards (Pianka 1975), small mammals (Rosenzweig and Winakur 1969), and insects (Murdoch et al. 1972). Thus, this metric was chosen to permit comparison of results from this study to those reported earlier. Rosenzweig and Winakur (1969) have also shown that the species abundance of small mammals over a gradient of habitats can be predicted by the proportion of vegetation in a certain vertical layer. Furthermore, evidence for the biological significance of these relationships has also been demonstrated by field experiments (Rosenzweig et al. 1975). These experiments were conducted

by artificial addition or removal of foliage layers and monitoring the response of the small mammal species to the modified habitats (Rosenzweig 1973). Also, by placing traps in natural habitat at different heights it was possible to show that the small mammal species utilized the foliage layers differentially (Rosenzweig et al. 1975). Thus, although the habitat measurements presented in Table 2 showed a high degree of correlation, I chose to characterize the habitats studied in the present report by FHD alone. The differences in foliage density and the height of the vegetation in the four habitats are presented in Fig. 7.

FHD was estimated in this study from all the foliage measurements conducted at 5-cm height intervals. Thus, instead of arbitrarily choosing three layers of vegetation (MacArthur and MacArthur 1961, Rosenzweig and Winakur 1969, Cody 1974), I calculated the overall degree of vertical diversity. Nevertheless, the nature of the results did not change when the FHD of three vegetation layers, used by Rosenzweig and Winakur (1969), was calculated.

The abundance of the three "native" species of the shortgrass prairie (*P. maniculatus*, *O. leucogaster*, and *S. tridecemlineatus*) exhibited negative correlation with increasing values of FHD (Fig. 8a). However, the abundance of the two "exotic" species (*M. ochrogaster* and *R. megalotis*) exhibited positive correlation with increasing values of FHD (Fig. 8b). Note that if lines are drawn between the points of each species, they will have different slopes. The difference between slopes probably reflects biological differences between the species such as home range size, social tolerance, and competitive ability.

Species diversity of the small mammals on the four treatments varied to a great extent throughout the study period (Fig. 9). The

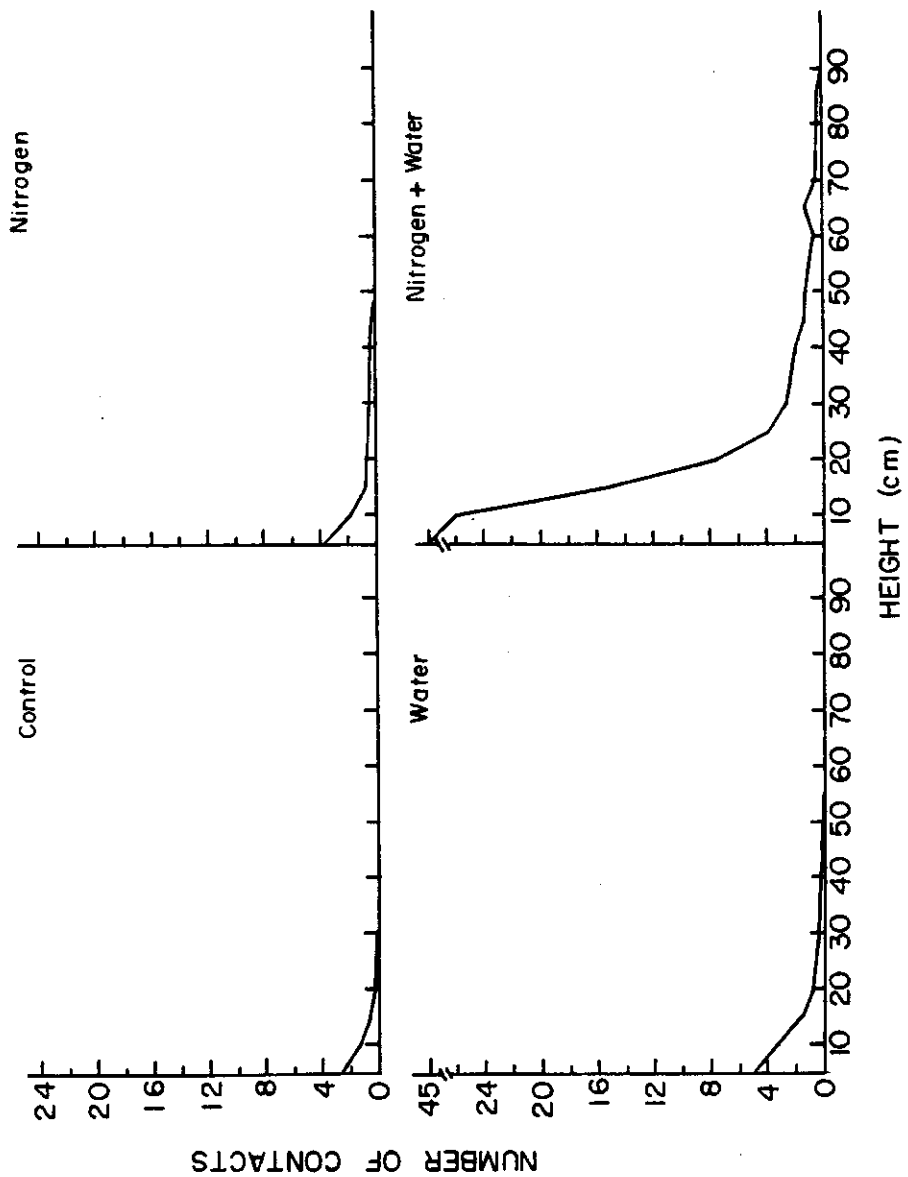


Fig. 7. The density of foliage in different height categories.

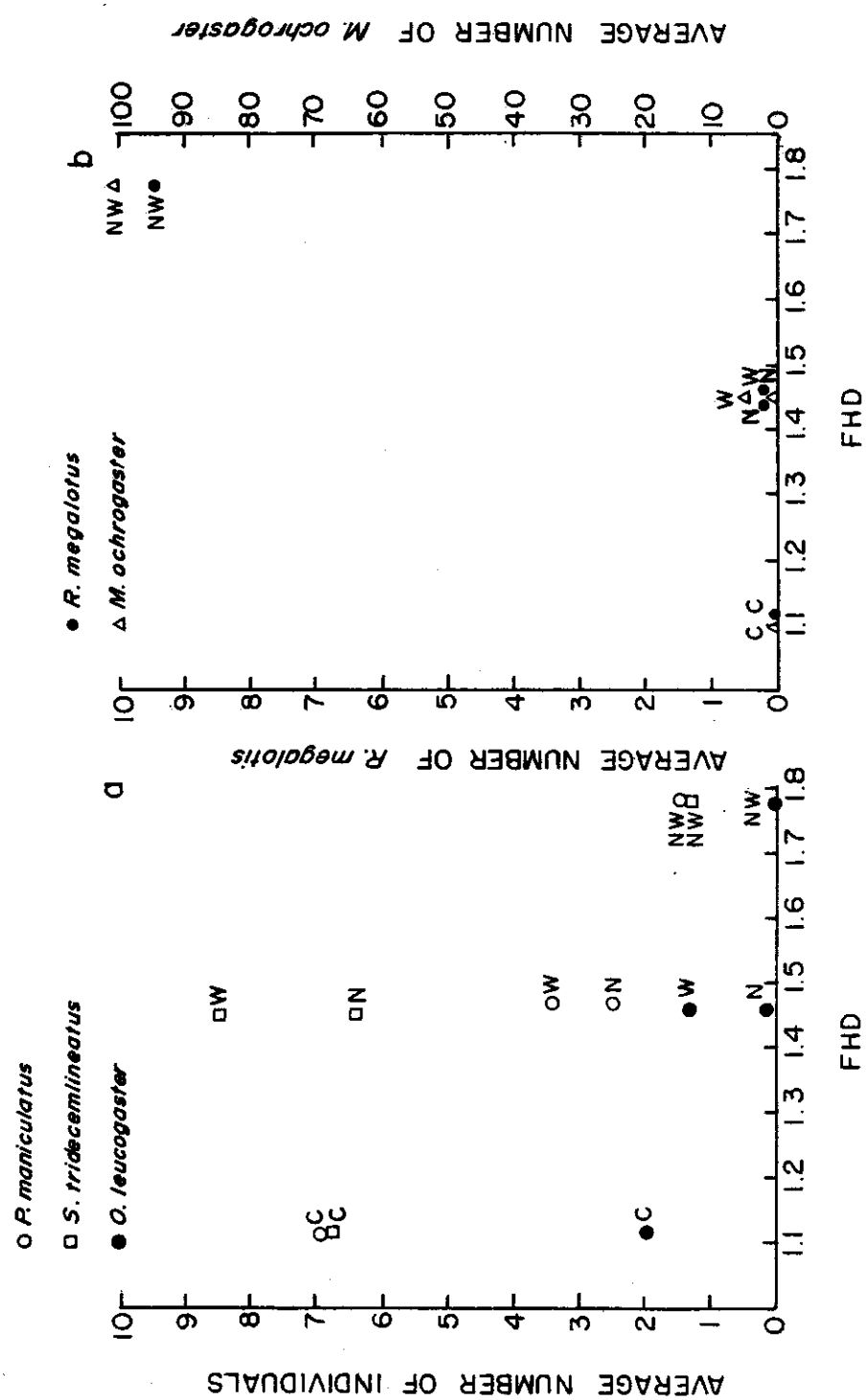


Fig. 8. Species abundance plotted against foliage height diversity (C, control treatment; W. water treatment: N. nitrogen treatment: NW. nitrogen + water treatment).

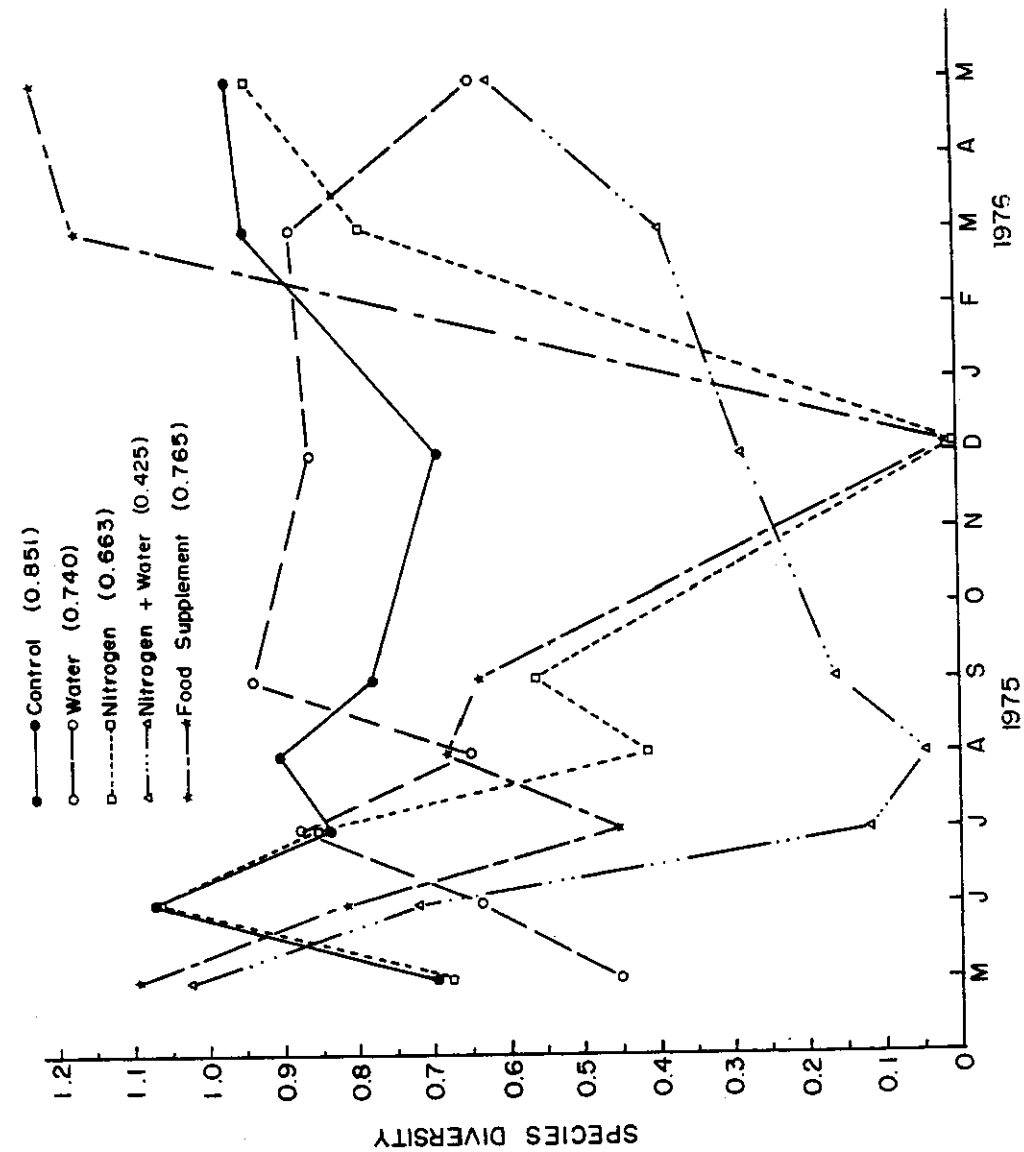


Fig. 9. Species diversity of the small mammal communities in the five treatments.

highest values of species diversity were recorded in May and June and the lowest values, usually during the winter months. This pattern of change in species diversity was partly caused by the fact that *S. tridecemlineatus* was hibernating from September to April. On the other hand, the differences in species composition between the four habitats and the fact that these habitats were adjacent to each other (Fig. 2), made it very likely for emigrants to be trapped in "suboptimal" habitats. This fact partly explains the month-to-month variation in species diversity. Note that species diversity for the nitrogen + water and the water treatments reached their lowest values earlier than on other treatments. This happened when *M. ochrogaster* was most abundant on both treatments and thus may suggest that competitive interactions between abundant *Microtus* population and the other species limit the abundance of the latter. Nevertheless, it was clear that the species diversity in the control treatment was higher than the species diversity on the rest of the treatments.

Negative linear correlation ($r^2 = 0.90$, $P < 0.05$) was found between species diversity and FHD (Fig. 10). Other variables of the habitat also showed high correlation with species diversity, but FHD was the best predictor of species diversity.

The negative correlation between species diversity and FHD is different from the results reported in the literature for natural habitats. In studies conducted in natural habitats on small mammals (Rosenzweig and Winakur 1969), lizards (Pianka 1975), and birds (MacArthur et al. 1966, Cody 1974) positive correlation was found between species diversity and FHD. The disagreement between the nature of the results found in natural and man-made habitats can probably be interpreted

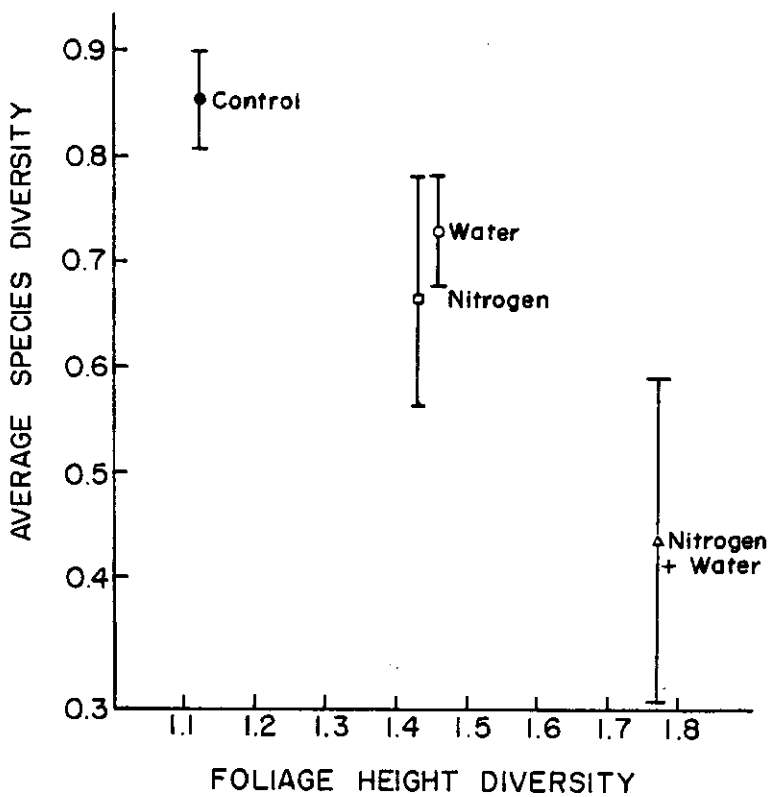


Fig. 10. Species diversity plotted against foliage diversity. The vertical line represents the standard error.

in terms of differences in colonization rates and the size of the stres plots. This is because the stress treatments can be regarded as small islands (2 ha, each) located in the middle of a "sea of shortgrass prairie habitat."

Natural gradient of grassland habitats shows that the number of small mammal species increased from shortgrass to tallgrass prairie habitat (French et al. 1976). *Peromyscus leucopus*, *Reithrodontomys montanus*, *Sigmodon hispidus*, *Mus musculus*, and *Blarina brevicauda* appeared in mixed-grass and tallgrass habitats but not in a shortgrass habitat (French et al. 1976). Brown (1973) postulated that the number of species that can be found in a given area is dependent on interactions between ecological, biogeographic, and evolutionary factors. The number of habitats or patches as an additional factor was suggested too (MacArthur et al. 1966, Rosenzweig et al. 1975). The evolutionary factor can probably be ruled out in the present study because of the short time involved. The biogeographic factor, on the other hand, has probably played an important role in determining the number of species in this study. Small mammal species that usually can be found in structurally similar habitats to those formed in the stress plots, probably have not invaded them because of geographical barriers, the size of the treatments, the short time that was available for colonization, or a combination of the above factors. Furthermore, ecological factors (e.g., competition) were probably also responsible not only for the different community compositions formed, but also for the number of species that colonized the area. A few individuals of *Mus musculus* were caught in the nitrogen + water treatment but did not persist in the area. A long list of evidence suggests that interspecific competition

between *Microtus* and *Mus* and between *Peromyscus* and *Mus* limits the distribution of the latter species (Wirtz and Pearson 1960, Caldwell 1964, Caldwell and Gentry 1965, DeLong 1966, Lidicker 1966, Batzli 1968). Thus, it is not unlikely that interspecific competition was responsible for the absence of stable population of *Mus musculus* in my study area.

Therefore, I concluded that biogeographical as well as ecological factors were probably the major causes that may explain the inverse relation between species diversity and FHD obtained in this study. A theoretical model has been provided by MacArthur and Wilson (1967) to account for variation in the diversity of species on islands. This model attributes the number of species to an equilibrium between rates of recurrent extinction and colonization as a function of the island size and its distance from the source populations. The model was late applied to organisms inhabiting caves (Culver 1970), mountain tops (Brown 1971), lakes (Barbour and Brown 1974), and was further develope for patchy environment (Levins and Culver 1971, Horn and MacArthur 197 Levin 1974). However, since the stress plots have only existed for a short time, and since little is known about the distribution of the potential invaders, this concept will not be discussed further. Never theless, two species (*M. ochrogaster* and *R. megalotis*) invaded the are. These species can be found in restricted habitats in northeastern Colorado (D. S. Dobkin, pers. comm., unpubl. data), and thus could invade the area rather rapidly.

Thus far I have discussed the difficulties that potential colonizers may face. I have also shown that the differential abundance of each of the species on the four habitats can be described by FHD.

However, another factor--interspecific competition for food--may have been responsible for the observed difference of the community compositions. Habitat preference and interspecific competition for food are not necessarily independent (Svärndson 1949; MacArthur 1972; Fretwell 1972; Morris and Grant 1972; P. R. Grant 1972, 1976), though usually it is not clear which is the cause and which is the effect. Different habitat priorities can cause a difference in the food taken, or similar diets can cause a difference in habitat utilization. Both may be the result of interspecific competition (MacArthur 1972).

Small Mammal Diet

To allow easy comparison between the diet of the small mammal species on the different habitats, the diet data were grouped into three categories: seeds, animal matter, and plant material (Figs. 11-14). The major (>5%) diet categories for insects (order level) and plants (species level except seeds) are presented in Appendix I. Because individuals of *R. megalotis* were misidentified in earlier samples of the population (see Methods), diet data were not available for this species. However, because it was possible to establish that in July 1975 only individuals of *R. megalotis* were caught in the nitrogen treatment, and thus, the diet of *R. megalotis* in this treatment and date is known. The feces consisted of 99% seeds and 1% plant material. This result is consistent with the findings of Fisler (1965) and Smith (1936). Fisler (1965) also reported that "the appearance of the stomach contents of [*R.*] *megalotis* remains constant throughout the year." Thus, I assumed that *R. megalotis* had similar diet throughout the study period and across the three treatments where it was captured, to the one diet sample analyzed.

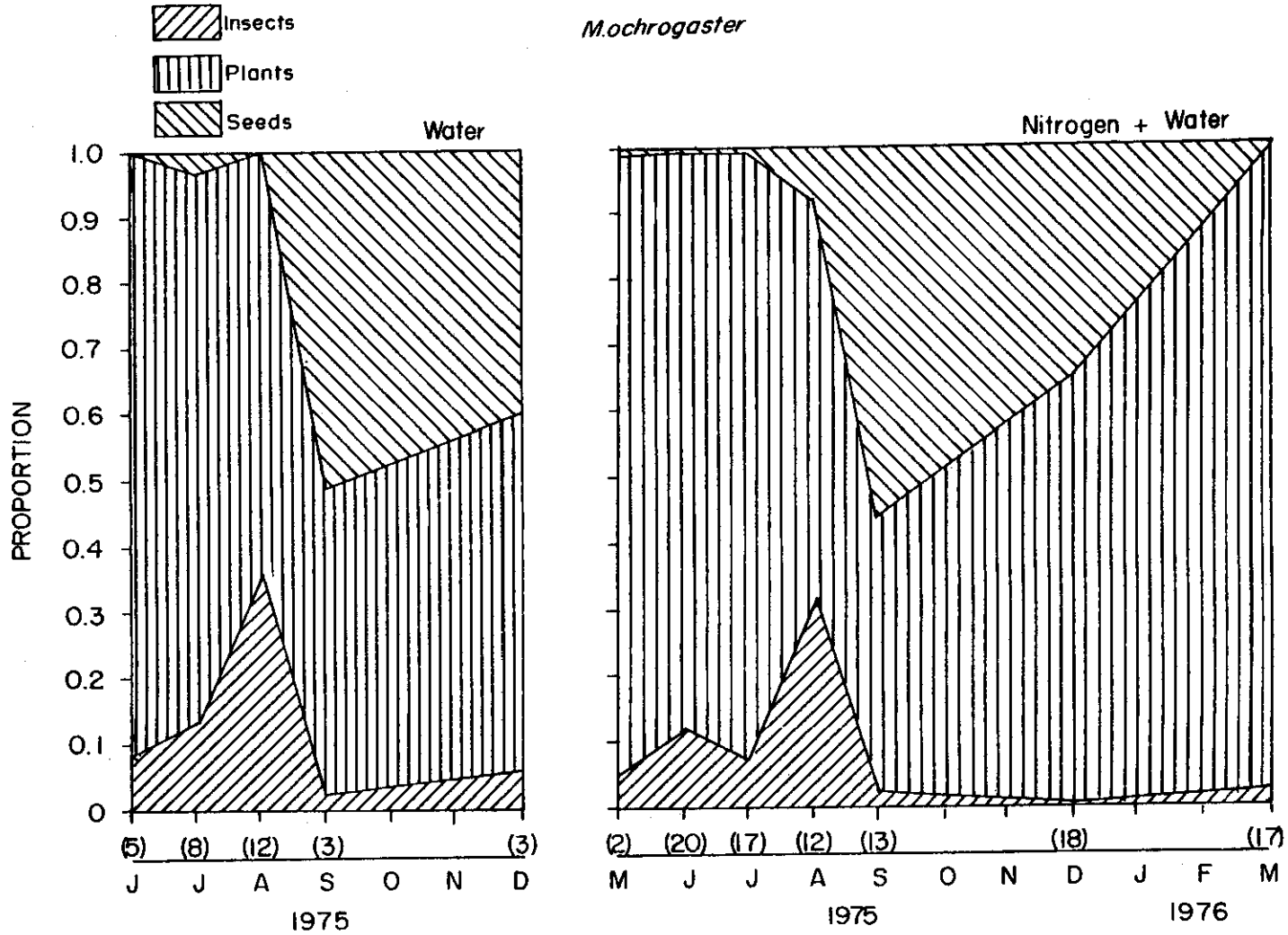


Fig. 11. Mean percent density of insects, plants, and seeds in the diet of *M. ochrogaster* during the study period. The numbers in parentheses represent the number of individuals from which

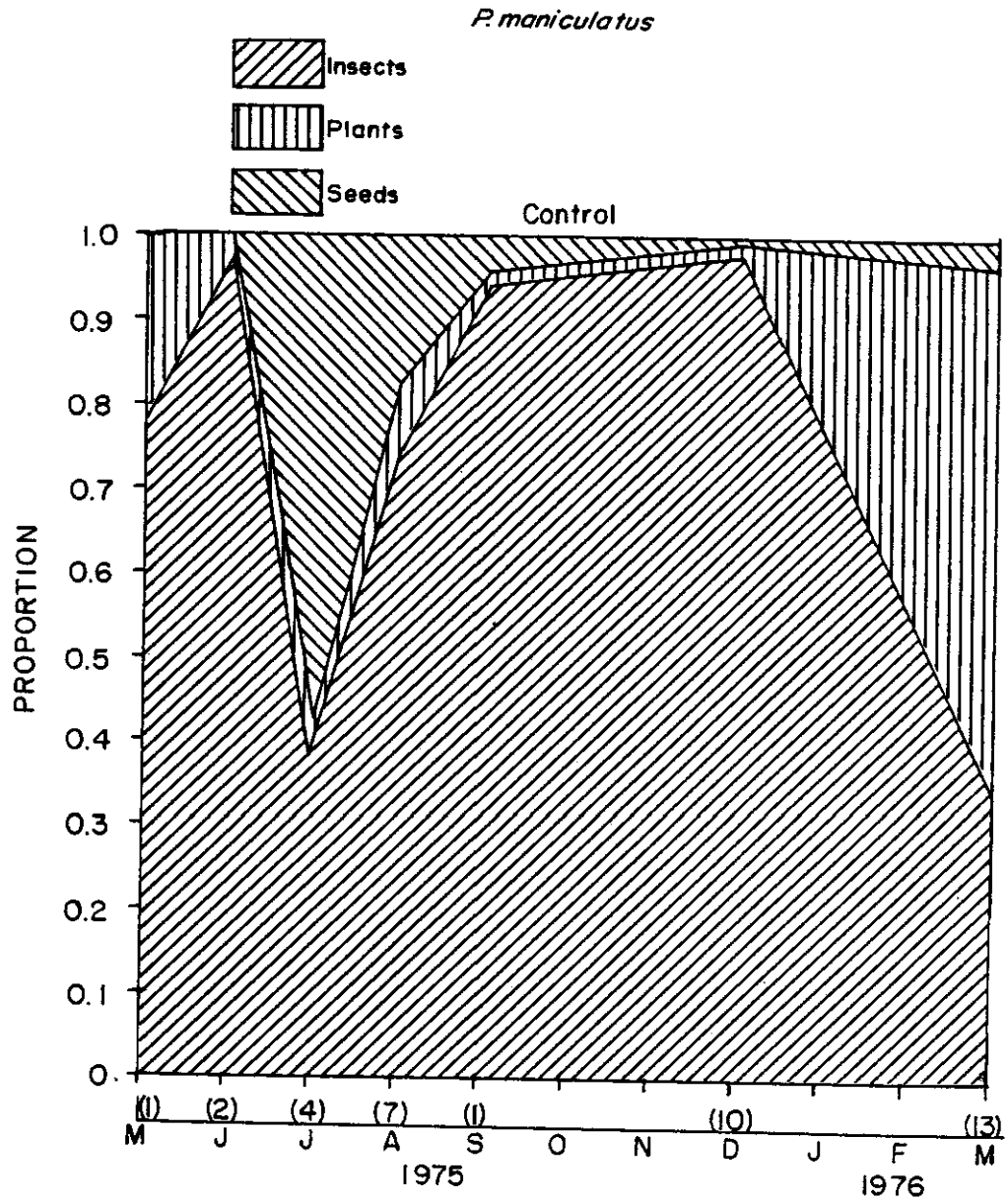


Fig. 12. Mean percent density of insects, plants, and seeds in the diet of *P. maniculatus* in the control treatment. The numbers in parentheses represent the number of individuals from which feces were collected.

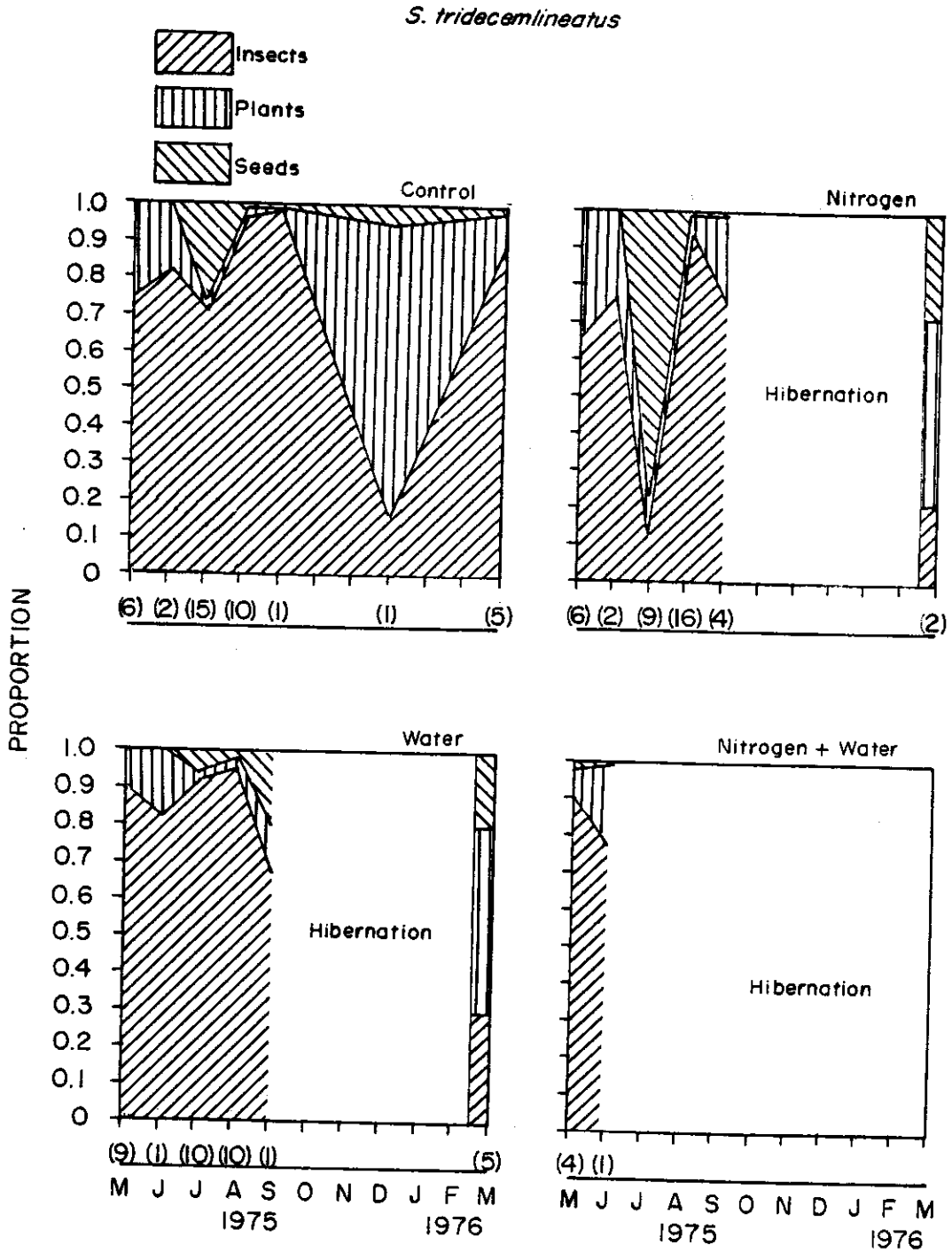


Fig. 13. Mean percent density of insects, plants, and seeds in the diet of *S. tridecemlineatus*. The numbers in parentheses represent the number of individuals from which feces were collected.

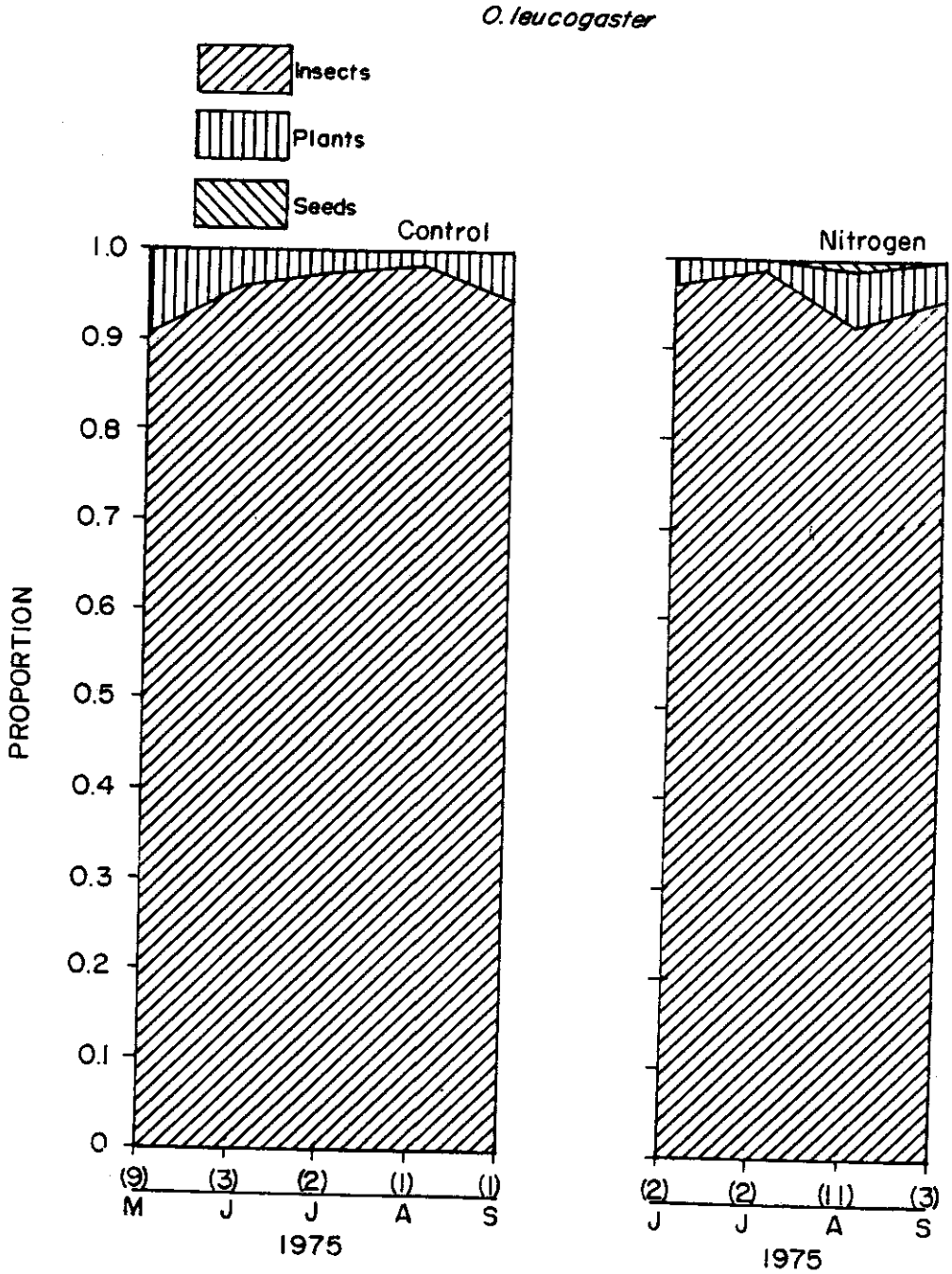


Fig. 14. Mean percent density of insect, plants, and seeds in the diet of *O. leucogaster*. The numbers in parentheses represent the number of individuals from which feces were collected.

The diet of the other members of the community changed considerab between sample dates (Figs. 11-14). By and large, it seems that most species overlap to a relatively great extent, at least during one or more sampling dates. For example, *M. ochrogaster*, which is primarily herbivore (Baker 1971), was found to take up to 40% insects in August 1975 (Fig. 11), and thus, exhibited a considerable amount of diet over lap with the more insectivorous species (e.g., *P. maniculatus* (Fig. 12 *S. tridecemlineatus* (Fig. 13), and *O. leucogaster* (Fig. 14)). Also, a the species, except *O. leucogaster*, were found to consume a relatively high proportion of seeds. *S. tridecemlineatus* usually hibernates duri the winter; however, a few individuals were active in December on the control treatment and their diet consisted of an unusually high propor tion of plant material (Fig. 13).

Under the assumption that the food was limited, and in the light the somewhat high degree of diet overlap exhibited by the species in some periods, interspecific competition for food may have been importa in determining the species distribution.

Fecal analysis is the best method to study the diet habits of a small mammal population when its dynamics is under investigation, sinc part of the population cannot be sacrificed for stomach analyses. However, differences in digestibility rate of different species may create a bias when comparing diets of different species. Because no other data were available, I assumed that the bias in the estimated proportions of the different prey species was of the same magnitude an direction for all the small mammal species and diet components. Thus, treated the proportion determined by the fecal analysis as the correct proportion of food taken.

Interspecific Competition

All food categories from each of the sampling periods were used to calculate competition indices using Levins' (1968) formula (Table 4, fo formula see Methods). Competition coefficients for habitat were also calculated with Levins' (1968) formula (Table 4). Competition coefficients for habitat were calculated for each sampling date, using the densities of the various species known to be alive in the different treatments. Thus, for each sample date the habitat competition, which was estimated across the habitats, measures the degree of competition between species over all the habitats. The food competition, on the other hand, measures the competition for food between species in each of the four treatments. However, the estimated competition indices measure only the potential competition between species in two different dimensions of the ecological niche. The realized competition between the species is some combination of both dimensions (Cody 1974, May 1975). This is because competition between species having similar diets, but utilizing different habitats, is low, and conversely, the competition between species that utilize similar habitats, but have different diets is also low. Because it was found that individuals of the same species usually had similar diet regardless of the habitat utilized (Table 5), the two measured dimensions of the ecological niche were assumed to be independent.

When the two dimensions of the habitat are independent, the realized competition between species is calculated by taking the product of the two competition matrices *elements* (May 1975). The result of the product competition elements is presented in Table 6. For each treatment and date, mean competition value of the community, computed as the

Table 4. Habitat (α_H) and food (α_F) competition calculated using Levins (1968) equation. For further information see text.

Date	Species	Habitat					Food														
							Control			Nitrogen				Water				Nitrogen + Water			
		1[a]	2	3	4	5	2	3	4	2	3	4	5	1	2	3	5	1	2	3	5
May	1 *Microtus ochrogaster*	1.00	0.32	0.45		0.96								1.00	0.05[†]	0.06[†]		1.00	0.23	0.05	0.01
	2 *Peromyscus maniculatus*	0.12	1.00	0.80		0.11	1.00	0.50		1.00	0.43			0.06[†]	1.00	0.23		0.12	1.00	0.33	0.00
	3 *Spermophilus tridecemlineatus*	0.14	0.67	1.00		0.12	0.34	1.00		0.25	1.00			0.06[†]	0.21	1.00		0.02	0.27	1.00	0.01
	5 *Reithrodontomys megalotis*	1.04	0.31	0.41		1.00												0.01	0.00	0.05	1.00
June	1 *Microtus ochrogaster*	1.00	0.42	0.40	0.00	0.89								1.00	0.05	0.06		1.00	0.18	0.27	0.01
	2 *Peromyscus maniculatus*	0.18	1.00	0.98	0.40	0.10	1.00	0.36	0.39	1.00	0.85	0.16		0.06	1.00	0.42		0.24	1.00	0.66	0.00
	3 *Spermophilus tridecemlineatus*	0.18	1.02	1.00	0.38	0.10	0.54	1.00	0.09	0.83	1.00	0.14		0.06	0.35	1.00		0.59	1.07	1.00	0.00
	4 *Onychomys leucogaster*	0.00	0.59	0.54	1.00	0.00	0.43	0.07	1.00	0.24	0.22	1.00									
	5 *Reithrodontomys megalotis*	1.11	0.29	0.27	0.00	1.00												0.09	0.00	0.00	1.00
July	1 *Microtus ochrogaster*	1.00	0.00	0.14	0.00	1.31								1.00		0.01	0.03	1.00		0.14[†]	0.01
	2 *Peromyscus maniculatus*	0.00	1.00	1.14	0.60	0.00	1.00	1.02	0.23												
	3 *Spermophilus tridecemlineatus*	0.05	0.37	1.00	0.48	0.44	0.67	1.00	0.38		1.00	0.12	0.84	0.03		1.00	0.06	0.29		1.00	0.00
	4 *Onychomys leucogaster*	0.00	0.33	0.80	1.00	0.44	0.50	1.25	1.00		0.08	1.00	0.00								
	5 *Reithrodontomys megalotis*	0.53	0.00	0.49	0.30	1.00					1.17	0.00	1.00	0.16		0.11	1.00	0.09		0.00[†]	1.00
August	1 *Microtus ochrogaster*	1.00	1.001	0.05	0.00	0.92								1.00		0.80		1.00			0.14
	2 *Peromyscus maniculatus*	0.00	1.00	1.04	0.77	0.00	1.00	0.14	0.48												
	3 *Spermophilus tridecemlineatus*	0.02	0.36	1.00	0.73	0.00	0.19	1.00	0.13		1.00	0.25		0.01		1.00					
	4 *Onychomys leucogaster*	0.00	0.40	1.10	1.00	0.00	1.14	0.24	1.00		0.50	1.00									
	5 *Reithrodontomys megalotis*	1.07	0.00	0.00	0.00	1.00												0.97			1.00
Sept.	1 *Microtus ochrogaster*	1.00	0.72	0.02	0.00	0.98								1.00	0.05	0.58		1.00	0.06		0.56
	2 *Peromyscus maniculatus*	0.34	1.00	0.77	0.58	0.33	0.10	0.53	0.34					0.07	1.00	0.46		0.07	1.00		0.94
	3 *Spermophilus tridecemlineatus*	0.01	0.58	1.00	0.74	0.00	0.31	1.00	0.50		1.00	0.78		0.30	0.17	1.00					
	4 *Onychomys leucogaster*	0.00	0.64	1.06	1.00	0.00	0.62	1.54	1.00		0.86	1.00									
	5 *Reithrodontomys megalotis*	1.02	0.73	0.00	0.00	1.00												1.47	0.08		1.00
Dec.	1 *Microtus ochrogaster*	1.00	0.13	0.59	0.00	1.06				1.00				1.00	0.01		0.41	1.00	0.01		0.36
	2 *Peromyscus maniculatus*	0.04	1.00	0.47	0.37	0.07	1.00	0.01	0.11		1.00			0.02	1.00			0.01	1.00		0.00
	3 *Spermophilus tridecemlineatus*	0.00	1.17	1.00	1.00	0.36	0.01	1.00	1.16			1.00									
	4 *Onychomys leucogaster*	0.00	1.17	1.20	1.00	0.00	0.07	0.81	1.00				1.00								
	5 *Reithrodontomys megalotis*	0.54	0.17	0.55	0.00	1.00								1.49			1.00	1.32	0.00		1.00
March	1 *Microtus ochrogaster*	1.00	0.41	0.14	0.00	1.16												1.00	1.62	0.05[†]	0.01
	2 *Peromyscus maniculatus*	0.12	1.00	0.90	0.40	0.19	1.00	0.71	0.11[†]	1.00	0.74		0.04		1.00	0.73	0.04	0.44	1.00	0.33[†]	0.04
	3 *Spermophilus tridecemlineatus*	0.04	0.99	1.00	0.39	0.11	0.92	1.00	1.16	0.76	1.00		0.28		0.53	1.00	0.20	0.02[†]	0.27[†]	1.00	0.01[†]
	4 *Onychomys leucogaster*	0.00	1.37	1.21	1.00	0.00	0.07[†]	0.81[†]	1.00												
	5 *Reithrodontomys megalotis*	0.85	0.47	0.25	0.00	1.00				0.18	1.28		1.00		0.18	1.27	1.00	0.01	0.18	0.05[†]	1.00

[a]The column species is corresponding to the numbered species in each date.

[†]No fresh pellets were available; the competition coefficient was estimated by averaging the coefficients obtained at time t - 1 and t + 1 when both were available. When only one was available, the same coefficient was used.

Table 5. The degree of intraspecific similarity between diets of *S. tridecemlineatus*, *M. ochrogaster*, and *O. leucogaster* on the different treatments. Similarity indices were calculated using Whittaker (1952) index of similarity. (C = Control, N = Nitrogen, W = Water, NW = Nitrogen + Water).

Treatment	May 1975				June 1975				July 1975			
	C	NW	N	W	C	NW	N	W	C	NW	N	W
S. tridecemlineatus												
W	0.71	0.71	0.62		0.17	0.24	0.22		0.62	--*	0.19	
C	--	0.74	0.78		--	0.20	0.49		--	--	0.41	
NW	--	--	0.59		--	--	0.63		--	--	--	
O. leucogaster												
C			--				0.74				0.54	
M. ochrogaster												
NW				--				0.47				0.60

Treatment	August 1975				September 1975				December 1975				March 1976			
	C	NW	N	W	C	NW	N	W	C	NW	N	W	C	NW	N	W
S. tridecemlineatus																
W	0.57	0	0.63		0.59	--	0.57		--	--	--		0.60	--	0.65	
C	--	--	0.84		--	--	0.56		--	--	--		--	--	0.59	
NW	--	--	--		--	--	--		--	--	--		--	--	--	
O. leucogaster																
C			0.94				0.37				--				--	
M. ochrogaster																
NW				0.53				0.80				0.80				0.64

*The calculation of diet overlap was not possible because the species was absent from one of the compared treatments, both treatments, or fresh fecal pellets were not available.

Table 6. The community matrices obtained on the different treatments during the study period. Competition coefficients are α_F - α_N of Table 4.

Date	Species	Control				Nitrogen					Water					Nitrogen and water				
		2*	3	4	ā†	2	3	4	5	ā	1	2	3	5	ā	1	2	3	5	ā
May	1 *Microtus ochrogaster*										1.00	0.02	0.03	**		1.00	0.07	0.02	0.01	
	2 *Peromyscus maniculatus*	1.00	0.40			1.00	0.34				0.01	1.00	0.18			0.01	1.00	0.26	0.00	
	3 *Spermophilus tridecemlineatus*	0.23	1.00		*0.32*	0.17	1.00			*0.26*	0.01	0.14	1.00		*0.07*	<.01	0.18	1.00	<.01	*0.05*
	5 *Reithrodontomys megalotis*																			
June	1 *Microtus ochrogaster*															0.01	0.00	0.02	1.00	
	2 *Peromyscus maniculatus*	1.00	0.35	0.16		1.00	0.83	0.06			1.00	0.02	0.02			1.00	0.08	0.11	0.01	
	3 *Spermophilus tridecemlineatus*	0.55	1.00	0.03	*0.23*	0.85	1.00	0.05		*0.34*	0.01	1.00	0.41			0.04	1.00	0.65	0.00	
	4 *Onychomys leucogaster*	0.25	0.04	1.00		0.14	0.12	1.00			0.01	0.36	1.00		*0.14*	0.11	1.09	1.00	0.00	*0.18*
	5 *Reithrodontomys megalotis*																			
July	1 *Microtus ochrogaster*															0.10	0.00	0.00	1.00	
	2 *Peromyscus maniculatus*	1.00	1.16	0.14							1.00		0.001	0.04		1.00		0.00	1.00	
	3 *Spermophilus tridecemlineatus*	0.25	1.00	0.18	*0.48*		1.00	0.06	0.38											
	4 *Onychomys leucogaster*	0.17	1.00	1.00			0.06	1.00	0.00	*0.18*	0.001		1.00	0.03	*0.03*	0.02		1.00	0.00	
	5 *Reithrodontomys megalotis*						0.57	0.00	1.00											*0.02*
August	1 *Microtus ochrogaster*										0.08		0.05	1.00		0.05		0.00	1.00	
	2 *Peromyscus maniculatus*	1.00	0.15	0.37							1.00		0.00			1.00			0.13	
	3 *Spermophilus tridecemlineatus*	0.07	1.00	0.10	*0.84*		1.00	0.18		*0.38*										
	4 *Onychomys leucogaster*	0.46	0.26	1.00			0.55	1.00			0.001		1.00		*0.00*					*0.69*
	5 *Reithrodontomys megalotis*																			
Sept.	1 *Microtus ochrogaster*															1.04			1.00	
	2 *Peromyscus maniculatus*	1.00	0.41	0.20							1.00	0.04	0.01			1.00	0.04		0.55	
	3 *Spermophilus tridecemlineatus*	0.003	1.00	0.37	*0.50*		1.00	0.58		*0.75*	0.02	1.00	0.35			0.02	1.00		0.01	
	4 *Onychomys leucogaster*	0.41	1.63	1.00			0.91	1.00			0.003	0.10	1.00		*0.09*					*0.36*
	5 *Reithrodontomys megalotis*																			
Dec.	1 *Microtus ochrogaster*					1.00										1.50	0.06		1.00	
	2 *Peromyscus maniculatus*	1.00	0.005	0.04			1.00				1.00	0.001		0.44		1.00	0.001		0.38	
	3 *Spermophilus tridecemlineatus*	0.01	1.00	1.16	*0.35*			1.00		*0.00*	0.001	1.00		0.00		<.01	1.00		0.00	
	4 *Onychomys leucogaster*	0.08	0.81	1.00											*0.39*					*0.27*
	5 *Reithrodontomys megalotis*								1.00											
March	1 *Microtus ochrogaster*										1.38	0.00		1.00		1.26	0.00		1.00	
	2 *Peromyscus maniculatus*	1.00	0.64	0.04		1.00	0.67		0.008							1.00	0.66	0.007	0.06	
	3 *Spermophilus tridecemlineatus*	0.91	1.00	0.45	*0.52*	0.75	1.00		0.03	*0.17*		1.00	0.66	0.01		0.05	1.00	0.30	0.008	
	4 *Onychomys leucogaster*	0.10	0.98	1.00								0.53	0.10	0.02	*0.27*	0.001	0.27	1.00	0.001	*0.12*
	5 *Reithrodontomys megalotis*					0.09	0.32		1.00			0.09	0.32	1.00		0.01	0.09	0.01	1.00	

*The column species is corresponding to the numbered species in each date.

†The interaction value for the community.

sum of the competition coefficients over the number of competition coefficients, was also calculated (Table 6). The mean competition valu represents the degree of interactions between all the community members (Lane 1975).

The values of the competition coefficients and the mean competitio value for the communities varied from treatment to treatment as could b expected from the observed species distribution (Table 2). However, th striking result was that the competition coefficients between most species pairs, in each of the treatments, also varied to a great extent from one sampling date to another (Table 6). The fact that competition coefficients between species pair may vary with time is an important aspect ignored by many scientists. From the long list of studies on competition known to me, only one paper considers the temporal variability of the competition coefficients (Lane 1975). Studies that concentrate on one season of the year can, thus, lead to incorrect conclusions on the degree of interaction between species.

MacArthur and Levins (1967) have suggested a theoretical limit of similarity between species beyond which coexistence is impossible. The limiting similarity is approached when similar normal distributions of resource utilization for two species have means which are displaced by one standard deviation (May and MacArthur 1972). Two such distributions have an overlap value of approximately 0.6 (May and MacArthur 1972).

The results presented in this study support the prediction that resources are not necessarily limiting through all seasons of the year (Fretwell 1972; J. A. Wiens, pers. comm.). Therefore, the competition coefficients may vary from low values (<0.6) indicating nonlimiting resources, to high values (>0.6) which probably indicate limiting

resources. The opposite may also be correct; during periods in which the resources are superabundant high ecological overlap is possible, and, conversely, during periods of resource shortage the ecological overlap is low. Schoener (1974b) has suggested a method to calculate the degree of competition between a species pair when the abundance o the resources is also considered. Unfortunately, this index could no be calculated because not all the food categories in the environment were sampled. Also, because only the energy stored in the resources known, rather than the quality of the resources, a calculation of thi index would be less than fully useful (see also Discussion below).

Although most of the competition coefficients were relatively small, some were quite large (Table 6). This suggests that the syste is unstable. To investigate the stability of the small mammal commur ties I generated one competition matrix for each treatment. The elements of these competition matrices consisted of the highest competit value recorded for each species pair in each treatment during the stu (Table 7). Thus, each of the four matrices contains a "bottleneck" (Fretwell 1972) for the interaction between species. Stability analy (May 1973) conducted on these competition matrices indicated that all the communities were not stable. This result, indicating that the co munities are unstable, is supported by the transient nature observed the species composition and abundance (Table 2), and the fact that so species exhibited high competition coefficients.

It is questionable if food was limiting at any time during the study. Grant et al. (1976) estimated that between 1971 and 1974 the total monthly consumption of plant material by small mammals never exceeded 4% of the standing crop on the same treatments studied in th

Table 7. Yearly competition matrices. The elements of each matrix are the highest competition value recorded for each species pair in each treatment during the study.

Species	Competition matrix*			
	1	2	3	4
Control				
1 *P. maniculatus*	1	1.16	0.37	
2 *S. tridecemlineatus*	0.91	1	1.16	
3 *O. leucogaster*	0.46	1.63	1	
Nitrogen				
1 *P. maniculatus*	1	0.83	0.06	0.01
2 *S. tridecemlineatus*	0.85	1	0.58	0.38
3 *O. leucogaster*	0.14	0.91	1	0.00
4 *R. megalotis*	0.09	0.57	0.00	1
Water				
1 *M. ochrogaster*	1	0.02	0.03	0.44
2 *P. maniculatus*	0.02	1	0.66	0.01
3 *S. tridecemlineatus*	0.01	0.53	1	0.03
4 *R. megalotis*	1.38	0.09	0.32	1
Nitrogen + water				
1 *M. ochrogaster*	1	0.66	0.11	0.55
2 *P. maniculatus*	0.05	1	0.65	0.01
3 *S. tridecemlineatus*	0.11	1.09	1	<.01
4 *R. megalotis*	1.50	0.09	0.02	1

*The column species is corresponding to the numbered species on each treatment.

present work. Monthly consumption of arthropods ranged from less than 1% to 34% of the arthropod standing crop (Grant et al. 1976). Similar results were obtained in other studies on the energetics of small mamm communities (Chew and Chew 1970, French et al. 1976). However, the above studies took into consideration only the energy demands of the small mammals and the energy stored in the plants and arthropods. Othe factors like nutrition (Pulliam 1975) may have been in limited supply. Grant et al. (1976) report that wild *Microtus* could not survive when they were brought to the laboratory and fed only forage that had over-wintered.

Thus, it seems that although from an energetic point of view small mammals are probably not food limited, other factors such as the amount of nutrients may be in short supply.

The niche breadth, a measure of the degree of generalization of species (Lane 1975), can be used to investigate the importance of compe tition for food between the species. If competition for food was an important factor, we might expect to find differences in the food niche breadth of a species (Table 8) when its competitor was present (partial niche) or absent (fundamental niche) (Vandermeer 1972). This type of analysis could be done with limitations for two species in this study: for *S. tridecemlineatus* when *O. leucogaster* was present or absent, and for *M. ochrogaster* when the combined individuals of two species, *P. maniculatus* and *R. megalotis*, were abundant or rare. In both cases, th niche breadths of the species were significantly smaller (t-test, $P < 0.02$) when the competitor was present than when it was absent (Tables 9 and 10). A similar type of niche breadth shifts in the presence of a competitor was observed in lizards (Schoener 1969, 1970; Jenssen 1973)

Table 8. Diet diversity (H') and niche breadth (B) based on diet of the small mammal species on the differen treatments.

Month	Treatment	*Peromyscus maniculatus* *		*Microtus ochrogaster*		*Spermophilus tridecemlineatus*		*Onychomys leucogaster*		*Reithrodontomys megalotis***	
		H'	B	H'	B	H'	B	H'	B	H'	B
May	Control	1.45	4.25			1.84	6.29				
	Nitrogen	1.45	4.25			2.02	7.54				
	Water	1.45	4.25			1.65	5.18				
	Nitrogen + water	1.45	4.25	0.99	2.70	1.63	5.12			0.06	1.06
June	Control	1.32	3.75			1.29	3.65	1.53	4.60		
	Nitrogen	1.32	3.75			1.46	4.29	1.20	3.31		
	Water	1.32	3.75	1.67	5.31	1.79	5.98				
	Nitrogen + water	1.32	3.75	1.77	5.85	1.14	3.12			0.06	1.06
July	Control	1.26	3.52			1.54	4.65	0.48	1.61		
	Nitrogen					0.67	1.95	0.76	2.14	0.06	1.06
	Water			2.31	10.07	1.01	2.75			0.06	1.06
	Nitrogen + water			2.12	8.32					0.06	1.06
August	Control	1.37	3.94			1.22	3.40	0.63	1.88		
	Nitrogen					1.36	3.91	0.74	2.09		
	Water			1.86	6.42	1.45	1.45	4.24			
	Nitrogen + water			2.28	9.79					0.06	1.06
September	Control	0.86	2.36			1.49	4.42	0.32	1.37		
	Nitrogen					1.79	5.99	1.34	3.82		
	Water	0.86	2.36	1.35	3.87	1.88	6.54				
	Nitrogen + water	0.86	2.36	1.32	3.73					0.06	1.06
December	Control	0.50	1.64			0.66	1.93	1.09	2.96		
	Nitrogen									0.06	1.06
	Water	0.50	1.64	1.60	4.97					0.06	1.06
	Nitrogen + water	0.50	1.64	1.54	4.68						
March	Control	1.92	6.85			1.74	5.71				
	Nitrogen	1.92	6.85			1.88	6.52			0.06	1.06
	Water	1.92	6.85			2.12	8.33			0.06	1.06
	Nitrogen + water	1.92	6.85	0.55	1.74					0.06	1.06

*The diet of *Peromyscus maniculatus* on all the treatments was assumed to be similar to the diet on the control (for further information see text).

**The diet of *Reithrodontomys megalotis* was assumed to be constant on all treatments during the study (for further information see text).

Table 9. Comparison of the average diet diversities and average niche breadths of *S. tridecemlineatus* when *O. leucogaster* was present (standard error in parentheses).

Species		N	Niche breadth	Diversity
O. leucogaster	Present	9	3.80 (0.42)	1.27 (0.12)
O. leucogaster	Absent	4	6.51 (0.38)	1.87 (0.06)
t-test value			3.87	2.97
P			0.003	0.013

Table 10. Comparison of the average diet diversities and average niche breadths of *M. ochrogaster* on the nitrogen + water treatment when the combined number of individuals of *R. megalotis* and *P. maniculatus* were abundant ($\geq$11) or rare ($\leq$4) (standard error in parenthesis).

Species		N	Niche breadth	Diversity
R. megalotis	Abundant	4	3.74 (0.93)	1.21 (0.27)
R. megalotis	Rare	2	9.06 (0.73)	2.20 (0.08)
t-test value			3.62	2.38
P			0.023	0.076

and birds (Werner and Hull 1976). Unfortunately, in both cases the change in the niche breadth by species in this study could have resulte from a seasonal change in food abundance. *O. leucogaster* was absent from both the nitrogen and the control treatments, and *R. megalotis* was absent from the nitrogen + water treatment only in the spring periods of both years. Note that in the spring the niche breadth of *S. tridecemlineatus* showed an increase in size while the niche breadth of *M. ochrogaster* showed a decrease in size. Thus, although the change in niche breadth may be a seasonal change, competition for food cannot be excluded. Furthermore, because the change in niche breadth was in opposite directions for the two species it seems likely that competition should be implicated in this change.

Even if food was always abundant and thus no competition for food occurred, interspecific competition still could have been important. P. R. Grant (1972) argued that competition for space also could be advantageous for the species. He claimed that natural selection should favor an overall reduced density in prey species utilized by a predator that exhibits numerical and functional response (Holling 1959). Reduced overall density will result from competitive interaction between such prey species which would lead to habitat selection. This is because the total density will be reduced when each species will be limited to one habitat. This type of competition will result in overall reduced overlap between habitat utilization of different species and may explain the distribution of the small mammal species observed in the present study. This type of relation has been experimentally shown to exist for *P. maniculatus* and *M. pennsylvanicus* (P. R. Grant 1972, 1976).

Furthermore, each species has a competitive advantage over the other species in its favorable environment (Grant 1976).

Further indirect evidence indicating that competition may be an important factor emerges in studies by Oftedahl (1976). Oftedahl artificially increased the vegetational structure and cover through th addition of straw and pine boughs to the shortgrass prairie. My experiment and that by Oftedahl were conducted simultaneously in a nearb area; similar vegetation occurred on my control plots and his plots. Neither *M. ochrogaster* nor *R. megalotis* invaded this experimental area Thus, it was possible to examine the impact of the presence of the two new species (and thus, perhaps, competition from these species) on the distribution and abundance of other species in my study area. No significant differences were found between the populations of *O. leucogaster* and *P. maniculatus* before and after the addition of the cover relative to the populations of these species on a control plot; however, there was a significant increase in the population density of *S. tridecemlineatus* on the cover treatment relative to the control treatment (Oftedahl 1976).

In my study the vegetation cover and structure was modified by the growth of the vegetation stimulated by the addition of nitrogen, water, or both. This increased biomass of vegetation, and thus, seed and insect biomass in my study also could be used as food which might allow higher population densities. However, the results of my study show a decrease in population numbers in two of the species (*P. maniculatus* an *S. tridecemlineatus*) which were rare on the nitrogen + water treatment. The third species (*O. leucogaster*) was absent from the water + nitrogen treatment throughout the study period. *P. maniculatus* was also less

common on both the nitrogen and the water treatments relative to the control treatment. *O. leucogaster* was absent from the water treatment and less common on the nitrogen treatment relative to the control treatment.

Another basic difference between my experiment and that of Oftedahl was that two treatments in my study were irrigated during the growing season (May through September). Thus, the reported differences in rodent communities could be explained in terms of differences in available moisture. However, if the difference in the amount of moisture between the two experiments was the only factor responsible for the habitat preferences exhibited by the species in my study and apparent lack of habitat preferences in Oftedahl's (1976) study, it seems reasonable that the difference should have disappeared during the 7 months when the treatments were not irrigated. The results in my study show that the differences in habitat utilization between the species were consistent throughout the year and appear to be unexplainable solely in terms of the difference in the type of vegetation cover or irrigation.

Thus, I concluded that the difference in the small mammal communities formed on the four treatments was not only the result of the increase in vegetation cover and biomass, but also other factors, like interspecific competition, probably played an important role in determining the community structure.

The evidence suggests that habitat priorities *per se* cannot explain the observed distribution of the small mammal species studied. To test whether interspecific interaction might be more important than habitat priority in determining community composition, a new experiment would be needed. In this experiment the treatment should be replicated and

fenced enough times so that the survival of each species in all habita can be measured in absence of competition. Unfortunately, this type o experiment has not been done to date. However, at least for *M. ochrogaster* the information available in the literature is probably sufficient to allow assessment of the importance of habitat type on th distribution of this species. The relationship between *Microtus* populations and vegetation cover has been documented in several studie (Eadie 1953, Zimmerman 1965, Batzli 1968). *Microtus* species do not occur in heavily grazed rangeland (Martin 1956) nor in mown fields (LoBue and Darnell 1959), although they reinvaded after regrowth of th vegetation (Batzli 1968). Thus, I can assume that the invasion of *M. ochrogaster* in 1971 was a response to the increase in vegetation cover and biomass in the nitrogen + water treatment. Given the biological characteristics of *Microtus* (Baker 1971), it seems unreasonable that *M. ochrogaster* has not invaded the shortgrass prairie habitat because of competitive interaction with the other small mammal species that exist there. Nevertheless, Grant (1976) showed experimentally that in the absence of competition, *Microtus* invades suboptimal habitats. However, the same argument is probably incorrect in explaining the distribution of the "native" species. *S. tridecemlineatus* and *P. maniculatus* were extremely rare in the nitrogen + water treatment, and *O. leucogaster* wa completely absent in this treatment. *P. maniculatus* has been shown to utilize *Microtus* grassland habitat when *M. pennsylvanicus* was removed, but limited its activity to the woodland part of the exclosure when *Microtus* was reintroduced to the exclosure in moderate densities (P. R. Grant 1971, 1972). Grant's experiments support the assumption that

competition induced by *M. ochrogaster* limited the distribution of the "native" species.

An experiment in which the two invaders (*R. megalotis* and *M. ochrogaster*) to the nitrogen + water treatment are excluded is being conducted presently. The results of this experiment will support or refute the hypothesis that competition played an important part in determining the species distribution and abundance.

In summary, indirect evidence suggests that interspecific competition has played an important role in determining small mammal abundance and community composition in different stress plots. Indirect evidence also suggests that habitat priority *per se* probably was responsible also for the observed distributions. Thus, it was concluded that both factors, habitat selection and interspecific competition, were responsible for the observed distribution; the relative importance of each factor cannot be determined from the present data.

Food Supplement Experiment

The abundance of food as a regulatory mechanism in population dynamics has received considerable theoretical discussion (Lack 1954a, Hairston et al. 1960, Slobodkin et al. 1967, Ehrlich and Birch 1967). Field experiments have produced controversial results. Bendell (1959) has shown that addition of food increased the population density of *Peromyscus leucopus*. Smith (1971) concluded that supplementary food is an important limiting factor in the population dynamics of *Peromyscus polionotus*. Fordham (1971) also showed a similar response to excess of food by *P. maniculatus*. Lack of response to food addition was reported for *M. californicus* (Krebs and DeLong 1965) and for *P. maniculatus* in a shortgrass prairie habitat (Oftedahl 1976).

In the light of the inconsistency of results from food supplementation experiments and the importance attributed to competition for food an experiment was initiated in May 1975 in which alfalfa pellets and whole oats were added to a 1-ha plot (Fig. 2). If food were initially limiting, addition of alfalfa and oats should have resulted in competitive release, and thus, increased population densities. However, no significant difference was found between the density of the small mammals in the control and food plots (Table 11). This result may sugges that food was not an important factor and that the observed densities the small mammals on the food treatment were determined by other factors. However, this conclusion may be misleading because the three native species that inhabited the food treatment during the study are primarily insectivorous and take seeds in relatively small amounts. Thus, the results of the food experiment cannot be interpreted as lack of competition for food between the species. Rather, the type of food that was added to this treatment did not increase the major food type availability for these species. Because the "native" small mammal species did not utilize heavily the food added and because in the winte time other seed consumers are rare in the area, the new resource accumulated slightly during the winter months. However, in March 1976 a new species, *Dipodomys ordii*, invaded the area and persisted in relatively high densities through August 1976 when the experiment was terminated (Table 11). Other consumers such as insects and birds (principally Horned Larks, *Eremophila alpestris*) also took advantage of the added food, but because large quantities were added, it was always available.

D. ordii can be found in northeastern Colorado mainly in roadside ditches (Flake 1971; pers. obs.) and areas of shortgrass prairie

Table 11. Number of individuals of the existing species on the food enriched plot and the control grid.

Time	Food Enriched Grid				Control Grid[a]		
	P. maniculatus[b]	*S. tridecemlineatus*[c]	*O. leucogaster*[d]	*D. ordii*	*P. maniculatus*	*S. tridecemlineatus*	*O. leucogaster*
Pre-treatment							
May	4	3	3	0	4.5	2.5	0
June	2	7	1	0	1	2	1.5
July	0	5	1	0	2	5.5	0.5
August	0	2	3	0	2	5	1
Food added							
September	0	1	2	0	3.5	4	1
December	0	0	1	0	5	1	1.5
March	7	3	0	6	5	4.5	1
Early May	3	4	1	4	4	6.5	1
Late May	3	2	1	5	2	9	0
June	1	13	2	9	5	7	0
July	1	11	1	4	2	17	0
August	0	0	1	5	0	0	1
TOTAL	21	51	19	33	36	60.5	8.5

[a] Number of individuals for this comparison calculated as the average number in the two control grids.

[b] No significant differences between treatment and control $X^2 = 0.01$, $P > 0.90$.

[c] No significant differences between treatment and control $X^2 = 0.53$, $P > 0.25$.

[d] No significant difference between control and treatment before and after adding food, $X^2 = 0.01$, $P > 0.90$.

dominated by fourwing saltbush (*Atriplex canescens*) (pers. obs.). However, this species does not reside in other habitat types of the shortgrass prairie. An intensive summer trapping in the last five summers failed to catch resident *D. ordii* in the nearby control area (Fig. 2). Also, trapping around the food treatment during this study failed to catch individuals of this species. The individuals of *D. ordii* caught on the food treatment apparently used burrows inside the area since animals released from traps retreated to nearby barrows, a since there was an abundance of food and tail prints of *D. ordii* near the burrows in this plot. Also, because the individuals were marked, it was possible to determine that most individuals of *D. ordii* were resident in the area.

D. ordii is mainly a seed-eating species (Brown and Lieberman 19 Rosenzweig et al. 1975), and thus, it is not surprising that it responded to the excess of seed supplemented. Diet analysis confirmed that oats consisted of 95% of the individual's diet. Therefore, it w concluded that the invasion of *D. ordii* to the food treatment was mos likely a response to the addition of the seeds. If this conclusion i correct, most shortgrass prairie habitats are not inhabited by *D. ordi* because food (seeds) availability is insufficient to support stable populations of this species. Also, the seed addition increased the species diversity of the small mammals in this plot relative to the other treatments (Fig. 10). It is still unknown whether seed availability *per se* limits the distribution range of *D. ordii* in shortgrass prairie habitat, or whether the availability of seeds of a certain siz is the limiting factor. The latter seems to be the case because *D.*

ordii is found in northeastern Colorado in locations dominated by plants which produce large seeds.

The response of *D. ordii* to excess food increased the species diversity of the small mammals in this plot to values which were higher than the species diversities of the small mammals on the other treatments (Fig. 10). This result supports the findings of Rosenzweig (1973) and Brown (1973, 1975). They concluded that species diversity of desert granivorous rodents increases as a function of food availability.

In summary, I have presented evidence that is consistent with the hypothesis that the distribution of *D. ordii* in the study area and probably in most shortgrass prairie habitats is limited by seed availability. The three "native" species did not respond to increase in food abundance, probably because the type of the food supplemented is not utilized heavily by these species in natural habitats.

Summary and Conclusions

Studying animal community structure in perturbed systems offers a unique opportunity to gain insight into the functioning of these communities (Smith 1970, Barrett et al. 1976). This is because species that have evolved to coexist in a certain type of environment are suddenly faced with patches of very unusual habitats. In these patches differences in community composition may be easier to detect than in the more homogeneous natural habitat. Also, if the perturbation results in a very different habitat type, rare species that usually lived in a marginal subhabitat (Hairston 1959) may become dominant and influence the distribution and abundance of the dominant species in the natural habitat.

The present study reports the response of a small mammal communit in a shortgrass prairie habitat to habitat manipulation. Six 1-ha plo were manipulated since 1971 through the application of water, nitrogen or both. Two additional 1-ha plots which were natural shortgrass prairie served as control. The response of the small mammal species t the perturbations between 1971 and 1974 has already been reported (Gra et al. 1976). The present study was conducted in 1975 and 1976 and wa partly designed to understand the mechanisms causing the differences between species abundance and distribution reported by Grant et al. (1976).

The vegetation biomass and structure in the six 1-ha stress plots responded dramatically to the perturbation treatments. The highest re- sponse was recorded in the nitrogen + water treatment, and intermediat responses were recorded in the water and the nitrogen treatments. The vegetation response resulted in structural representatives of the natural gradient ranging from shortgrass prairie to habitat equivalent to tallgrass prairie. Thus, through the application of the stress treatments a local representation of habitats which otherwise can be found only on a large geographical area has formed.

Two new species of small mammals (*Microtus ochrogaster* and *Reithrodontomys megalotis*) have colonized the nitrogen + water treated areas. These two species usually inhabit only restricted patches in northeastern Colorado.

The three "native" species (*Peromyscus maniculatus*, *Spermophilus tridecemlineatus*, and *Onychomys leucogaster*) have responded differ- entially to the change in vegetation cover, biomass, and structure. Both processes, colonization by new species and the differential

response of the "native" species, appear to have caused the formation of different small mammal community compositions in the four treatments.

I assumed that two factors, habitat selection and interspecific competition, have determined the observed distribution, and I tried to analyze their relative importance.

The abundances of the species over the habitat gradient could be predicted by FHD; the "native" species abundances exhibited negative correlation with increased FHD, while the two "exotic" species exhibited positive correlation with FHD.

A negative correlation was found between species diversity and FHD. This result, which is different from what has been found in natural habitats (Rosenzweig and Winakur 1969), is interpreted in terms of colonization rates. Biogeographic as well as ecological factors might explain the inverse relation.

The importance of interspecific interaction was analyzed by calculating competition coefficients for the food and habitat dimensions of the ecological niche. A simple stability analysis revealed that all the communities studied were unstable. This result may explain why the communities fluctuated in terms of species abundance and composition. A comparison with another study (Oftedahl 1976) in which the habitat structure was also changed but the two "exotic" species did not invade suggests that interspecific competition played an important role in determining the observed species distribution and abundance. Although it was not possible to distinguish between the relative importance of habitat selection and interspecific competition, it was shown that both processes were probably co-acting.

The importance of food as a factor, which was responsible for population regulation, was investigated in a separate 1-ha plot to whi alfalfa pellets and whole oats were added on a 2-week schedule. None the three "native" species responded to the excess amount of food. However, a new species, *Dipodomys ordii* which usually cannot be found habitat types of the shortgrass prairie ecosystem, invaded the area an persisted in a relatively high population density. Because this speci was not trapped in the control plots or around the food treatment, it was concluded that the species invaded the area as a response to the excess amount of seed supplemented. This experiment validated the prediction that species diversity increases when the productivity increases (Brown 1973, 1975; Rosenzweig 1973). This experiment also suggests that seed abundance is probably the factor that limits the distribution of *D. ordii* in some habitats of the shortgrass prairie.

Interspecific competition, habitat selection, and food abundance represent only three mechanisms suggested to account for species abundance and distribution. Only *Microtus ochrogaster* was abundant enough to allow investigation of other factors which may regulate the population abundance.

MICROTUS POPULATION DYNAMICS

Many hypotheses have been suggested recently to account for fluctuations in small mammal population densities. Cole (1954) has postulated that the changes in population density can be explained by random events. Elton (1925) suggested that fluctuations are caused by disease outbreaks at dense population, and later he (Elton 1929) argued that weather may be responsible. Lack (1954b) reasoned that fluctuations are caused by food shortages at peak population, and that these shortages cause mortality. Later Pitelka (1964), Batzli and Pitelka (1970), Batzli (1975) and others postulated that microtine populations, at peak densities, deplete the available nutrition in the plant food resulting in population declines. Pearson (1964, 1966, 1971) suggested that mammalian carnivore predation during a crash and especially during the early stages of the subsequent population low determines to a large extent the amplitude and timing of the microtine cycle of abundance.

Christian and Davis (1964) claimed that phenotypic changes are adequate to explain why populations decline. They suggested that endocrine feedback mechanisms can regulate and limit population growth in response to increase in overall "social pressure." Chitty (1967), on the other hand, argued that hypotheses involving predation, endocrine imbalance, disease, or food depletion were insufficient to explain cyclic changes in vole population density. He proposed that cyclical fluctuations are due to changes in the selective advantages of certain genotypes as density changes. He contended that as the population increases, so does mutual interference. Thus, selection favors aggressive genotypes at the expense of other components of fitness, especially viability. Consequently, the aggressive types are more susceptible to

nonspecific mortality factors, and this susceptibility sets the stage for the population decline. Krebs and his students (Krebs 1964, 1966; Krebs et al. 1969, 1976) have presented inconclusive evidence in favor of Chitty's hypothesis. Recently Freeland (1974) hypothesized that the loss of individuals from vole population at peak densities is the direc result of reduced viability induced by the consumption of plants or plant parts containing toxic compounds. This hypothesis was challenged by Batzli and Pitelka (1975) and by Schlesinger (1976).

Although each of the above hypotheses seems to offer an explanatic for the cyclic changes in population density, none of them can explain all the observed events during the cycle, and probably more than one of the discussed mechanisms is responsible for the cyclical phenomenon (Lidicker 1973, Wilson 1975).

The purpose of this paper is not to offer a new hypothesis. Rather, I want to point to some difficulties in interpreting and comparing the results obtained from studying noncyclic population of *M. ochrogaster* in manipulated shortgrass prairie with the recent theories and intensive field work conducted by Chitty and Krebs.

Results

Population Status

The total number of individuals known to be alive on the two replicates of the nitrogen + water treatment since 1971 is presented in Fig. 15a. Although no winter trapping has been conducted between 1971 and 1974, it seems that the data represent the dynamics of the two populations of *M. ochrogaster*. This is because the two populations showed a fairly uniform pattern of population changes with peaks in late summer

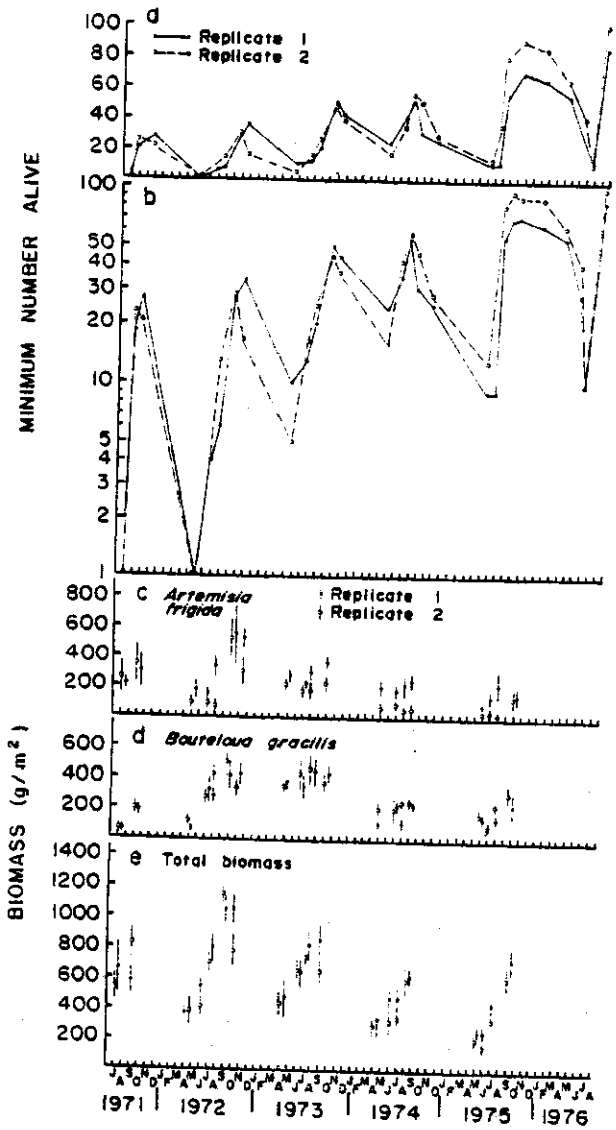


Fig. 15. Minimum number of individuals of *M. ochrogaster*, mean biomass of *B. gracilis*, *A. frigida*, and total plant biomass in the two replicates of the nitrogen + water treatment. The data of Grant et al. (1976) were used to reconstruct the population density of *M. ochrogaster* between 1971 and 1974. The vertical lines represent the standard error.

or fall and minimum numbers in April and May. In April of 1974 the minimum sizes of the two populations were somewhat larger than the minima for all other years. This relatively higher density could repre sent the real minimum of this spring or it could be that by the time th sample was taken the two populations were already increasing after an earlier minimum in this year.

The general picture of the dynamics of the two populations is that of fairly regular annual fluctuation with peaks in late summer and lowest density in late spring. No other multi-year fluctuations of 2-t 4-year cycle, which are so common in microtines, could be detected. Every year the two populations declined to approximately the same minim size (Fig. 15a). Indeed, regression analysis of the minimum population size, as a function of year, produced slopes that were not significantl different from zero ($P = 0.33$ in replicate 1 and $P = 0.09$ in replicate

The level of populations after the nonbreeding season has been termed "primary density" by Varshavskii et al. (1948). Martin (1956) reported that in a 2-year study of *M. ochrogaster* in northeastern Kansa the population declined to a similar density after the nonbreeding seasons. However, in Martin's study which was conducted in tallgrass prairie (Table 12) the "primary density" was much higher than the one observed in the present study (50 and 16 individuals, respectively).

Another characteristic of the population dynamics was the progressively linear increase in peak population abundances from year to year during the study period (Fig. 16), though the two populations were growing at different rates ($t = 2.46$, $P = 0.04$). Hamilton (1937) and Hoffman (1958) also found a progressive yearly increase in population peak densities in *M. pennsylvanicus* and *M. californicus*, although in

Table 12. Locality, habitat, and population status of *Microtus* referenced extensively in this report.

Species	Locality	Habitat	Status	Reference
M. ochrogaster *M. pennsylvanicus*	Southern Indiana	Tallgrass	Cycling	Krebs et al. (1969) Gains and Krebs (1971) Gains et al. (1971) Myers and Krebs (1971a) Krebs (1970) Keller and Krebs (1970)
M. ochrogaster	Northeastern Kansas	Tallgrass	Cycling	Martin (1956) Fitch (1957)
M. pennsylvanicus	Manitoba, Canada	Old field	Cycling	Iverson and Turner (1974)
M. pennsylvanicus	Ithaca, New York	Grassland	Cycling	Hamilton (1937)
M. pennsylvanicus	Southern Indiana	Tallgrass	Cycling	Krebs et al. (1973)
M. californicus *M. montanus*	Northern California	Annual grassland Mountain meadows	Cycling	Hoffman (1958)
M. californicus	Northern California	Annual grassland and weeds	Cycling	Pearson (1960, 1964, 1966, 1971)
M. californicus	Northern California	Annual grassland	Cycling	Batzil (1968) Krebs (1966) Krebs and DeLong (1965) Batzli and Pitelka (1970, 1971)
M. californicus	Brooks Island	Annual grassland	Cycling	Lidicker (1973)
M. townsendii	British Columbia	Grassland	Cycling	Krebs et al. (1976)
M. agrestis *C. glareolus*	England	Grassland	Cycling	Chitty and Phipps (1966) Chitty (1952, 1967)
M. oeconomus	Alaska	Taiga	Cycling	Whitney (1973)

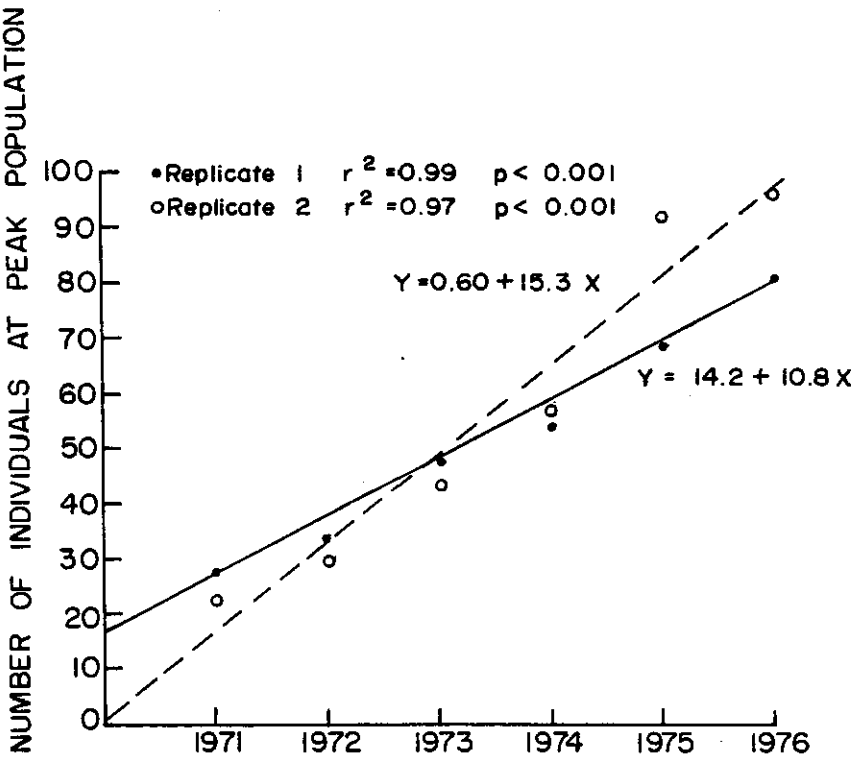


Fig. 16. Number of *M. ochrogaster* individuals known to be alive at peak populations between 1971 and 1976. The two slopes are significantly different (P = 0.04).

both studies the progressive increase in density was within a defined cycle. (For locality and habitat used in the above studies, see Table 12.)

In order to allow for easy comparison between the data presented in this study and those collected by other investigators (Pearson 1966, Krebs et al. 1969, Lidicker 1973) the data presented in Fig. 15a were replotted on a semi-logarithmic scale (Fig. 15b). Before continuing with the discussion some terminology should be clarified. In a regular cycle most populations follow a pattern that includes a population increase phase, peak population phase, and a decline phase. Chitty (1955, 1967) described three patterns of cyclic population declines. Krebs (1964) has adopted these definitions and also described other patterns. However, a decline within the peak phase, namely, a spring decline within two high population densities, was usually disregarded and interpreted as common phenomenon of small mammal populations which is probably associated with social strife at the beginning of the breeding season (Myers and Krebs 1971a). This type of decline within the peak phase can reduce the population to a moderate or to extremely low size. A decline of the type described for *M. ochrogaster*, to a level of 13 individuals (Krebs et al. 1969, their Fig. 5), or even to eight individuals (Myers and Krebs 1971a, their Fig. 4) was not interpreted as a population crash that usually follows the peak phase. A population crash is usually considered to exist when the population declines from a high peak density to an extremely scarce density of about three individuals per hectare (Pearson 1966, Krebs et al. 1969). If this terminology is adopted for the present study, then the two populations of *M. ochrogaster* described in this study were at their "peak phase" at least

since June of 1972 (Fig. 15b). Within this "peak phase" the population were fluctuating annually simply due to differences between the breedin periods (when the number of new recruitments entering the trapable populations offset the number dying) and the nonbreeding period (when the populations were declining as a result of natural mortality).

The two populations of *M. ochrogaster* exhibited similar patterns o population density changes over time. However, there were differences in density between the two populations. From 1971 to 1974 this density difference ranged from a few individuals to 20 in October 1972 and in August 1973 (Fig. 15a). With one exception (May 1976) from 1975 to 197 a consistent difference in the order of 20 individuals was found betwee the two populations. Furthermore, the two populations exhibited a significant difference ($P = 0.04$) in the growth rate of peak densities (Fig. 16).

Although the two replicates of the nitrogen + water treatment were only a few meters apart (Fig. 2), few individuals moved from one replicate to the other. Only 12 individuals from a total of 228 individuals which were caught more than once, moved between the replicates.

Because the two populations exhibited a considerable difference in density in 1975 and 1976, and since most of the analysis is conducted for this period, I chose to analyze the two populations separately.

In summary, whatever terminology we may prefer to use, it is clear that the two populations studied were not exhibiting the usual 2- to 4-year cycle, and instead they were undergoing a regular annual fluctuation in abundance as well as progressively increasing in peak densities.

Habitat

The yearly progressive increase in peak population densities might have resulted from progressive increase in their food biomass on the two replicates of the nitrogen + water treatment. A large proportion of the vole's diet in 1975 and 1976 was found to consist of blue grama (*Bouteloua gracilis*) and fringed sagewort (*Artemisia frigida*), and it was assumed that the same proportion was taken in earlier years. The total herbage biomass probably represents the total production of the area and the amount of cover (Mueller-Dombois and Ellenberg 1974). The average monthly biomass of blue grama, fringed sagewort, and total herbage biomass in the growing seasons since 1971 are presented in Figs. 15c,d,e. No significant correlation was found between vole abundance and the total (dead and alive) herbage biomass ($r = 0.25$), blue grama biomass ($r = 0.17$), fringed sagewort biomass ($r = 0.18$), or the sum of the latter two ($r = 0.24$). This was probably because the *Microtus* populations were progressively increasing from year to year while the herbage biomass reached its peak in 1972 and then decreased (Fig. 15). Thus, I concluded that the amount of food or cover available in the two replicates of the nitrogen + water treatment probably did not regulate the population densities, and therefore, could not account for the progressive increase in vole's abundance.

Because only in 1975 and 1976 the *Microtus* populations were sampled throughout all the seasons of the year and because the data collected from individuals between 1971 and 1974 were not as extensive as in the last 2 years of the study, most of the following discussion is concentrated on the data collected in 1975 and in 1976.

Demographic Parameters

Recently, several investigators have pointed to the relationship between population demographic parameter changes and the cycle phases (Chitty and Phipp 1966, Chitty 1967, Krebs et al. 1969). Because of th importance attached to these demographic changes during the cycle, it i necessary to compare these components between cycling and noncycling populations. A comparison such as this may reveal the differences between the two population types and, thus, may point to the significance of some of the demographic components leading to an understandin of the factors that determine the cycles.

Reproduction. I used the position of the testes as an index of reproductive conditions in males, and the size of the nipples and appa ent pregnancy condition as a measure of reproduction for the females. The reproductive activity of the individuals was measured by recording the external appearance of live-trapped *M. ochrogaster*, and thus only a crude measure of the reproductive activity was obtained (Krebs et al. 1969).

The two sexes in both replicates showed a similar pattern of reproductive activity (Fig. 17). Females on replicate 2 exhibited higher reproductive activity in early May and June relative to replica 2. In both replicates a steady decrease in reproductive activity followed the initial peak until December, when only one female per replicate was found in breeding condition. Subsequent to December, th proportion of fecund females increased and in late May of 1976 all the females in the populations were in reproductive condition. The propor tion of males in reproductive condition was similar in both replicates and showed similar pattern to that found in females. The proportion o

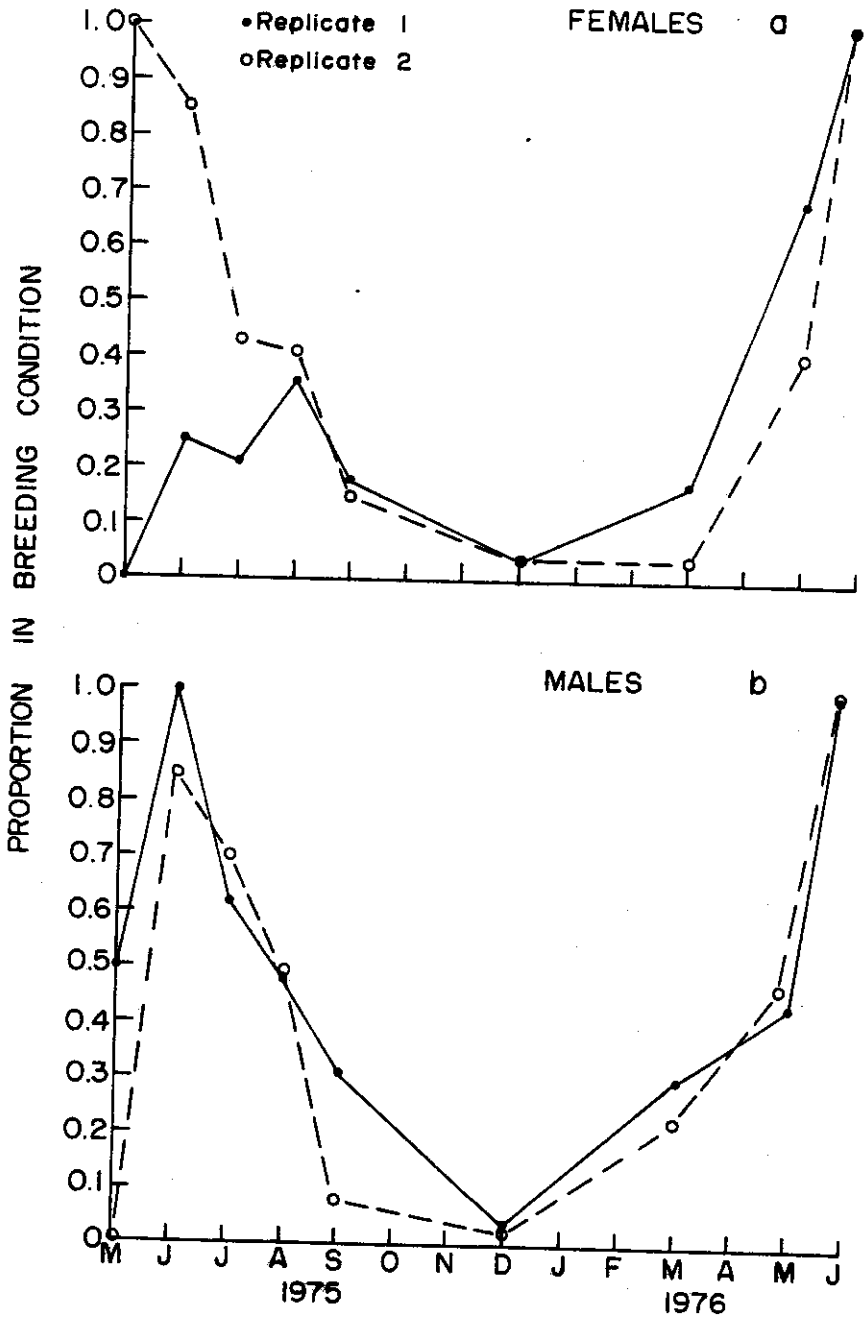


Fig. 17. Proportion of male and female *M. ochrogaster* in breeding condition in the two treatments of the nitrogen + water treatment.

fecund females in May, June, and July of 1975 was lower on replicate 1 relative to replicate 2. Although the difference obtained in early spring was based on small sample size, I believe that it accurately represents the difference between the two populations. This fact along with lower densities of both males and females on replicate 1 relative to replicate 2 (Fig. 18) may explain why the two populations attained different densities at peak population in 1975. Krebs et al. (1969) found that in *M. ochrogaster* the "reproductive intensity" of adults, as measured by crude external sexual characteristics, seemed independent o the cycle phases and showed only yearly variation. However, Keller and Krebs (1970) claimed that the cyclic peak cannot be accounted for by th differences in the reproduction during the main breeding season alone, and concluded that "the reproduction during the fall, winter, and spring before the peak has appreciable effect on the number of reproduc ing animals in the following season." Only a negligible number of individuals in reproductive condition (one of both sexes on each replicate) was observed in my study during the winter period (Fig. 17). Nevertheless, in the last 3 years of the study the populations of *M. ochrogaster* attained similar peak densities to those reported by Krebs et al. (1969) and in earlier years to those reported by Myers and Krebs (1971a). Also, the smallest populations in the last 2 years were only about 10 individuals per replicate. Furthermore, it seems that the population density in May did not determine the population size at the peak. Some 24 individuals inhabited replicate 1 in April of 1973 and the peak density attained that year was 54 individuals. However, in 1976 10 individuals which inhabited the same replicate in May yielded 8 individuals in August of the same year. The *Microtus* populations in

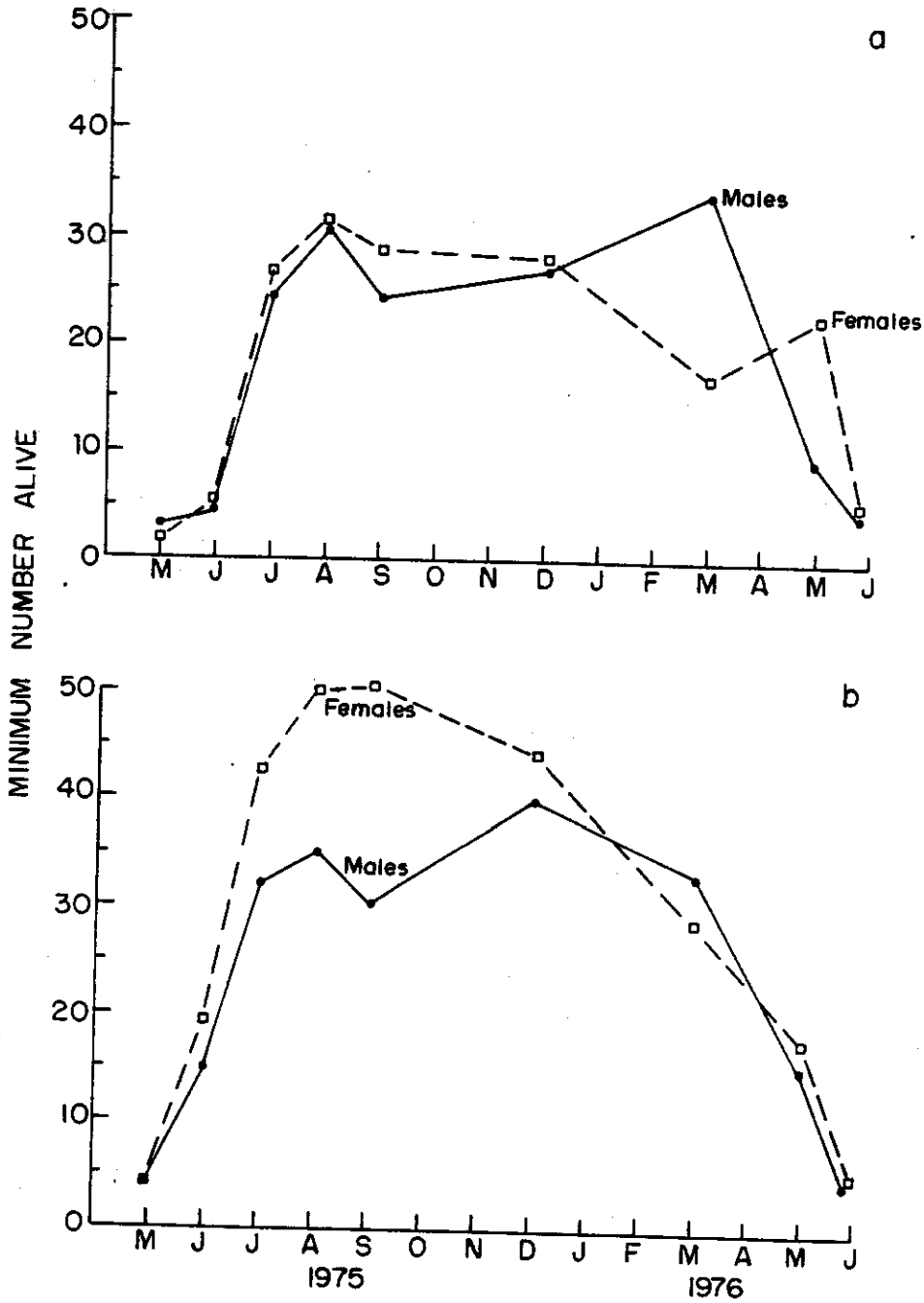


Fig. 18. Minimum number of male and female *M. ochrogaster* in the two replicates of the nitrogen + water treatment (a = replicate 1; b = replicate 2).

this study were able to obtain these high densities faster than the populations of *M. ochrogaster* reported by Krebs et al. (1969) (2.5 months and 1 year, respectively). Thus, I concluded that reproductive activity in the season prior to the peak is not necessary to produce th high numbers observed at peak population densities. This high rate of increase can be explained by the fact that *Microtus* is polyestrous and has a short gestation period of 21 days (Hatfield 1935, Hamilton 1941, Fitch 1957). Also, fertilization is possible immediately after young are born (Hamilton 1937). These characteristics probably prompted Hoffman (1958) to state that microtines have the highest rate of increa known for mammals.

Mortality. Mortality in a live-trapping study is equated with disappearance of individuals from the trapable population and, thus, includes dispersal (Krebs et al. 1969). Very few immigrants were caugh on different grids and they will be discussed later.

Mean survival rate per month was high and relatively constant in males and females of both replicates during the increase phase, the pea phase, and early decline phase (Fig. 19). However, survival rates in the late decline phase decreased to a very low level. This happened as most of the individuals on the two replicates disappeared. Survival rates for *M. agrestis* higher than 0.7 (per 4 weeks) through most of the year were described by Chitty (1952), D. Chitty and H. Chitty (1962), H. Chitty and D. Chitty (1962), and Newson and Chitty (1962). High survival rates were also reported throughout most of the cycle phases o *M. ochrogaster* (Krebs et al. 1969). Chitty and Phipps (1966) describe a sudden severe population loss in late spring similar to the one foun in this study. During this severe loss the population lost in a short

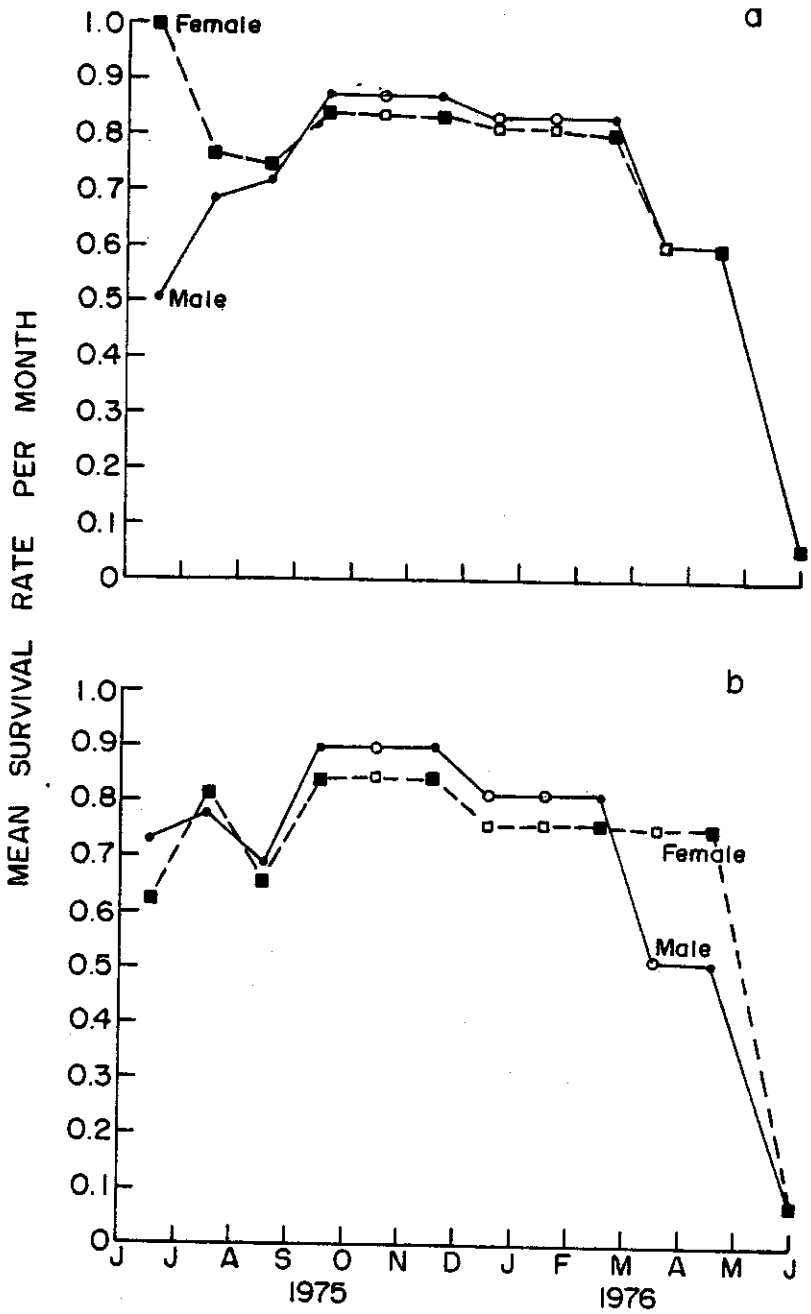


Fig. 19. Mean survival rate per month of male and female *M. ochrogaster* in the two replicates of nitrogen + water treatments (a = replicate 1; b = replicate 2). Solid symbols represent actual measurements; open symbols represent interpolation.

period exceeded the proportion lost in several months. Chitty and Phipps (1966) concluded that the steady losses during the winter were probably due to predation, disease, and other factors peculiar to the locality, and the sudden losses were probably the result of interspecific strife peculiar to the species. No indication was found that individuals in the decline phase were more susceptible to mortality thar individuals in earlier phases of the cycle (Chitty 1967, Krebs et al. 1969). The mean survival rate for both sexes was highest in the peak phase (0.82), intermediate in the increase phase (0.72), and lowest during the decline phase (0.44). The differences between the three mear survival rates are not significant ($P = 0.71$), although the survival rates during the increase and peak phases are significantly ($P = 0.05$) higher than the survival rate during the decline phase. Krebs et al. (1969, their Table 7) obtained a similar pattern of survival rate changes during a 2-year cycle, although survival rates in the increase phase were slightly higher than survival rates in the peak phase. Hoffman (1958) believed that mortality was the most important factor regulating population size of *M. californicus*. He claimed that mortality in the nonbreeding season is related to the size of the population which enters this period. The same conclusions could be reached for my study, since populations of different densities reached similar low levels each spring (Fig. 15). However, this hypothesis does not explain why most of the mortality occurred in less than 1 month in the spring of 1976. Martin (1956) reports that individuals which were born in the fall seem to have a longer life expectancy. He argued that thes animals, born in fall and early winter, were more vigorous than their older competitors, and therefore, were better able to survive the

winter. In Fig. 20 the survival rates of three cohorts are presented. (A cohort is defined here as the unmarked individuals first captured at a given sample.) These survival rates which were calculated from the individuals of both replicates to increase the sample size can be used to observe general biological trends in the three cohorts. It can be seen (Fig. 20a) that the August cohort individuals survived better than those of July and September, although the three cohorts had the same survival rate in May 1976 when most of the population disappeared. Individuals that were first caught in August and presumably born in July were probably growing in a period when the abundance of new vegetation was higher (new vegetation growth in the nitrogen + water treatment occurred in June) relative to those born in early June and belong to the July cohort. On the other hand, the August cohort individuals were growing in a less dense environment (and thus less intraspecific competition) than those born in August and belong to the September cohort. This may be the reason for better early survivorship of the August cohort individuals relative to those belonging to July and September cohorts. Males were surviving better than females in the July cohort (Fig. 20c,d), while females were doing better in the August cohort. I do not have an explanation for the difference between the survival rates of the two sexes.

In summary, the survival rates of male and female *M. ochrogaster* in one annual fluctuation seem similar to those reported of cyclic population (Krebs et al. 1969).

Sex ratios. The sex ratio of the two replicate populations fluctuated throughout the year (Fig. 21). Females dominated during late summer and winter and males dominated in the other periods of the year.

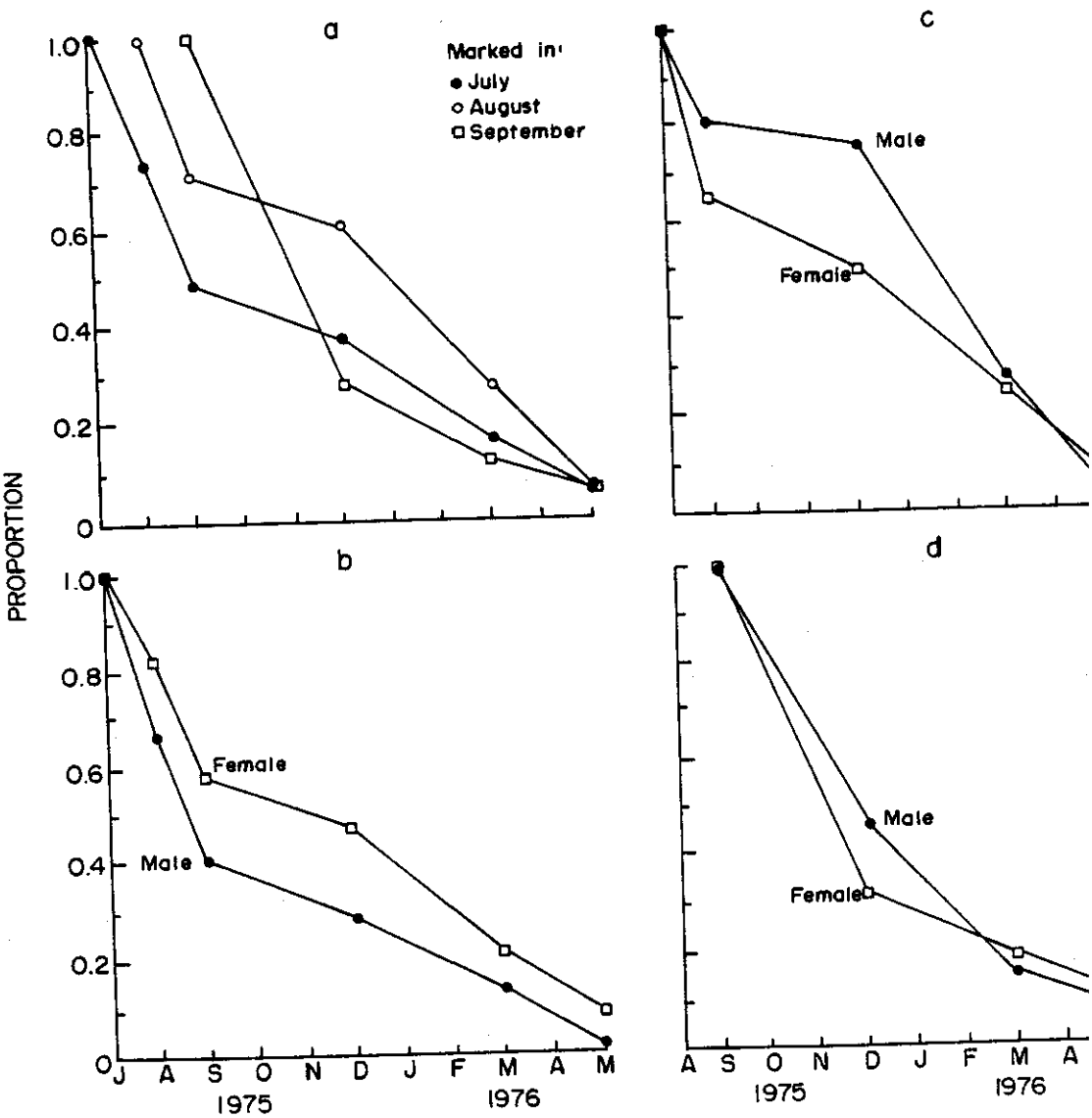


Fig. 20. Percentages of individuals first captured in July, August, and September, surviving in subsequent months (a = males and females combined; b = cohort of July; c = cohort of August; d = cohort of September).

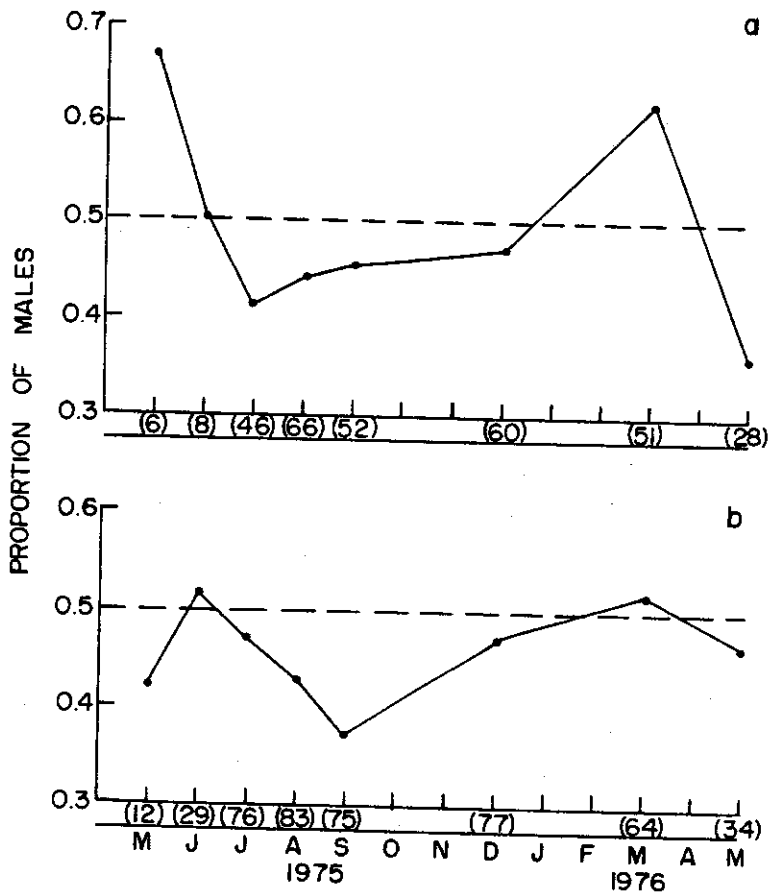


Fig. 21. Proportion of males in the two populations of *M. ochrogaster* in the nitrogen + water treatment. The numbers in parentheses represent the sample size (a = replicate 1; b = replicate 2).

The sex ratio calculated from resident individuals (i.e., from those animals known to be alive) of both replicates showed that males were only 46% of the trapable populations ($X^2 = 4.35$, $P = 0.05$). On the other hand, when the sex ratio of newly captured individuals was measured, no significant difference was found between the proportion of males in the population and the hypothesized 1:1 ratio ($X^2 = 0.132$, $P < 0.90$). Myers and Krebs (1971b) showed the same result and suggested that the skewed sex ratio may have importance in cycling vole populations. Laboratory matings of *M. ochrogaster* also yielded an approximate 1:1 sex ratio for the entire populations (Myers and Krebs 1971b). This either means that for some reason the potential sex ratio of 1:1 is altered in natural populations of *M. ochrogaster* or that once captured males have a significantly poorer probability of being recaptured (i.e. trap-shy). Martin (1956) suggested that the deviation from 1:1 sex ratio is caused by greater wandering tendency of males (see also Hamilton 1937).

In summary, annually fluctuating populations of *M. ochrogaster* showed the same system of distorted sex and thus there are no grounds t accept Myers and Krebs' (1971b) suggestion that the distorted sex ratio may have demographic consequences in cycling small rodent populations.

Body weight. No significant difference was found between mean weights of individuals (Table 13) from the two replicates averaged over the study period ($P = 0.31$, Appendix IV). Also, no significant difference was found between the mean weights of males and females ($P = 0.45$, Fig. 22). Thus, the individuals for each sex from both replicates were combined for further analysis. Both sexes in this study showed a significant change in weight with time ($P = 0.003$), although the variation

Table 13. Mean body weight and standard error for male and female *M. ochrogaster* on the two replicates of the nitrogen + water treatment. Numbers in parentheses represent the sample size.

Replicate	Sex	May	June	July	August	September	December	March	May
1	Males	35.0±0.00 (1)	39.5±1.61 (3)	40.0±0.97 (15)	40.1±0.77 (25)	43.2±1.01 (18)	38.5±0.60 (21)	41.9±1.08 (32)	44.6±1.38 (5)
	Females	--	41.5±0.29 (3)	43.3±1.03 (19)	41.8±1.11 (29)	46.8±1.66 (19)	38.1±0.68 (23)	37.9±0.70 (13)	42.7±1.14 (15)
2	Males	35.0±0.00 (1)	42.2±1.15 (10)	41.9±0.76 (26)	40.3±0.55 (22)	42.5±0.67 (27)	40.4±0.96 (19)	42.8±1.11 (26)	42.5±1.19 (11)
	Females	36.7±0.44 (3)	42.1±2.02 (9)	43.2±0.82 (32)	43.6±0.89 (34)	44.4±1.06 (38)	38.9±0.65 (24)	37.4±0.82 (18)	43.5±1.86 (12)

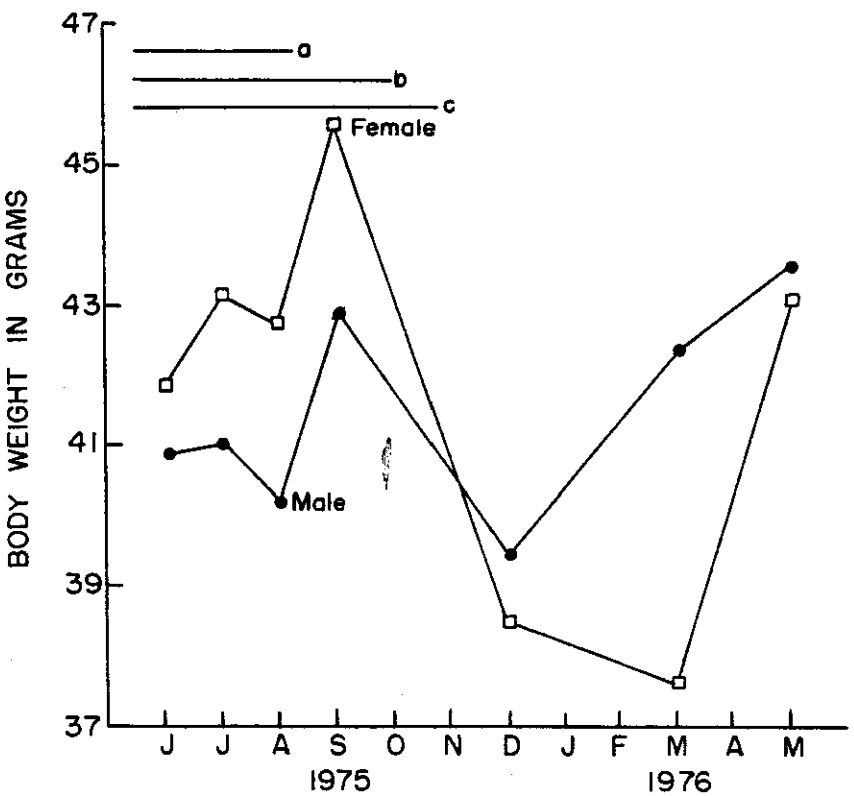


Fig. 22. Mean body weight of male and female *M. ochrogaster* in the nitrogen + water treatment. If the distance between sexes within any month is greater than a, the means are significantly different at 95% level. If the distance between any pair of means within either sex is greater than b, the points are significantly different at the 95% level. If the distance between any pair of the 14 means is greater than c, the points are significantly different at the 95% level.

in the females' mean weight was higher than in males (Fig. 22). Martin (1956) also reported that female *M. ochrogaster* were likewise heavier than males, probably due to a high proportion of pregnant females. Generally, the weights of both sexes were highest during late spring and summer and lowest in winter, with a peak weight in early fall (Fig. 23). The differences between the mean weights in late spring and early summer, and those in winter and early fall are significant ($P < 0.05$) (Fig. 23). A similar trend of yearly change in mean weights was found in *M. pennsylvanicus* (Hamilton 1941, Iverson and Turner 1974), *M. oeconomus* (Whitney 1973), and *M. agrestis* (Chitty 1952). This is in spite of the fact that these studies were conducted in different locations and habitats (Table 12). Iverson and Turner (1974) concluded that the weight decrease in the winter resulted primarily from a combination of recruitment of small animals and weight loss by older individuals. In the present study, I found that these two factors were also responsible for the drop in mean weight during the winter period. Examples of weight changes of different individuals are presented in Fig. 24. On the other hand, many of the individuals first caught in the winter sample generally weighed little, although some individuals were heavy. Thus, the mechanisms proposed for low weights during the winter period (Iverson and Turner 1974) seem appropriate to this study. Wunder et al. (1976) showed that weight specific oxygen consumption of *M. ochrogaster* caught in winter is 24% higher at 27.5°C and 29% higher at 7.5°C than that of summer animals. However, the total energetic costs to maintain an animal is the same at 27°C for both summer and winter animals. At 7.5°C the total energetic cost is less in winter animals than in summer (Wunder et al. 1976). Thus, they suggested that *M. ochrogaster*

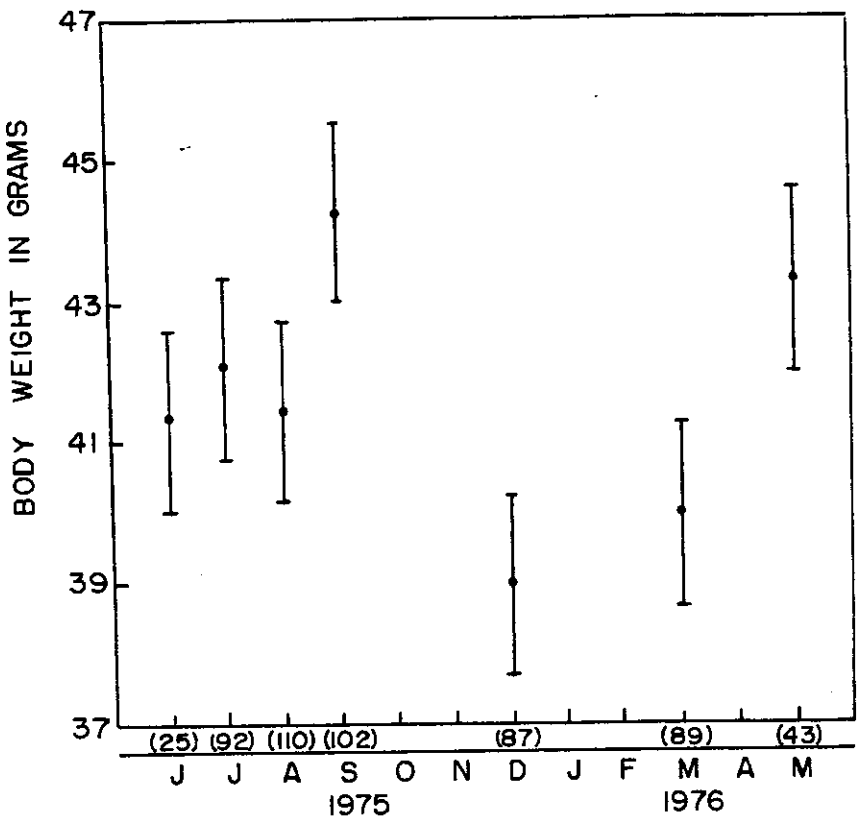


Fig. 23. Mean body weight of *M. ochrogaster* in the nitrogen + water treatment. The numbers in parentheses represent the sample size. The vertical lines represent 95% confidence limit.

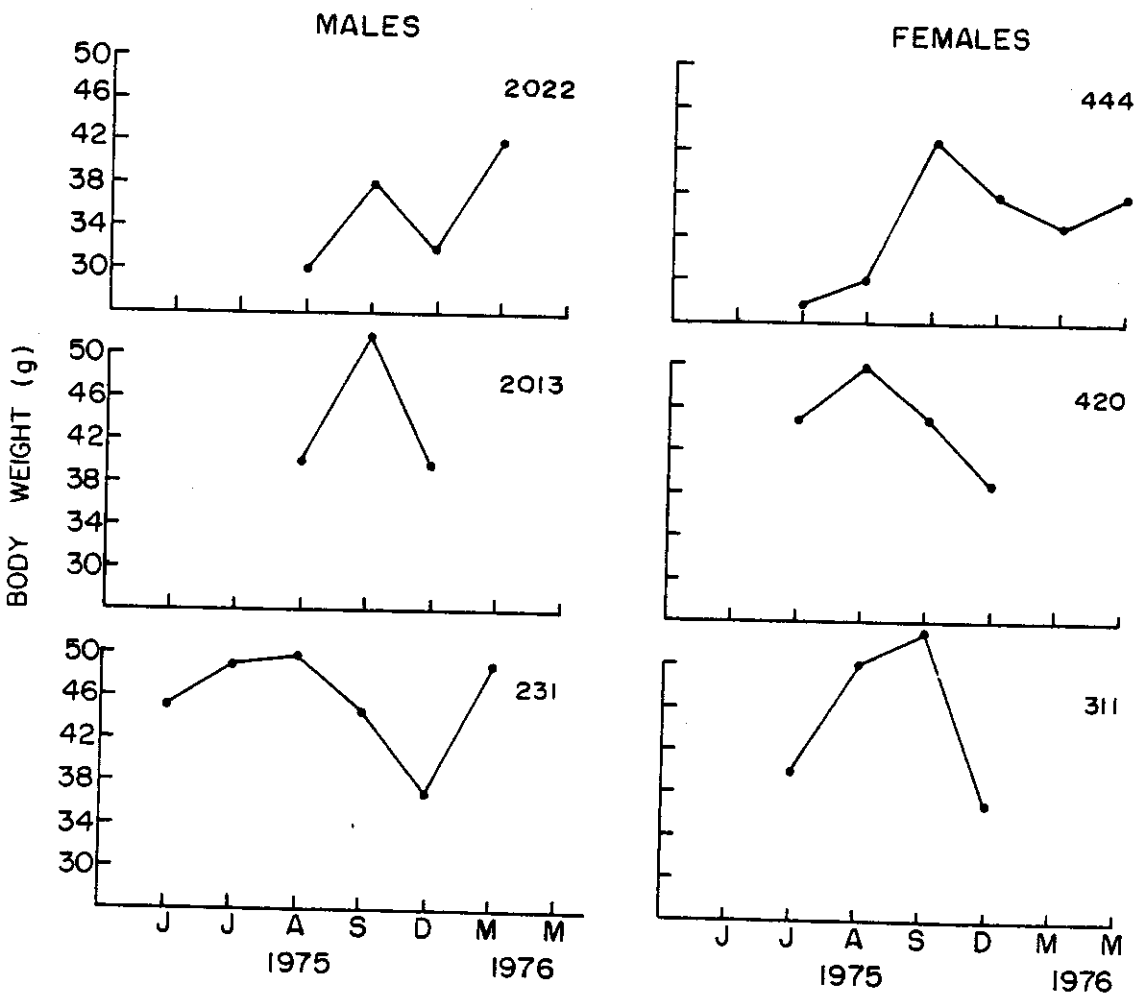


Fig. 24. Selected body weight changes of male and female *M. ochrogaster*. The numbers represent the individual number.

compensate for increased weight-specific thermogenesis in winter by lowering body weight. Lowered body weight, however, can be caused by higher energetic demands for thermo-regulation and lower food quality during the winter time.

It has been shown that in cyclic populations of microtines the population peak and late increase phases are characterized by having adult males of relatively heavy body weight (Krebs 1964, 1966; Krebs et al. 1969; Keller and Krebs 1970). In the early increase and decline phases these heavy males are apparently rare or completely missing. Keller and Krebs (1970) found evidence suggesting that the breeding in the middle of the increase phase in *M. ochrogaster* is carried out by animals which are of unusually high body weight (higher than 46 g). Myers and Krebs (1971a) have shown for the same species that the heavy males emigrate during the peak phase and suggested that selective emigration may cause a genetic change in the population. Because such significance has been attached to males with high body weight, a careful comparison between males in cyclic and noncyclic populations seems very important.

The body weight distributions of males captured during 1975 and 1976 noncycling populations are presented in Fig. 25. It seems that males with body weights higher than 46 g were present through most of the annual cycle, though they were missing in early May 1975 when the populations reached their lowest densities and were scarce in December and June 1975. The 46-g weight level was established (Keller and Krebs 1970) only to allow quick comparison of high weight distributions and has no biological significance. The presence of heavy males found in this study agrees with the weight change reported in cycling populations

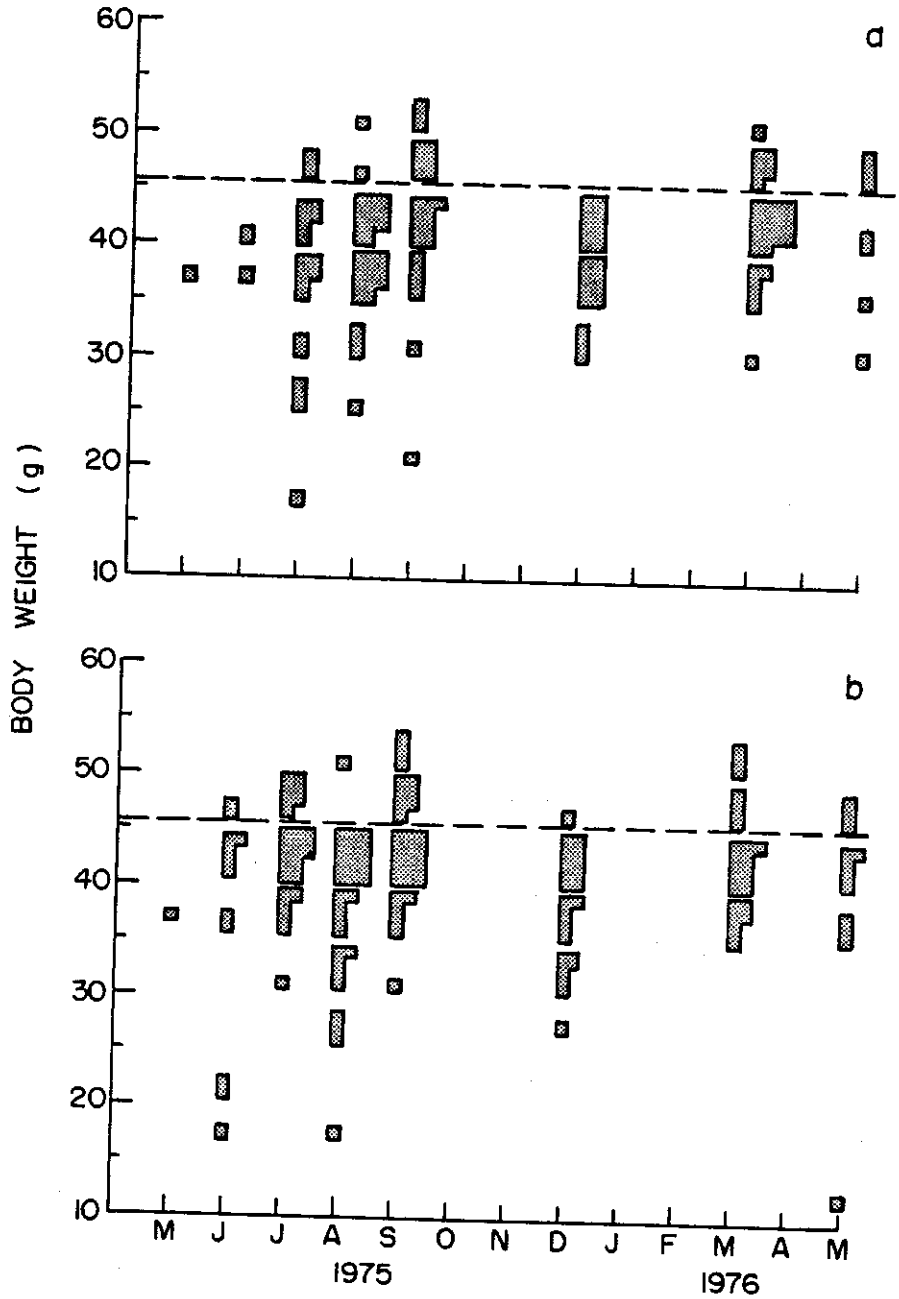


Fig. 25. Body weight distribution of *M. ochrogaster* males in the nitrogen + water treatment. Each small square represents one vole. Data grouped into 4-g intervals. (a = replicate 1, b = replicate 2).

except that heavy males were present and abundant in my study during th decline phase (Fig. 25) while they were missing in the decline phase of a cycling population (Krebs et al. 1969, their Fig. 21). However, the mean weight of the breeding males was significantly higher than the mea weight of nonbreeding males ($P = 0.002$).

In summary, although the male body weight distribution is somewhat different in annually fluctuating populations of *M. ochrogaster*, it is found that males in reproductive conditions were significantly heavier than males in nonreproductive conditions.

Population fluctuation. In a live-trapping program "mortality" is usually defined as the sum of actual mortality and emigration. Reprodu tion is likewise defined as the sum of two processes: birth and immigr tion. Thus, the population fluctuations observed in this study are the result of these two defined processes of mortality and reproduction.

The two populations of *M. ochrogaster* showed an enormous rate of increase in late spring of 1975 and 1976. In both replicates each yea the populations increased from an annual minimum of approximately 10 individuals to over 70 individuals per hectare in only 2 months (Fig. 16). This occurred at a growth rate of 110% per week. This value is much higher than that reported for a single fenced population of *M. ochrogaster* which reached abnormal densities (Krebs et al. 1969:594). The tremendous rate of increase (Fig. 26) was replaced by approximatel zero population growth during the peak phase in August through Decembe The high rate of increase that followed the nonreproductive period accounts for the great increase in abundance, and thus contradicts the conclusion of Keller and Krebs (1970) that breeding during the

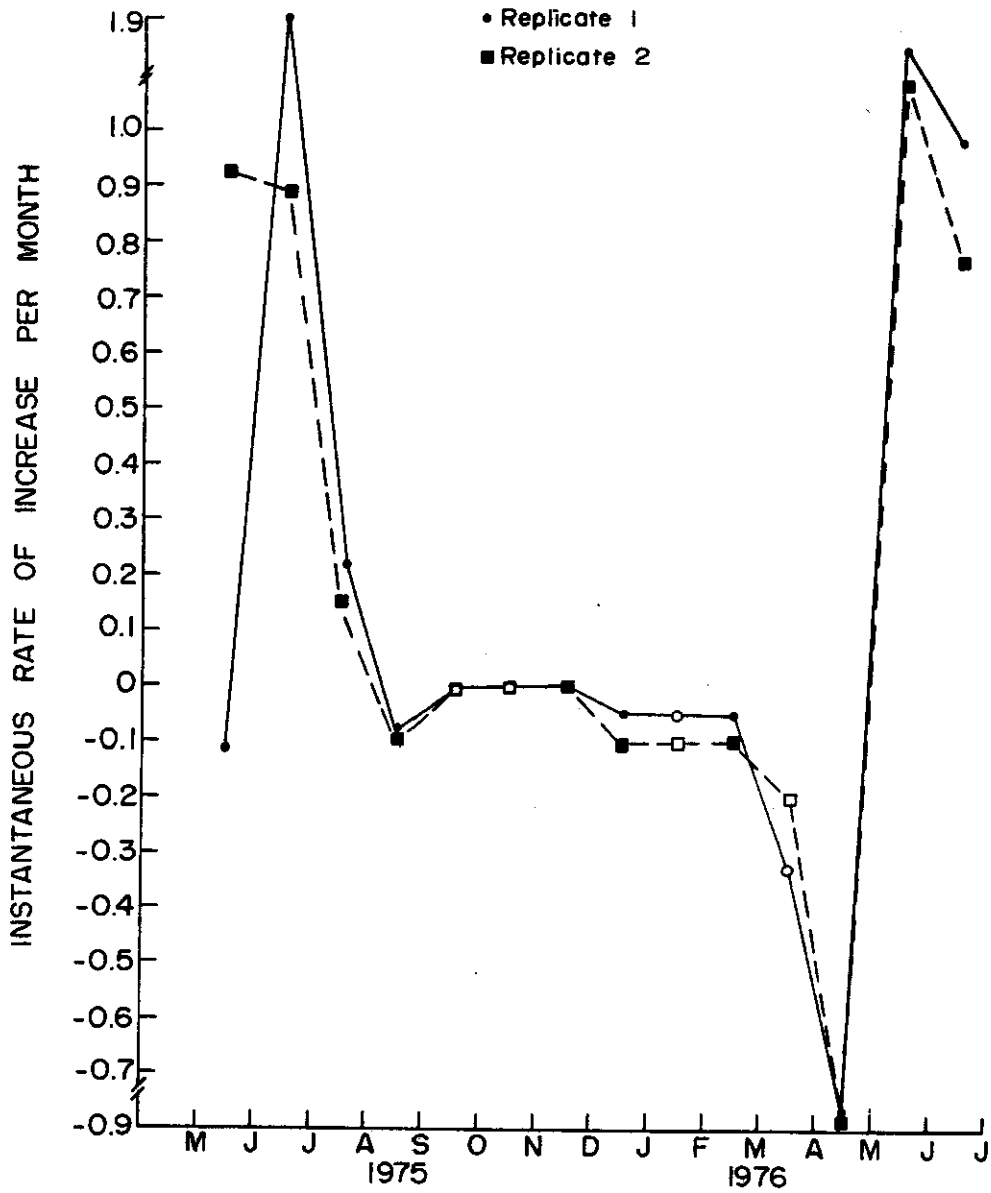


Fig. 26. Instantaneous rates of population increase in *M. ochrogaster* (solid symbols represent actual measurements, open symbols represent interpolation).

nonreproductive season has appreciable effect on the peak density attained in the following season.

Activity. Reports on the activity period of microtines are contradictory. Martin (1956) concluded from a live trapping study that *M. ochrogaster* is mostly diurnal, while Calhoun (1945) in laboratory studies reported that the same species is nocturnal. Davis (1933) reported that *M. agrestis* is nocturnal, and Hatfield (1935) concluded that *M. californicus* is also nocturnal. Hatt (1930) reported that *M. pennsylvanicus* is nocturnal while Hamilton (1937) concluded that the same species is active mainly during the daytime. Thus, it seems that different species of microtines as well as populations of the same species in different locations and habitats may be active during different parts of the day.

During winter and early spring (December 1975 and March 1976, respectively) voles in my study were trapped three times a day (0800, 1400, and 2200). Thus, it was possible to compare the activity pattern of individuals of *M. ochrogaster*. No significant difference ($P = 0.30$) was found between the mean number of individuals caught per trap-hour i the three periods of the day considered in either March or December (Table 14 and Appendix IV). These results suggest that in December and March individuals of *M. ochrogaster* were equally active during each tra period. Similar results were reported for *M. californicus* using automatic photographic recorders (Pearson 1960). However, the day was divided into three unequal periods which were scheduled to minimize tra mortality. Thus, individuals could have been active only during the daylight hours and still be represented in the three trapping periods.

Table 14. Mean number of individuals of *M. ochrogaster* caught per hour of trapping during December and March samples in different periods of the day. Sample size (number of trapping days) in parentheses.

Time of day	Mean number of individuals caught/hr ± standard error	
	December	March
Assuming active all hours		
2200 to 800	1.8 ± 0.1 (4)	0.9 ± 0.13 (4)
800 to 1400	2.4 ± 0.65 (2)	1.5 ± 0.25 (3)
1400 to 2200	1.7 ± 0.21 (3)	1.7 ± 0.61 (4)
Assuming active only during the daylight hours		
600 to 800	9.0 ± 1.46 (4)	4.1 ± 0.42 (4)
800 to 1400	2.4 ± 0.65 (2)	1.5 ± 0.25 (3)
1400 to 1800	3.4 ± 0.46 (3)	3.5 ± 1.20 (4)

Under the assumption that individuals were active only during the daylight hours (approximately 0600-1800), activity was greatest in earl morning, intermediate in late afternoon, and smallest in late morning and early afternoon. The differences between this activity pattern wer significant ($P = 0.02$) between all the periods (Table 14 and Appendix I).

In summary, although it seems that individuals of *M. ochrogaster* were equally active throughout the day, the result was changed if the individuals were active only during the daylight hours.

Home range. Pearson (1960) working with *M. californicus* in annual grassland has shown that several individuals, probably family groups, all use the same runway system. He concluded that with increasing population the number of mice using each runway system remains constant but the number of runway systems and, therefore, habitat utilization increase. Lidicker and Anderson (1962), and Batzli (1968) who worked the same habitat type and species also supported this suggestion. If Pearson's (1960) hypothesis is correct and several mice use the same runway system regardless of population density, we should expect to fi similar home range size in high and low population density.

To determine home range sizes for the mice I studied, I used two kinds of information. First, I used the mean maximum distance travele by an individual that was captured at least twice as an indication of the size of the home range, following the approach of Southwood (1966) Second, I used radiotelemetry on selective males to determine their position and movement in my study site (Appendix V). Both methods showed that the size of the home range was independent of population density (Table 15). Both methods may not measure accurately the home

Table 15. Home range size (± standard error) of *M. ochrogaster* in low and high population density. Numbers in parenthesis represent the sample size.

Population size	Home range size[a/] (m^2)	Index of the home range size[b/] (m)
Low[c/]	113.5 ± 46.2 (4)	18.88 ± 2.5 (53)
High[d/]	217.3 ± 87.9 (4)	15.87 ± 1.14 (131)
t-test	0.008	1.24
Probability	>0.50	>0.30

[a/] Home range size was calculated by measuring the area enclosed by at least 8 points recorded by radiotelemetry equipment. Only individuals inhabiting replicate two of the nitrogen + water treatment were used in this experiment.

[b/] The maximum average distance traveled, calculated from all marked individuals caught more than once on the nitrogen + water treatment.

[c/] The average number of individuals in a low population was 38 when the home range size was measured by the radiotelemetry equipment and 68 when the maximum average distance index was estimated.

[d/] The average number of individuals in a high population was 89 when the home range was measured by the radiotelemetry data and 148 when the maximum average distance index was estimated.

range size, since the method of analysis based on mean maximum distanc traveled may be biased by the number and location of traps, and mice carrying transmitters have been shown to reduce their activity (Hamly and Falls 1976). However, if both techniques were biased similarly by low and high population densities, one has to conclude that home range size was independent of the population density.

Dispersal. Dispersal has been suggested as a potential mechanism for population regulation in small mammals (Dice and Howard 1951, Errington 1956, Sadlier 1965, DeLong 1967, Healey 1967), and Howard (1949, 1960) has suggested a genetic basis for dispersal in small mammals. Myers and Krebs (1971a) have shown that the frequencies of two alleles are somewhat different between dispersing and resident individuals of *M. ochrogaster* and *M. pennsylvanicus*. A similar result for *M. townsendii* was obtained by Krebs et al. (1976) who suggested that emigration acts as a selecting force during the population increase, a through this mechanism the composition of the resident population changes from socially tolerant to socially intolerant individuals. Th change in the quality of the individuals is assumed to cause populatic decline (Chitty 1967). Neither the genetic composition of the residen nor the dispersing individuals in my study is known. Nevertheless, a comparison between the weight of resident and dispersing individuals i cyclic and noncyclic populations can be made.

The two replicates of the water treatment plots which were adjace to the nitrogen + water treatment plots carried only a few individuals of *M. ochrogaster*. Because the population of voles in the water treatment plots was always very low (indeed, some censuses revealed no vole in these plots), I concluded that the individuals caught on this

treatment were emigrants from the two nitrogen and water plots. The fact that two marked individuals (out of a total of 19) were marked on the nitrogen + water replicates before moving to the water treatment further supports this conclusion. Most of the individuals found on th water treatment weighed less than individuals on the nitrogen + water plots. The average weight of males on the water treatment was 20.4 g (n = 10) while the average weight of the same sex on the nitrogen + water treatment was 39.9 g (n = 297). The average weight of females or the water and the nitrogen + water treatments was 31.7 g (n = 11) and 39.6 g (n = 244), respectively. The difference of the mean weight of both sexes in the two treatments was significant ($P < 0.0001$). Myers and Krebs (1971a) have shown the same result, namely, that males and females that dispersed from a cyclic population of *M. ochrogaster* were significantly lighter than resident individuals. The same pattern existed in *M. pennsylvanicus* (Myers and Krebs 1971a).

In summary, no difference was found between the weight of resident and dispersing individuals of *M. ochrogaster* in cyclic and noncyclic populations.

Discussion and Summary

It has been suggested that the interaction between microtines and their food supplies is instrumental for the production of cyclic population fluctuations (Lack 1954b; Pitelka 1959, 1964; Schultz 1964; Batzli and Pitelka 1970). Other investigators have shown that high population densities can reduce their food abundance (Schultz 1964, Batzli and Pitelka 1970). If the interaction between the microtines and their food supply, and the biomass of the food, determines the population density,

a positive correlation should be expected between the vole density ar biomass of their food resources. No such correlation could be found this study. Thus, I concluded that neither food nor cover regulated vole population sizes. This conclusion is in agreement with the expe ment conducted by Krebs and DeLong (1965) where food supplemented to population of *M. ochrogaster* (Krebs et al. 1969) did not prevent popu tional declines. Also, a fenced population of *M. ochrogaster* (Krebs al. 1969) reached abnormally high densities before overgrazing their food resources while a control, unfenced population declined after reaching much lower densities. Thus, it seems that although high pop lations of *Microtus* do reduce their food supply (Batzli and Pitelka 1970), the density of the microtines is decreased in normal situation before reaching food limitation.

Chitty (1967) has hypothesized that cyclic changes in population densities of voles are a result of selection for certain genotypes in different phases of the cycle. The hypothesis states that as the pop lation increases, mutual interference causes differential emigration reduced reproductive rate for certain genotypes. Mutual interference through differential reproduction, mortality, and dispersal causes th selection for aggressive individuals which are characterized by accen ated spacing behavior, thus resulting in reduction in population den- sity. After the population decreases to a low level, selection favor high reproductive behavior. Intensive field work to test this hypoth esis (Krebs 1964, 1966; Chitty 1967; Krebs et al. 1969, 1976) has produced inconclusive results. Gains et al. (1971), Gains and Krebs (1971), and Krebs et al. (1976) have shown that during the cycle of *M. ochrogaster* there is a change in the frequency of certain genotypes ir

the population. However, at this point in time we do not know if these changes are the cause or the effect of the cycle (Myers and Krebs (1971a). Other work on demographic parameters (Krebs et al. 1969) and on genetic and behavioral changes during the cycle (Krebs 1970, Myers and Krebs 1971a) has produced only indirect evidence in favor of the Chitty hypothesis, and the results for *M. pennsylvanicus* seem more convincing than the results for *M. ochrogaster*.

Fenced populations of *Microtus* have been shown to reach extremely high densities and exhibit no cyclic fluctuations (Krebs et al. 1969). Because the fence prevented both emigration and immigration, it has been hypothesized that dispersal is necessary for normal population regulation and population cycling in *Microtus* (Krebs et al. 1973). Krebs et al. (1973) have also suggested an experiment to test this hypothesis. They suggested that a fenced plot with one-way exit doors would allow normal population regulation and cycling due to emigration of individuals from the study plot.

The two replicates of the nitrogen + water treatment in my study were located in a virtual sea of shortgrass prairie habitat which is apparently unfavorable to voles. The fact that *Microtus* travels through shortgrass prairie habitat is evidenced by the fact that they naturally colonized my study area in 1971. However, the area is also located far from any known dense populations of *M. ochrogaster*. Monthly searches for populations of *M. ochrogaster* in the environment around the study area were conducted from 1975 to 1976. This was done by directly searching for microtine runways. Only two low density populations were found, each 1.6 to 2 km away from the study area. However, even if a small dense population of *M. ochrogaster* existed in a nearby area, the

probability that high numbers of individuals would have dispersed from it and reached the small study site was negligible. Thus, it is reasonable to assume that while emigration from my study area was possible, (perhaps even frequent) immigration is most likely negligibl In Fig. 27 I diagramed the differences between the three situations discussed: "normal" populations, fenced populations, and isolated populations. In "normal" populations in which cycling occurs, both immigration and emigration are possible. In fenced populations neithe migratory process can exist and the results are extremely high population densities and the elimination of the cyclic fluctuation. However in an isolated population only emigration usually occurs in any regula fashion while immigration is probably negligible. The result of such situation in my study is a "normal" population density, but no multipl year cyclic fluctuation. Thus, it seems that emigration itself might explain the "normal" or regulated densities observed in the present study, but it does not seem to explain the cyclic fluctuation of microtine populations. The result of this study also suggests that immigration may be the important factor causing cyclic behavior. Unfortunately, I cannot explain how selection can favor such a process because immigrants to one area are the emigrants from another area. Even equilibrium between immigration and emigration rates of certain genotypes cannot explain the importance of emigrants in determining th cycle. If we assume that the emigrant population suffers severe mortality before settling in an area, the number of immigrants to any are would be smaller than the number of emigrants. This process is propos to explain the change in gene frequency observed in cycling population (Gains and Krebs 1971), and thus the cycle. However, in isolated

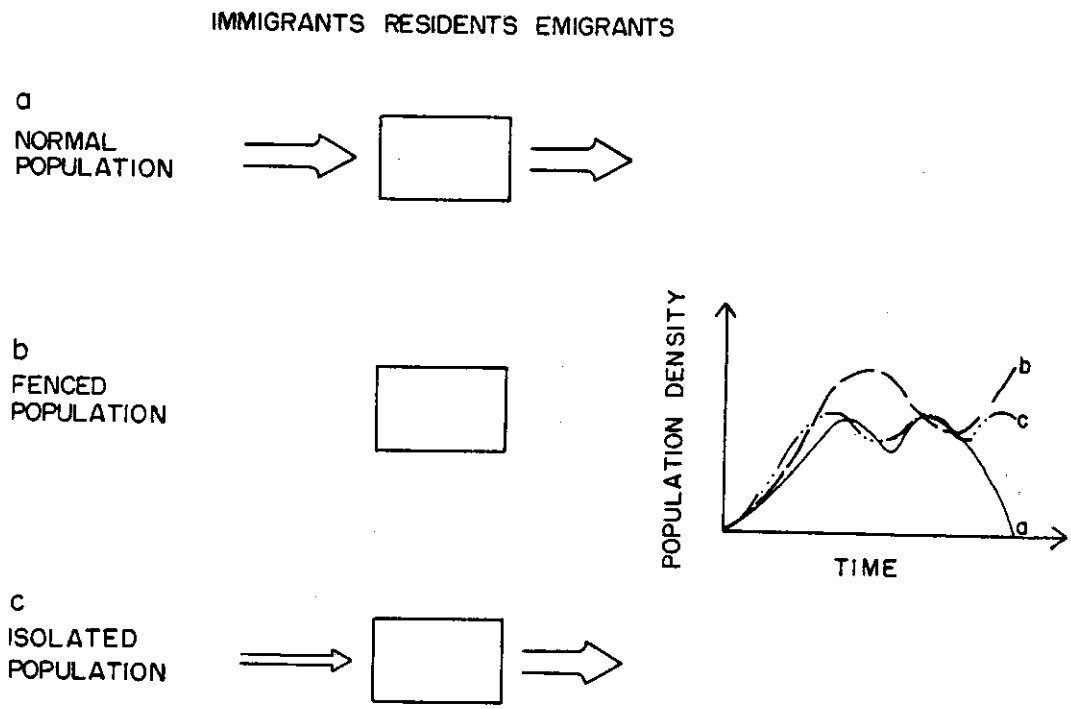


Fig. 27. Graphical illustration of the relative importance of emigration and immigration on the population density and pattern of change in *M. ochrogaster*.

populations only emigration occurs, and thus, the rate of change in population's phenotypic composition would be even higher than in a "normal" population. One may speculate that the annual cycle observ in the present study resulted from such rapid change in the populati genotypic frequency, or that self-regulation through natural selecti does not exist. This former speculation is supported by the fact th the populations in the present study, which only underwent annual cycling, showed similar demographic and body weight patterns as popu lations which fluctuate in a regular 2- to 4-year cycle.

An annual fluctuating population of *M. californicus* was studied Lidicker for 13 years on Brooks Island. This population exhibited a typical pattern of density changes of high peak density in 1 year th was followed by a lower peak density in the second year. This popul tion also exhibited difference in biological characteristics (like molting episodes and delayed breeding season) in consecutive years. These differences between consecutive years were interpreted as 2-ye cycle (Lidicker 1973). Many of the biological characteristics that exhibited 2-year cycle in Lidicker's work were not measured in this study. However, it is clear that the populations of *M. ochrogaster* described in this study showed a different pattern of peak density changes from those reported by Lidicker (1973), and no multiple-year cycle could be detected. However, Lidicker's study questions the importance of dispersal in determining the cycle because in island populations both emigration and immigration are probably negligible.

Pearson (1964, 1966) has suggested that the timing of the cycle determined by predation pressure. He reports evidence supporting his hypothesis that predators determine the timing of the population decl

and the duration of the low phase. No observations of predation were made in this study, and thus, I cannot judge the importance of predation. Also, I did not look for toxins in the microtine's food and thus cannot assess Freeland's (1974) hypothesis. Nor was disease as a cause for a population decline specifically tested. Variation in the climatic conditions that influence plant growth was probably minimal because yearly variation in the amount of precipitation was obviated by artificial irrigation of the plots. Thus, it seems that climate probably played a minimal role in determining the population densities.

I must conclude that food supply was probably not important in limiting population densities in my study. I also conclude that emigration is probably not a necessary factor for the cyclic behavior of microtines, although immigration may play a role in determining the existence and the length of the cycle. However, the causes for cyclic fluctuation in microtine populations still remain unsolved.

POPULATION DYNAMICS MODEL

Numerous attempts to model the population dynamics of one or mo animal populations have been reported in the literature. The early attempts have concentrated on simple two-equation systems with two t three parameters which were presumed to have biological importance (Volterra 1926, Lotka 1932, Gause 1934, Watt 1968, Royama 1971). Th first parameter, intrinsic rate of increase, represents the populati net growth rate; the second represents the carrying capacity of the environment in the absence of competition; and the third, applied on when more than one species is involved, represents the competition between species, namely, the decrease in the rate of increase of spe i caused by an individual of species j as compared to the decrease i the rate of increase of species i caused by an individual of species Although it is extremely difficult to measure these parameters in natural populations, when known, the population dynamics (total numb of individuals) of the species can be predicted to literally infinit time. Furthermore, because the equations are simple, an analytical analysis of the population densities can be conducted for the equili rious state. Leslie (1945) enlarged part of the above approach to include age and sex groups.

Recently models of population dynamics of animals have been included in ecosystem models (Wiegert 1975, Van Dyne and Abramsky 1975 Anway 1976, and references cited by these authors). These models (o submodels) of population dynamics emphasize the energetic demands of population but usually do not directly consider the interactions betv populations which were of greater importance in earlier, more simple models. However, recent models are very detailed and provide

information on sex and age groups, changing energetic demands of individuals in different seasons and reproductive stages, and weights of individuals. Weather conditions and food availability are also simulated in other parts of the model so better representation of the interactions between the organisms and their environment is possible. Thus, the information included in the three parameters of the simple models is subdivided into components and used more specifically in detailed models. Since the detailed models require specific informatio such as food abundance and weather, they usually have been run for relatively short time spans for which these data are available. Also, because of the complex nature of these models, analytical analysis cannot be done.

Simple models are thus more general than complex models and are usually used to specifically address such general questions as how many species can coexist in a certain habitat, and to provide information on species abundances (Cody 1974). Complex models, on the other hand, ignore the first question and concentrate on more detailed information which addresses the second question.

Most of the models reported in the literature, however, assumed that the populations modeled were closed populations and thus no emigration or immigration of individuals and species could take place. This probably results from dispersal usually being ignored by ecologists or being considered of little significance in population dynamics and regulation (Lidicker 1975).

Exceptions are the models reported by Levins and Culver (1971), Horn and MacArthur (1972), and Levin (1974). These simple models

(usually two equations) incorporated the dispersal rate between habit patches as mechanisms for population dynamics and species coexistence

Although only a few attempts have been made to study dispersal rates in natural populations (Krebs et al. 1976), many theories were developed to account for population regulation (Andrewartha and Birch 1954; Howard 1960; Lidicker 1962, 1975; Healey 1967; also see section *Microtus* Population Dynamics) and for the number of coexisting specie in a given habitat (MacArthur and Wilson 1967). The theory points to the importance of emigration in population regulation and suggests th inter- and intraspecific competition, as well as genetic characteristics, play an important role in determining their magnitude.

The results reported in earlier sections herein also point to th importance of emigration and immigration in determining species compo tion, species abundance, and population regulation. Indeed, because certain species exhibited a noncontinuous presence in some of the habitats studied (Table 2), the dynamics of this population cannot be described without incorporating dispersal.

In this study I tried to apply some of the theories on the role dispersal to a population dynamics model. The model is somewhat simi to the theoretical model suggested by Grant (1976).

Model Development and Overview

The major objective of the model was to introduce emigration and immigration to a population dynamics model. Thus, the emphasis was devoted to simulate the transient character of the studied communitie of small mammals and not the actual population densities.

The model simulates the population dynamics of five small mammal species (*P. maniculatus*, *M. ochrogaster*, *R. megalotis*, *S. tridecemlineatus*, and *O. leucogaster*), that inhabit four different habitat types. The results of the 1-year field study of these species were reported previously in this paper.

Forrester's (1961) approach was utilized to construct the model. According to this approach two factors of the system change through time: the state variables and the flows of information and material. Although these two interact to give the dynamics of the system through time, the agents of action are the flows (Anway 1976).

The model is a system of difference equations operating on a 2-week time step for 1 year and includes 3 driving variables, 34 state variables, and 70 flows. The model is coded in SIMCOMP 3.0 and runs in 26 seconds on a CDC 6400 computer.

The three driving variables are the density of small mammal species in the environment outside the study area, habitat priority index, and mean temperature calculated for 2 weeks (Fig. 28).

In developing the model four processes were considered: reproduction, mortality, emigration, and immigration. Because the main goal of the modeling effort was to implement emigration and immigration into a population dynamics model, most of the effort was given to them. For this reason mortality and reproduction were simulated simply by time-dependent coefficients taken from literature or estimated in this study (Table 16).

In each habitat type the species densities are represented in state variables to which individuals are flowing from the sources as a function of the reproduction status of the population and flowing out to the

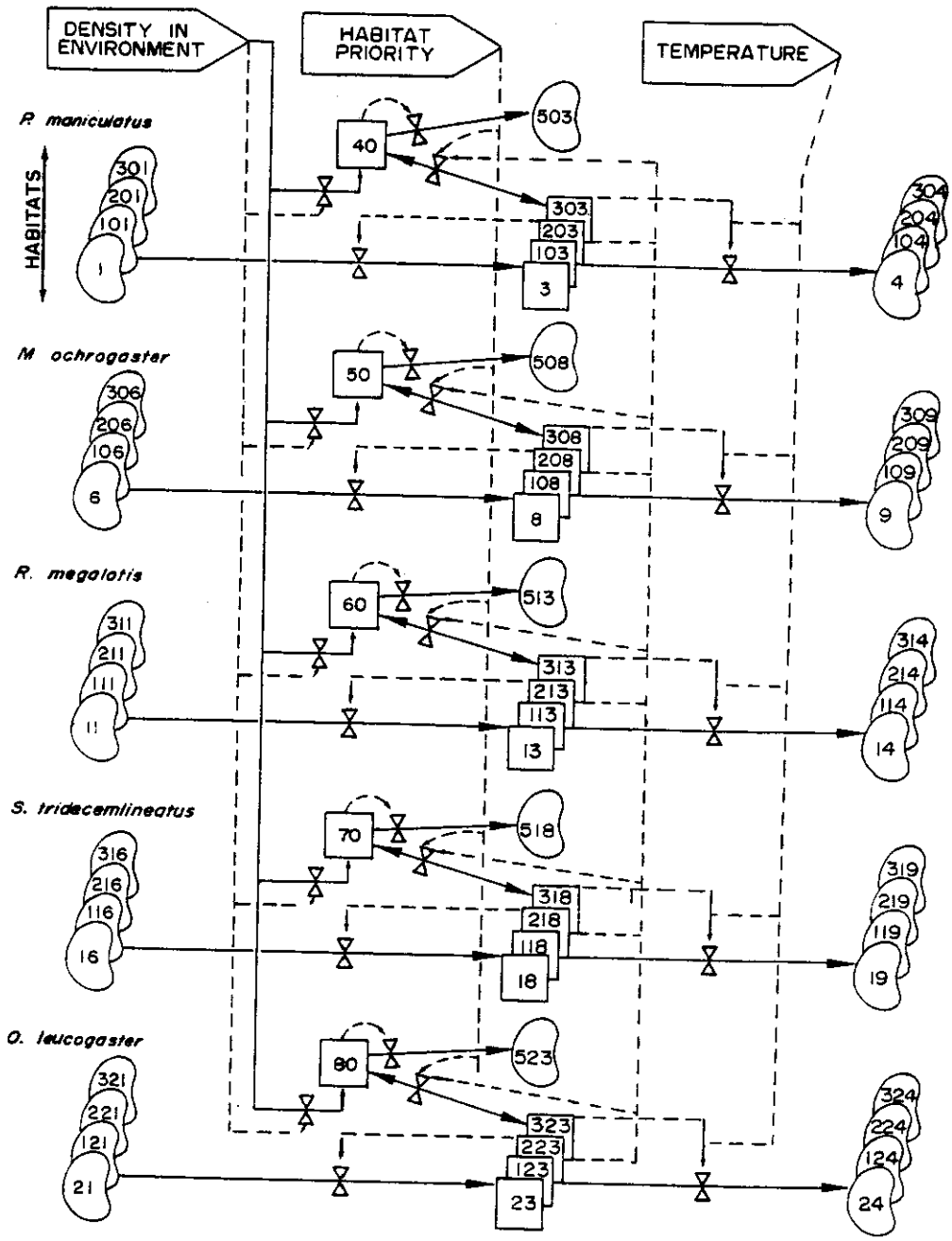


Fig. 28. Box-and-arrow diagram of the population dynamics model. The solid arrows represent individuals flow and the broken arrows represent information flow. Each arrow represents four flows to the corresponding variables. Squares represent the state variables. The kidney shape structure on the left represents the sources and on the right the sinks.

Table 16. Sources of input variables used in the model.

Parameter	Source
Species: *P. maniculatus*	
Proportion of adults	Peticrew and Sadlier (1974)
Proportion of pregnant females	Flake (1971)
Litter size	Flake (1971)
Sex ratio	Flake (1971)
Mortality rate	Beer and Macleod (1966)
Population densities in the studied area	Data (Table 2)
Population density in the environment	Data (Table 2)
Distance between treatments	Data
Size of treatments	Data
Competition indices	Data (Table 6)
Habitat priority	Estimated
Threshold density for emigration	Estimated
Species: *M. ochrogaster*	
Proportion of adults	Martin (1956)
Proportion of pregnant females	Data (Fig. 17)
Litter size	Keller and Krebs (1970)
Sex ratio	Data (Fig. 18)
Mortality rate	Martin (1956)
Population densities in the studied area	Data (Table 2)
Population densities in the environment	Estimated
Distance between treatments	Data
Size of treatments	Data (2-ha)
Competition indices	Data (Table 6)
Habitat priority	Estimated
Threshold density for emigration	Estimated

Table 16. Continued.

Parameter	Source
Species: *R. megalotis*	
Proportion of adults	Estimated
Proportion of pregnant females	Fisler (1965)
Litter size	Fisler (1965)
Sex ratio	Fisler (1965)
Mortality rate	Fisler (1965)
Population densities in the studied area	Data (Table 2)
Population densities in the environment	Estimated
Distance between treatments	Data
Size of treatments	Data
Competition indices	Data (Table 6)
Habitat priority	Estimated
Threshold density for emigration	Estimated
Source: *S. tridecemlineatus*	
Proportion of adults	Flake (1971)
Proportion of pregnant females	Flake (1971)
Litter size	Flake (1971)
Sex ratio	Flake (1971)
Mortality rate	Rongstad (1965)
Population densities in the studied area	Data (Table 2)
Population densities in the environment	Data (Table 2)
Distance between treatments	Data
Size of treatments	Data
Competition indices	Data (Table 6)
Habitat priority	Estimated
Threshold density for emigration	Estimated
Starts hybernation	September
Ends hybernation	April

Table 16. Continued.

Parameter	Source
Species: *O. leucogaster*	
Proportion of adults	Estimated
Proportion of pregnant females	Flake (1971)
Litter size	Flake (1971)
Sex ratio	Egoscue (1960)
Mortality rate	Estimated
Population densities in the studied area	Data (Table 2)
Population densities in the environment	Data (Table 2)
Distance between habitats	Data
Size of treatments	Data
Competition indices	Data (Table 6)
Habitat priority	Estimated
Threshold density for emigration	Estimated

sinks as a function of the mortality rate. Emigration is simulated functions of inter- and intraspecific interaction. Immigration is simulated as a function of weighted index calculated from habitat priority index, size of the habitat, and distance between habitats. key to compartments and parameter names (or numbers) is presented in Appendix VI, their values in Appendix VII, and the model code in App dix VIII.

The Model

Reproduction

Reproduction is simulated by using data taken from the literatu or from the data reported in earlier sections (Table 16). The numbe individuals born to each species in the four habitats is determined simply by a series of time-dependent coefficients.

$$(\text{Number born})_{ijt} = \left[\left(\begin{matrix}\text{Proportion}\\ \text{of adults}\end{matrix}\right)_{it} \cdot \left(\begin{matrix}\text{Proportion}\\ \text{of females}\end{matrix}\right)_{it} \cdot \left(\begin{matrix}\text{Proportion of}\\ \text{fecund female}\end{matrix}\right) \cdot \left(\begin{matrix}\text{Litter}\\ \text{size}\end{matrix}\right)_{it}\right] \cdot \left(\begin{matrix}\text{Population}\\ \text{size}\end{matrix}\right)_{ijt}$$

where i = 1, 2, ..., 5 small mammal species

j = 1, 2, ..., 4 habitat types

t = 1, 2, ..., 26 2-week time steps

Proportion of adults, proportion of females, proportion of fecu females, and litter size are assumed to be similar for a given speci in all four habitats.

Mortality

Mortality is also simulated as simple time-dependent coefficients largely taken from the literature (Table 16). During cold weather (T 4.2°C) the mortality is increased by 5%.

$$(\text{Mortality})_{ijt} = \begin{cases} \left(\begin{matrix}\text{Population}\\ \text{size}\end{matrix}\right)_{ijt} \cdot (\text{Mortality})_{it} & \text{for } T°C > 4.2 \\ \left(\begin{matrix}\text{Population}\\ \text{size}\end{matrix}\right)_{ijt} \cdot \left[(\text{Mortality})_{it} + 0.05 \cdot (\text{Mortalit}\right. & \text{for } T°C \leq 4.2 \end{cases}$$

where i, j, and t are the same as in the reproduction. Mortality rates are similar for a given species in all four habitats.

Emigration

Emigration rate is generally considered to be a function of intra- and interspecific interaction between species. As the number of individuals occupying a certain habitat increases, the habitat becomes less suitable (due to depletion of resources or aggressive interactions) to support more individuals (P. R. Grant 1972). Thus, for each population in a given habitat a threshold density, above which individuals are forced to leave, exists. Lidicker (1975) has termed this type of emigration as "post-saturation" dispersal. Krebs et al. (1976), with indirect evidence, support Howard's (1960) suggestion that the dispersing individuals are genetically different from the resident. The genetic differences between individuals are not incorporated in the model.

Interspecific interaction between species is assumed to operate similarly to intraspecific interaction (Grant 1976), although no genetic

basis was suggested for dispersal of individuals due to interspecific interactions.

In the model, emigration rate is determined as a function of the amount of intra- and interspecific competition. The amount of competition imposed on each species in each of the four habitats is calculat as the ratio between the amount of competition suffered at time t and the maximum amount of competition observed in this system (α_{ij} max = 1.62, see Table 6). This ratio is assumed to be directly correlated with the emigration rate. For each species in the four habitats a threshold density value is given under which no emigration is possibl

Thus, when the density of a species in a given habitat is above threshold density,

$$(\text{Emigration})_{it} = \left(\sum_{i=1}^{5} N_{it} \cdot \alpha_{it}\right) / \left(\sum_{i=1}^{5} N_{it} \cdot \alpha_{max} \cdot K_2\right)$$

where α_{it} is the amount of competition induced in a given habitat by species i on species j at time t, N_{it} is the population densities of species in a given habitat at time t; the constant (K_2) represents th relation between the relative amount of competition suffered by a species and the emigration rate and is estimated by simulation runs.

Because it is assumed that individuals leaving their familiar ho range suffer higher mortality than residents (Errington 1956, Pielows 1962, Metzgar 1967, Ambrose 1972), 20% of the emigrants are assumed t die. The emigrants of each species are stored in a state variable an these individuals are the source for immigrants.

Immigration

In each time step emigrants of a given species are redistributed between habitats or leave the area for the surrounding environment. This is done according to three categories: inverse square root of the distance between habitats, habitat size, and habitat priority index. The data for the first two categories were obtained by direct measurements while the habitat priority was estimated as an index ranging from zero to one. This was done according to the relations between species abundance and FHD presented in Fig. 8. The three criteria are weighted in the following way:

$$(\text{Immigration})_{ijt} = \left[5 \cdot \left(\begin{matrix}\text{Habitat}\\ \text{priority}\end{matrix}\right)_{ij} + 2 \cdot \left(\begin{matrix}\text{Habitat}\\ \text{area}\end{matrix}\right)_{j} + \left(D^{\frac{1}{2}}\right) \right] / \left[8 \cdot \left(\begin{matrix}\text{Number of}\\ \text{immigrants}\end{matrix}\right)_{it} \right]$$

where D = the distance between the source of immigrants (which is assumed to be in the middle of the study area) and a given habitat type.

The three criteria are weighted to rank their importance. Habitat priority index was assumed to be the most important factor that determines the immigration rate, the habitat size received an intermediate importance, and the distance was already weighted by taking the inverse square root of the distance.

In each time step, individuals emigrate as a function of competition, some (20%) die, and the rest are redistributed among the habitats and the environment around the study area (see below). An illustration of possible movement of individuals is presented in Fig. 29.

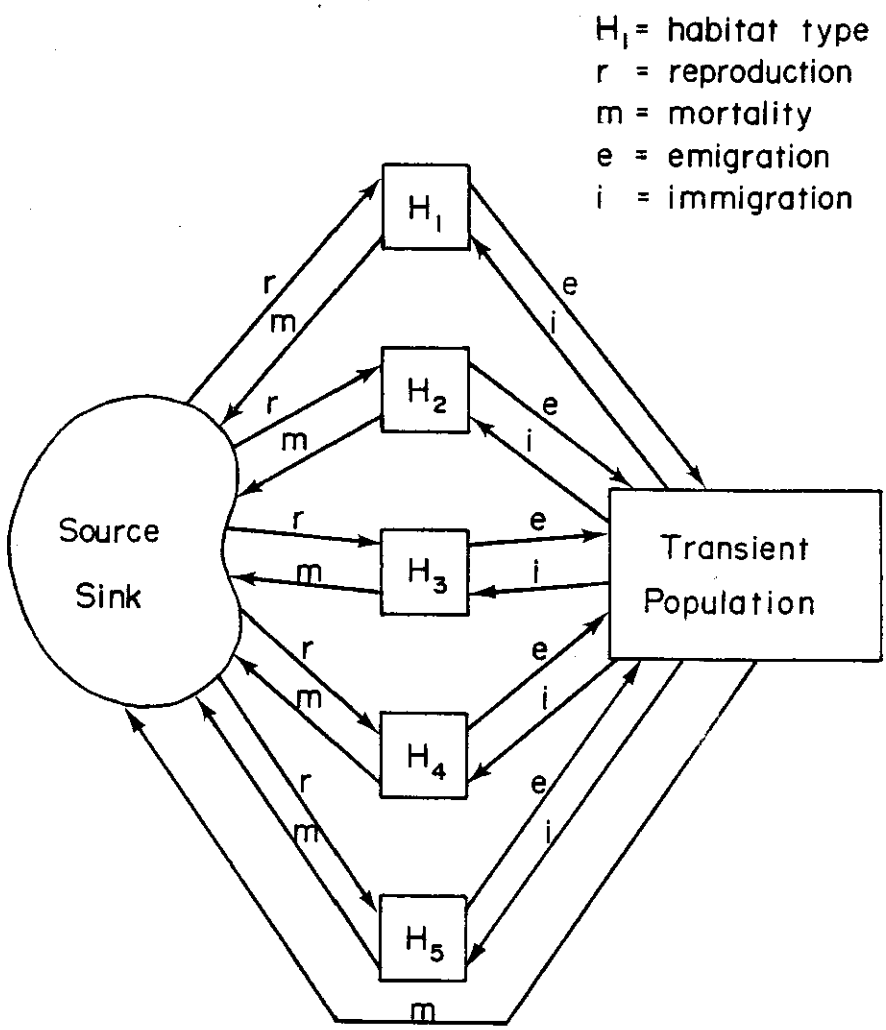


Fig. 29. Schematic illustration of possible dispersal of individuals of one species.

Environment

Individuals of the five small mammal species studied also inhabited the environment surrounding the studied area. These populations can serve as source for immigrants to the studied area and as sink for emigrants from the studied area. The size of the area from which immigrants may enter the studied area was estimated in the following way. The mean dispersal distance for individuals of *P. maniculatus* (Dice and Howard (1951) and other desert rodents (French et al. 1968) is approximately 300 m. A similar mean dispersal distance was assumed for other species. From the mean dispersal distance the area of the environment from which emigrants could invade the studied area can thus be estimated. The data for the densities of the "native" small mammal species were assumed to be equal to those found on the control treatment (Table 2). For the two "exotic" species an arbitrarily low density (0.05/ha) was assigned. The number of individuals that emigrate from the environment and the number of individuals that immigrate to the environment is determined in the same way as the number of emigrants and immigrants in the four habitats.

Hibernation

One of the species *S. tridecemlineatus* hibernates between September and March. This is simulated by an exogenous event that removes all individuals of this species to a dummy state variable in September. A second event reintroduces the individuals of *S. tridecemlineatus* to the system in March. Mortality was assumed to be the only process that influenced hibernating individuals. However, it was found that during warm days, a few individuals of *S. tridecemlineatus* became active. This

was simulated as a function of temperature. Some 15% of the hiberna individuals became active when the mean maximum temperature exceeded 8.5°C.

Model Results and Discussion

The major objective of this simulation model was to apply two processes, emigration and immigration which have been hypothesized t account for species distribution and abundance (Lidicker 1975), to a deterministic simulation model. This type of approach was selected describe the population dynamics of the small mammal species because most species (*O. leucogaster*, *R. megalotis*, and *P. maniculatus*) exhibited discontinuous residency in some of the habitats studied (Tab 2). Because new processes which are not fully studied (Krebs et al. 1976) are incorporated, the performance of the model is judged accor to its ability to simulate the population trends rather than the pop tion densities.

The simulation results exhibited good agreement with the observ data. The observed data were characterized by discontinuous residen of some habitats by several species. This was simulated rather accu rately by the model (Figs. 30-34, model 1). According to the simula results *O. leucogaster* utilized the control treatment throughout the study period but only utilized the nitrogen treatment part of the ye (Fig. 34, model 1). *R. megalotis* exhibited discontinuous residency the nitrogen and the water treatments and was absent from the contro treatment (Fig. 32, model 1). *P. maniculatus* and *S. tridecemlineatus* exhibited the lowest density in the nitrogen + water treatment.

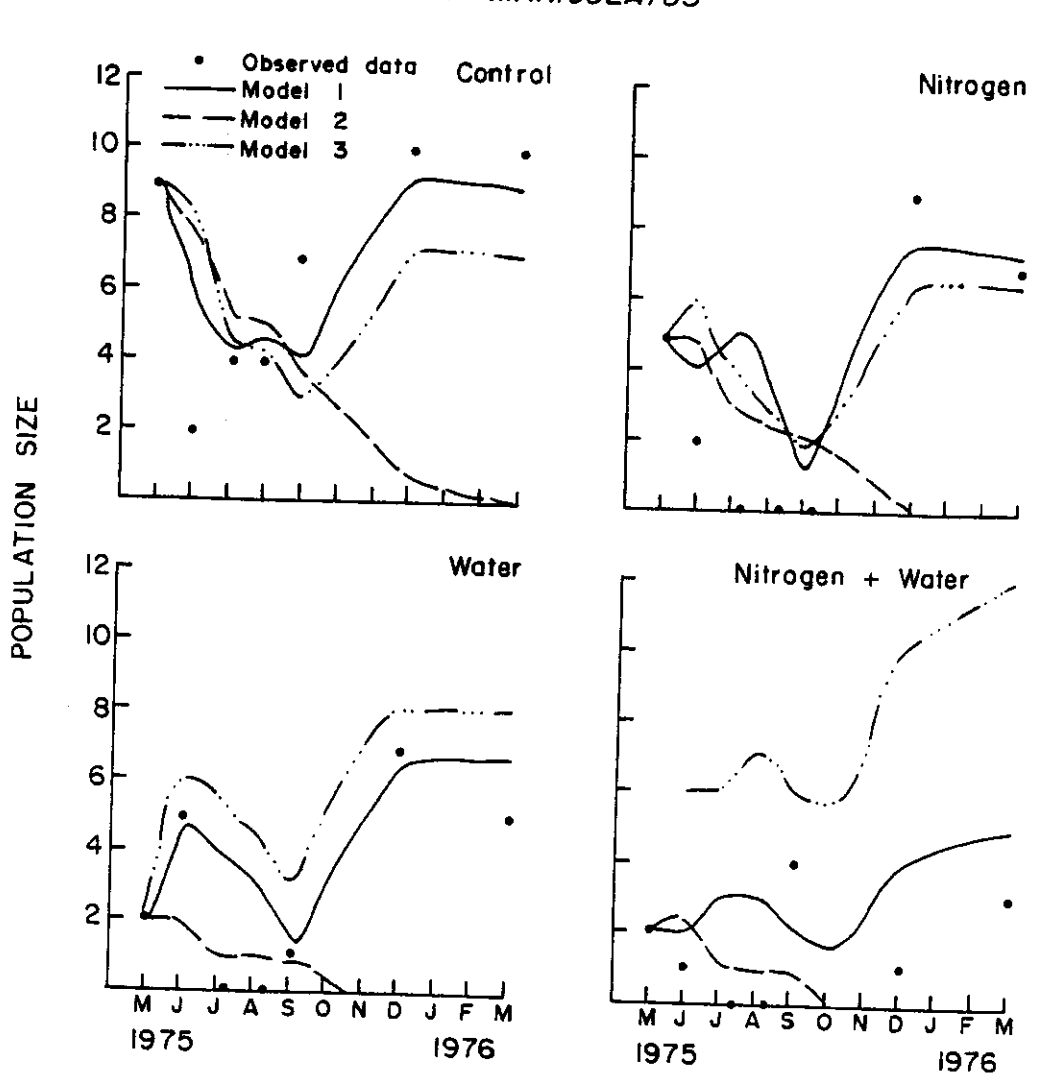


Fig. 30. Population density of the *P. maniculatus* in the four treatments. Dots represent the observed data. Model 1 is the control run simulation results. Model 2 is the simulation results when no emigration or immigration were possible. Model 3 is the simulation results when equal habitat priority values were assigned for all habitats.

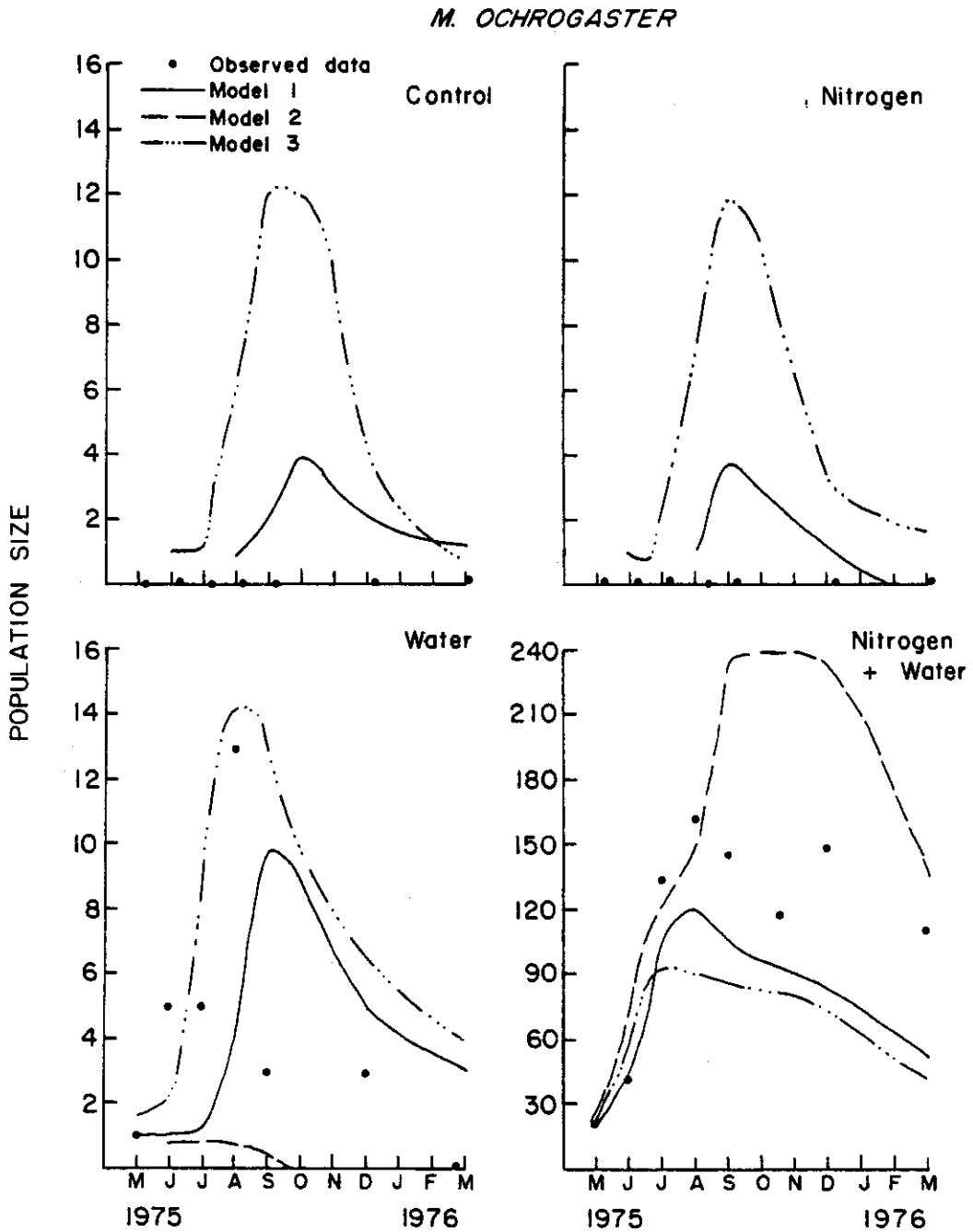


Fig. 31. Population density of *M. ochrogaster* in the four treatments. For footnotes, see Fig. 30.

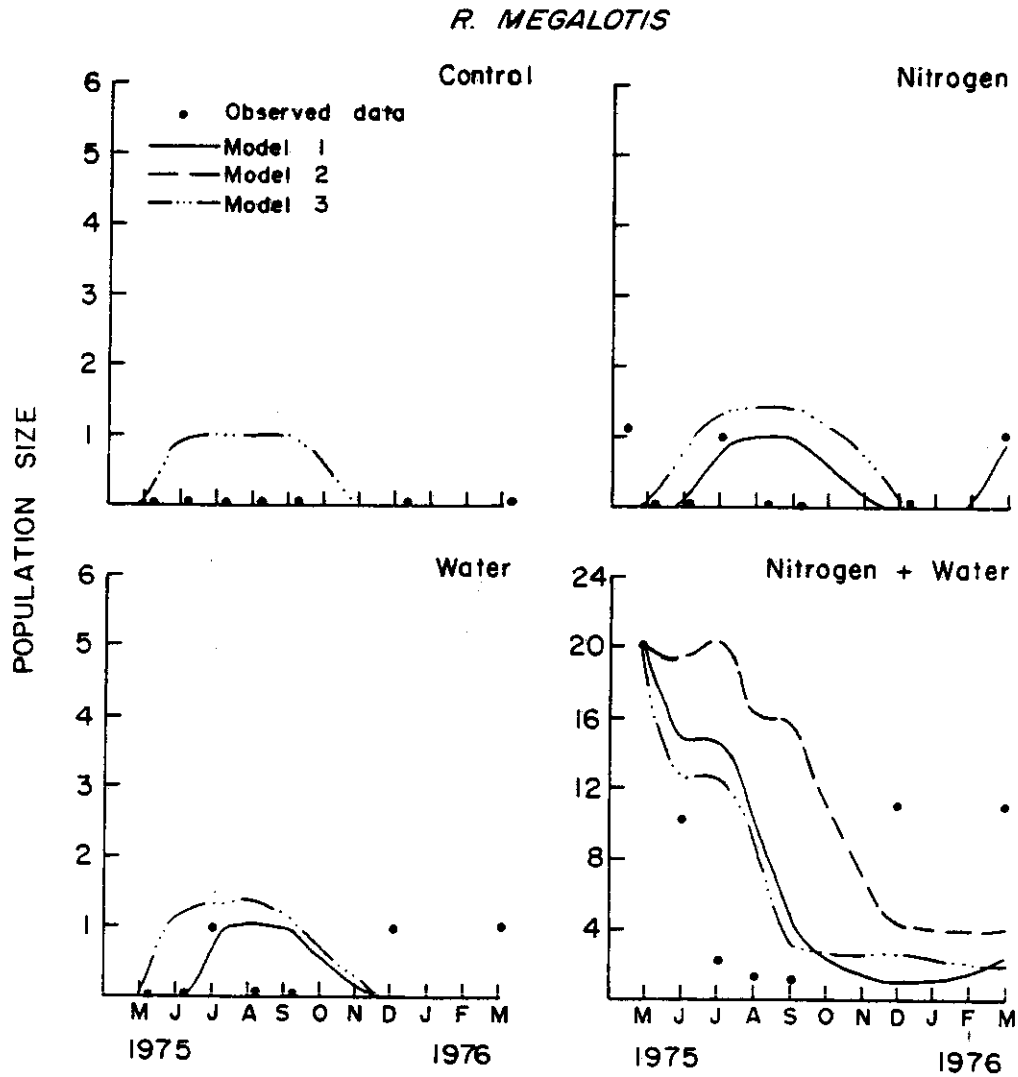


Fig. 32. Population density of *R. megalotis* in the four treatments. For footnotes, see Fig. 30.

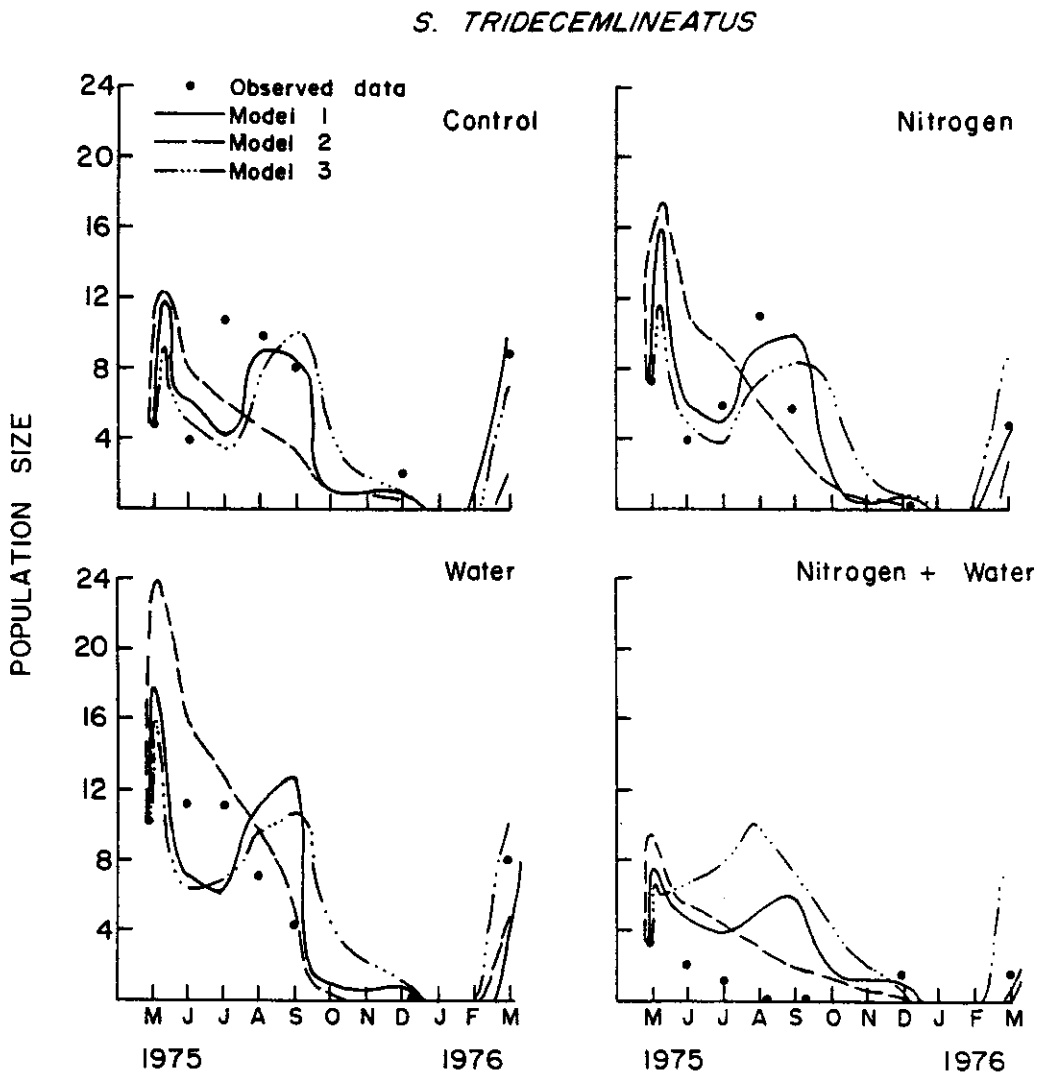


Fig. 33. Population density of *S. tridecemlineatus* in the four treatments. For footnotes, see Fig. 30.

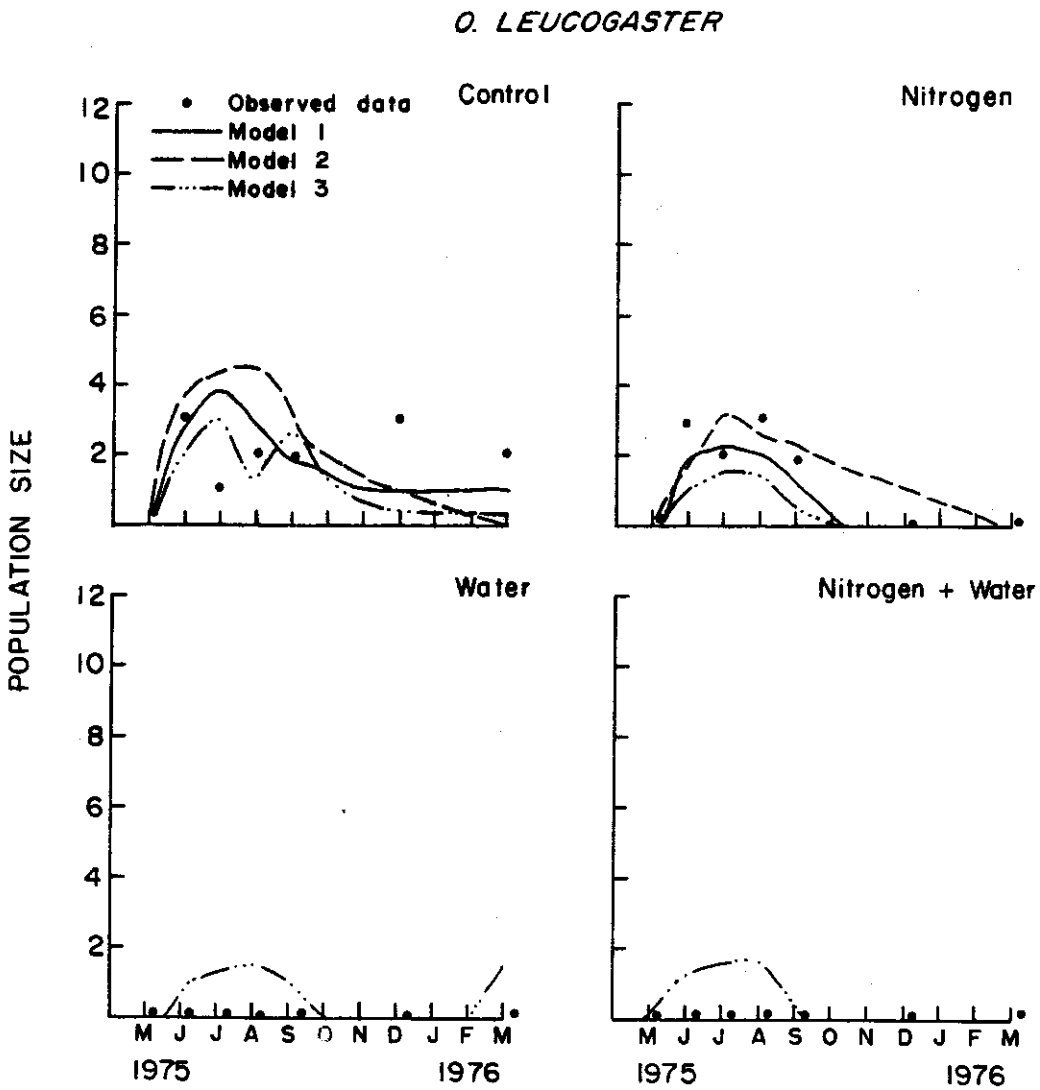


Fig. 34. Population density of *O. leucogaster* in the four treatments. For footnotes, see Fig 30.

The same trends of discontinuous residency were found in the field data, although both *P. maniculatus* and *S. tridecemlineatus* exhibited discontinuous presence in the nitrogen + water treatment according to the observed data, but not in the model results.

The major disagreement between the simulation results and the observed data is that *M. ochrogaster* was found, although in low density, in both the nitrogen and the control treatments in the simulation results but not in the observed data (Fig. 31, model 1).

M. ochrogaster reached high density in the observed and simulated results in the nitrogen + water treatment (Fig. 31). Krebs et al. (1976) reported that at similar densities of *M. townsendii* many individuals emigrated from the population. Assuming that individuals of *M. ochrogaster* behave in a similar way as individuals of *M. townsendii*, many individuals of *M. ochrogaster* emigrated in the present study durin the peak population period. Some of these individuals probably dispersed through the control and the nitrogen treatments but failed to enter traps. Avoidance of traps by small mammals outside their familia home range has already been shown (Fisler 1966). Thus, the fact that n individuals of *M. ochrogaster* were trapped in the control and the nitrc gen treatments can be attributed to behavioral constraints which were not built into the model.

The differential habitat utilization of the small mammal species was also reflected through their density (see section on Community Structure). *M. ochrogaster* and *R. megalotis* were most abundant in the nitrogen + water treatment. *O. leucogaster* and *P. maniculatus* were mo abundant in the control treatment, and *S. tridecemlineatus* was most abundant in the water treatment. These differences between the specie

comparison between the simulated and observed data of each species on the four treatments, I calculated an index which measures the goodness of fit between the simulated and observed results. This was done by summation of the square deviation of the model results from the observed results. The index was scaled by the mean observed density (Table 17). Thus, the goodness of fit for a given species in each of the four treatments is

$$\begin{pmatrix}\text{Goodness}\\ \text{of fit}\end{pmatrix}_{ij} = \sum_{i=1}^{t}\left[\begin{pmatrix}\text{Observed}\\ \text{data}\end{pmatrix}_{ij} - \begin{pmatrix}\text{Simulation}\\ \text{results}\end{pmatrix}_{ij}\right]^2 / \begin{pmatrix}\text{Mean observed}\\ \text{density}\end{pmatrix}_{ij}$$

where $j = 1, \ldots, 4$ habitat types

$i = 1, \ldots, 5$ species

$t = 1, \ldots, 7$ times.

It can be seen (Table 17) that from a total of 25 goodness-of-fit indices, only six are higher than 20.

The simulated density of *M. ochrogaster* exhibited the worst fit with the observed data. However, in both the water and the nitrogen + water treatments the general trends of the simulated results are similar to the observed data. Generally the fit of the simulated species densities on the nitrogen + water treatment exhibited the worst fit to the observed data (Table 17). In this treatment only a few individuals of species other than *M. ochrogaster* were usually caught. An experiment presently being conducted in which individuals of *M. ochrogaster* are removed from one replicate of the nitrogen + water treatment suggests that the other species in this treatment were competitively excluded by *M. ochrogaster*. Because only low densities of the other species were observed in the nitrogen + water treatment, the calculated competition

Table 17. Goodness of fit of the model to the observed data calculated as Σ (observed data-simulation results)^2/mean observed density. (When the mean observed density was zero, the index is given as the sum of the deviations only.)

Species	Control	Nitrogen	Water	Nitrogen + water	Total
M. ochrogaster	11.0	22.0	35.6	120.0	188.6
P. maniculatus	1.7	17.1	9.7	21.3	52.8
R. megalotis	0.0	7.5	9.0	51.7	68.2
S. tridecemlineatus	7.8	4.6	11.1	65.1	88.6
O. leucogaster	11.7	2.3	0.0	0.0	14.0
Total	35.2	53.5	65.4	258.1	412.2

removed from one replicate of the nitrogen + water treatment suggests that the other species in this treatment were competitively excluded by *M. ochrogaster*. Because only low densities of the other species were observed in the nitrogen + water treatment, the calculated competition coefficients were relatively low. Nevertheless, the simulated population densities of all species except *M. ochrogaster* and *R. megalotis* in the nitrogen + water treatment were lower than their densities in other treatments (Figs. 30-34, model 1).

The simulation model also failed to predict the increase in the density of *R. megalotis* in the nitrogen + water treatment during the winter of 1975 and spring of 1976 (Fig. 32, model 1). *R. megalotis* was extremely rare (1 individual) during the summer months of 1975. The increase in density in December may have been the result of emigration from an unknown source. It is very likely that because *R. megalotis* is extremely rare on most shortgrass prairie habitats and the above potential source was not simulated, the model results disagree with the observed data.

The goodness of fit between the model results and the observed data for each species in the four treatments can be ranked as follows: *O. leucogaster* > *P. maniculatus* > *R. megalotis* > *S. tridecemlineatus* > *M. ochrogaster* (Table 17).

The major reason for the disagreements between the model results and the observed data is lack of appropriate data. The mortality and some of the reproduction estimates were taken from the literature (Table 16) from studies that were conducted in different regions and habitats and, thus, are probably different from the mortality rates in the studied area. However, in spite of these constraints, the transient

character of the small mammal species as well as the densities of the small mammals are simulated with good agreement with the observed data.

The model can be further tuned to fit the observed data by changir more constants to time-dependent variables. This can be done with the threshold density for emigration, maximum competition value, and the relation between competition and emigration. However, I believe that a this point in time more field data in which dispersal can be studied a needed. In these studies the relation between competition and emigration should be determined and only then, further model tuning will be valuable.

The number of individuals that were born, died, emigrated, and im migrated from each of the four treatments is summarized in Table 18. can be seen that for some species emigration and immigration accounted for higher changes in their population densities than reproduction and mortality. This result supports Lidicker's (1975) suggestion that dis persal plays an important role in population regulation.

It should be asked whether the percent of individuals that emigrated from each habitat, according to the simulation results (Table 19), exhibited reasonable agreement with field studies. Briese and Smith (1974) reported that a minimum of 27% of the mortality of *M. townsendii* can be accounted for by dispersal. In *M. pennsylvanicus* dispersal accounted for 15% to 70% of the mortality (Myers and Krebs 1971a). Thus, I concluded that the number of emigrating individuals simulated by the model (Table 19) was in good agreement with field studies.

I am not familiar with any detailed model of population dynamics which different habitat types, interactions between species, and

Table 18. Yearly summary of the number of individuals that were born, died, emigrated, and immigrated for each species and treatment (C = control, N = nitrogen, W = water, NW = nitrogen + water).

Species	Habitat	Reproduction	Mortality	Emigration	Immigration
P. maniculatus	C	42	56	62	91
	N	33	43	39	26
	W	30	39	34	61
	NW	17	26	18	31
	Total	122	164	153	209
M. ochrogaster	C	0	4	4	8
	N	0	3	4	7
	W	2	11	9	19
	NW	401	227	225	125
	Total	403	245	242	159
R. megalotis	C	0	0	0	0
	N	1	2	4	1
	W	1	2	1	4
	NW	11	17	16	7
	Total	13	21	21	12
S. tridecemlineatus	C	8	14	35	57
	N	12	15	17	41
	W	17	20	50	68
	NW	5	9	4	18
	Total	42	58	106	184
O. leucogaster	C	5	5	1	2
	N	3	3	1	1
	W	0	0	0	0
	NW	0	0	0	0
	Total	8	8	2	3

Table 19. Percent of individuals that emigrated (according to the simulation results) from the four treatments calculated from "gross mortality" (mortality + emigrants).

Species	Treatment			
	Control	Nitrogen	Water	Nitrogen + Water
P. maniculatus	47	54	46	41
M. ochrogaster	50	66	45	48
R. megalotis	0	63	30	49
S. tridecemlineatus	70	71	70	29
O. leucogaster	28	31	0	0

dispersal are simulated. However, simple two-equation models, in which different habitat types, interactions between species, and dispersal are included, exist (Levins and Culver 1971, Horn and MacArthur 1972, Levin 1974). The conclusion arrived at from analyzing these simple models is that higher numbers of species may coexist in the same habitat when dispersal occurs than when dispersal is ignored. Thus, because of continuous emigration from a nearby source, species can be found in habitats that usually are not occupied by them.

The results of the present model agree with the above conclusions. Because dispersal was simulated, *R. megalotis* was found in the water and the nitrogen treatments (Fig. 32, model 1). For the same reasons *M. ochrogaster* was found in relatively high densities in the water treatment (Fig. 31, model 1), and *O. leucogaster* exhibited discontinuous residency in the nitrogen treatment (Fig. 34, model 1). For further discussion on the importance of dispersal see the section on Model Experiments.

All models should be verified and validated (Wiens and Innis 1974). Garratt (1974) stated that "verification concerns itself with the establishment of the correctness of a model" and involves: (1) tests of the correctness of the computer code, (2) tests to determine the accuracy of the assumption and hypothesis upon which the model is based, and (3) tests of the agreement of observed data and model predictions, using as inputs the data employed in the construction of the model.

"On the other hand, validation is primarily concerned with the determining the usefulness of the model as evidenced in the accuracy of its predictions" (Garratt 1974). For validation a new set of data not used in the construction of the model is needed.

The present model was verified and found to simulate the population densities with good agreement to the observed data. However, the assumption built into the emigration process cannot be verified until more information is available. Likewise, validation of the model is not possible at present because data are not available.

Sensitivity Analysis

The behavior of the model can be studied by performing simple sensitivity analysis (Wiens and Innis 1974). Sensitivity analysis can give some idea about the soundness of the model structure and point at variables to which the model is very sensitive. The latter can be used as an indicator of the accuracy needed when data are collected (Wiens and Innis 1974).

To conduct the sensitivity analysis I adopted the approach suggested by Wiens and Innis (1974). According to this approach experimental runs, in which one or more parameters or input data are changed are compared with the "control" run. The magnitude of the response is calculated as [altered value - control value] ÷ control value. The response of the model is measured as the relation between yearly total number of emigrants and immigrants in the control and experimental rur

I chose to change only those parameters which were associated wi the simulation of dispersal and mortality and, thus, treated the valu of reproduction as correct estimates. The reason is that while very little is known about dispersal and in most cases it is hard to disti guish natural mortality and emigration (Lidicker 1975), reproduction be estimated in a field study.

In Table 20 I summarized the response of the model to a change in one or more input parameters. Only few examples that were found to be typical for the model response are listed.

The model was found to be sensitive to changes in the slope of the line that describes the relation between the competition suffered by a species and the emigration rate (altered Parameter No. 1, Table 20). This finding suggests that this relation may be of great importance in the regulation of natural populations. The model was less sensitive to changes in the value of maximum competition and mortality of emigrants and residents (altered Parameters No. 2, 3, and 4, respectively, Table 20). No changes in the model results were observed when mortality induced by cold weather was changed.

When the values of the competition coefficients suffered by one species were changed, the model showed higher sensitivity (altered Parameters No. 6 and 7, Table 20) relative to changes in the threshold density for emigration (altered Parameters No. 8 and 9, Table 20).

The model exhibited the highest sensitivity to changes of the density of *P. maniculatus* in the environment (altered Parameter No. 10, Table 20). A similar result was obtained for the other "native" species. This suggests that the density of a population from which emigrants may come has great influence on the population dynamics of other nearby populations.

In summary, the model exhibited high sensitivity to changes in the relation between competition and emigration and changes in the density of individuals in the environments. Lower sensitivity of the model was found in small changes in the values of the competition coefficients, mortality, and threshold density for emigration.

Table 20. Summarization of the effects of altering the model constants of input variables on model output estimates of total emigration and immigration. Magnitude of alteration is expressed as percentage of control value. The sensitivity of output estimates to alteration of input is measured as the percent change in output : percent change in input. C = control treatment, N = nitrogen treatment, W = water treatment, NW = nitrogen + water treatment.

Altered parameters	Treatment	Magnitude of alteration (%)	Ratio of output change : input change	
			Emigration	Immigration
Constant that controls the relation between competition and emigration	C	+20	1.46	1.07
	N	+20	1.39	1.08
	W	+20	1.37	0.95
	NW	+20	0.28	0.47
	C	-20	1.31	1.01
	N	-20	1.24	1.27
	W	-20	1.31	0.95
	NW	-20	0.09	0.27
Maximum competition	C	+20	0.68	0.60
	N	+20	0.69	0.56
	W	+20	0.79	0.52
	NW	+20	0.17	0.25
	C	-20	0.97	0.79
	N	-20	0.99	0.73
	W	-20	0.95	0.65
	NW	-20	0.06	0.11
Mortality of emigrants	C	+20	0.29	0.31
	N	+20	0.25	0.31
	W	+20	0.31	0.33
	NW	+20	0.11	0.33
	C	-20	0.32	0.35
	N	-20	0.29	0.35
	W	-20	0.26	0.33
	NW	-20	0.11	0.36
Mortality of residents	C	+20	0.53	0.16
	N	+20	0.49	0.17
	W	+20	0.47	0.20
	NW	+20	0.57	0.44
	C	-20	0.97	0.38
	N	-20	0.94	0.38
	W	-20	1.10	0.52
	NW	-20	2.08	1.65

Table 20. Continued

Altered parameters	Treatment	Magnitude of alteration (%)	Ratio of output change : input change	
			Emigration	Immigration
Mortality from cold weather	C	+20	0.00	0.00
	N	+20	0.00	0.00
	W	+20	0.00	0.00
	NW	+20	0.00	0.00
	C	-20	0.00	0.00
	N	-20	0.00	0.00
	W	-20	0.00	0.00
	NW	-20	0.00	0.00
Competition on *P. maniculatus*	C	+20	0.48	0.27
	C	-20	0.24	0.27
Competition on *O. leucogaster*	C	+20	0.66	0.00
	C	-20	1.28	0.23
Threshold for emigration of *P. maniculatus*	C	+20	0.32	0.27
	C	-20	0.06	0.00
Threshold for emigration of *M. ochrogaster*	NW	+20	0.04	0.04
	NW	-20	0.00	0.00
Density of *P. maniculatus* in the environment	C	+20	1.69	1.65
	N	+20	1.90	1.73
	W	+20	1.76	1.64
	NW	+20	1.39	1.45
	C	-20	1.21	1.26
	N	-20	1.30	1.20
	W	-20	1.47	1.23
	NW	-20	1.39	1.29

The response of the model to parameter change is also illustrated to allow easy comparison in Fig. 35. It can be seen that most parameter changes caused higher changes in emigration relative to immigration. This is probably because most changes were done on parameters directly connected with emigration.

Model Experiments

In a modeling exercise of this nature, where theory with little supporting data is applied, it is probably more instructive to examine the model response to big changes in the proposed mechanisms. To test the response of the model to the mechanisms proposed for emigration and immigration and the importance of dispersal I made two experimental runs. In the first run (model 2) emigration and immigration were prevented and in the second run (model 3) habitat priority was set to be equal for all species in the four habitats. The control run when no modifications were made represents model 1.

The five species responded differentially to the removal of dispersal. *P. maniculatus* became extinct in all four treatments (Fig. 30, model 2). This result indicates that 2 ha represent a small area for this species and its population dynamics is dependent on emigration.

M. ochrogaster, on the other hand, exhibited high population density in the nitrogen + water treatment when dispersal was eliminated (Fig. 31, model 2). However, its population on the water treatment could not sustain itself by reproduction. Removal of dispersal also eliminated the transient character of *R. megalotis* in the water and the nitrogen treatments (Fig. 32, model 2).

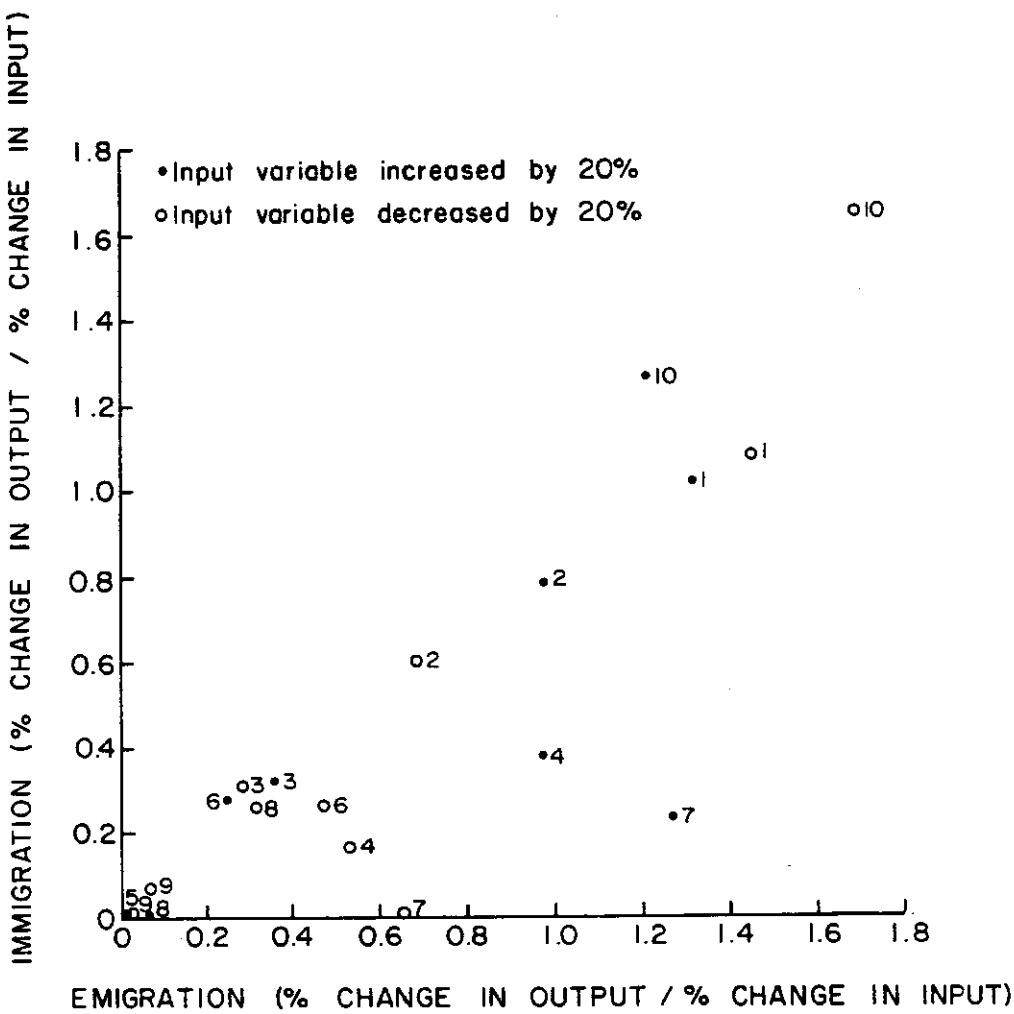


Fig. 35. The relation between percent change in input variable to percent change in output variable of emigration and immigration in the control treatment. The numbers correspond to the parameter value in Table 20. (For further information, see Table 20).

S. tridecemlineatus exhibited higher densities in early summer wher dispersal was eliminated, relative to its densities when dispersal was simulated. However, the densities of *S. tridecemlineatus* were lower in late fall of 1975 and spring of 1976 (Fig. 33, models 2 and 1, respectively).

O. leucogaster generally exhibited higher densities when dispersal was removed relative to its densities when dispersal was simulated (Fig 34, models 2 and 1, respectively).

Thus, the removal of dispersal eliminated the transient character of the communities and the simulated population densities exhibited poo agreement with the observed data. Furthermore, both *P. maniculatus* on all treatments and *M. ochrogaster* on the water treatment became extinct in a relatively short time. This result suggests that even when a habi tat is suitable for the requirements of a given species, local extinctions are likely when dispersal is prevented. This supports the conclusions reached by May (1973) and Roff (1974) that dispersal is a necessary process that prevents local extinctions.

The general trend of the simulation results when the habitat priority indices of all species were set equal for the four habitats is that a smaller difference between the species densities in the four habitats was obtained relative to the control run (Figs. 30-34, models and 1, respectively). Furthermore, all species were found on all treat ments and thus the differential habitat utilization exhibited by the species was partly removed. Both *O. leucogaster* and *R. megalotis* were found in the four treatments (Figs. 34 and 32, respectively, model 3).

Thus, equal indices of habitat priority changed the model results and the community compositions. This result agreed with the results of

an experiment conducted by Wecker (1963). In these experiments Wecker showed that species of small mammals exhibited preference for different habitat types.

In summary, the removal of dispersal from the simulation model resulted in significant changes that point to the importance of dispersal in species abundance and distribution. When the habitat priority indices of the species were assumed to be equal, the differential habitat utilization exhibited by the small mammals was partly removed.

Summary and Conclusions

Emigration and immigration are considered to be an important factor in population regulation (Errington 1956; Lidicker 1962, 1975). However, because of the difficulty in measuring these processes in the field, very little is known about their actual importance (Myers and Krebs 1971a). In the few field studies where emigration was measured, it was found to account for up to 70% of what usually is defined as mortality (Myers and Krebs 1971a).

The causes for emigration are usually attributed to genetic causes favored by natural selection (Howard 1960, Myers and Krebs 1971a) as well as intra- and interspecific competition between individuals (Fretwell 1972, Lidicker 1975, Grant 1976).

The results of the present field study also support the hypothesis that emigration and immigration may be responsible for species distribution (section on Community Structure) and species abundance (section on *Microtus* Population Dynamics).

A population dynamics simulation model was built in which emigration was considered a function of competition and immigration a function of

habitat priority index, habitat size, and the distance between habitats. Genetic differences between individuals was not considered.

The simulation results exhibited good agreement with the trends of the natural populations. The transient pattern of the small mammal communities and the differential habitat utilization exhibited by the species was simulated by the model. The densities of the simulated species also exhibited satisfactory agreement with the observed data.

Sensitivity analysis in which input parameters were increased or decreased showed that the model is sensitive to the value of the constant that describes the relations between competition and emigration and the density of individuals in the environment. Other variables like competition and mortality had only small impact on the model results. When the habitat priority indices of the species were set equal for all habitats, all the species were found to utilize the four habitats and thus the differential habitat utilization observed in the species was not simulated. On the other hand, when the processes of emigration and immigration were removed, the transient character of the small mammal species disappeared.

The model, simple as it is, points to the importance of emigration and immigration in determining species distribution and abundance. However, more field work in which dispersal can be studied (see Suggestions for Future Work, No. 5, 6, and 7) is necessary before the model could be validated and the relative importance of the processes discussed could be determined. A report of the modeling effort and costs is summarized in Appendix IX.

SUGGESTIONS FOR FUTURE WORK

1. It was shown in this work that the nitrogen + water treatment which had the highest amount of herbage and arthropod biomass and also exhibited the highest vertical foliage diversity had the lowest small mammal species diversity. Nevertheless, it had the highest number of individuals which belong to two "exotic" species. The distance between the nitrogen + water treatment and structurally similar habitats was proposed to be the reason for the low species diversity. This assumption can easily be tested by introducing one or more species that usually inhabit tallgrass prairie to the nitrogen + water treatment.

2. It was shown in this study that the small mammal species differentially utilized the four studied habitats. Another study, in which the distribution of the small mammal species in the natural habitats of the shortgrass prairie ecosystem, will help to confirm the relation between small mammal species abundance and distribution and habitat structure. This type of study may also contribute to our understanding of the role of the two "exotic" species on the observed "native" species distribution.

3. The small mammal community composition formed in the three man-made habitats was hypothesized to be an outcome of habitat priority and interspecific competition. However, the relative importance of each factor could not be determined in the initial study. Experiments in which potential competitors would be removed from an area would point to the importance (or lack of importance) of interspecific competition in determining the species distribution and abundance of the small mammals.

4. It was suggested that *D. ordii* avoided most of the shortgrass prairie subhabitats because of seed shortage. However, this hypothesis was based on studies performed on one grid. Replication of this experiment is necessary to support this hypothesis. Also, it was not clear from the experiment if seed type or seed size availability limited the distribution of *D. ordii*. An additional experiment in which one type o seed in different sizes would be supplemented in different areas would clarify this point.

5. The result of this study suggested that immigrants rather than emigrants are probably responsible for the cycle observed in most microtine populations. This suggestion was based on the studied populations of *M. ochrogaster* being semi-isolated and thus while emigration was probably normal, immigration was most likely very low. This hypothesis can be tested by fencing one of the nitrogen + water replicates. The second replicate can serve as control. By leaving one part of the fenced replicate open and thus forcing emigrants to enter pitfall traps (by drift fences), emigration rate can then be measured and immigration avoided. Electrophoresis analysis would help to determine the genetic composition of emigrants and resident individuals.

6. The simulation model results are probably most appropriate to suggest future research. The most important result, which is basic to the mechanism of emigration built into the model, is the suggested relation between competition and emigration. This relation can probably be tested in fenced grids where the species densities are known. One-way doors would help to detect emigrants.

7. More studies of small mammals in natural habitats that I have suggested in Suggestion No. 2 (above) will also serve to validate the

model. The data used to build the model were taken from a small area and thus for most species only few individuals were present. By sampling small mammals in natural habitats many replicates can be established and thus a better understanding of the patterns of the species population dynamics can be obtained.

GENERAL SUMMARY

The community structure of five small mammal species (*Peromyscus maniculatus, Microtus ochrogaster, Reithrodontomys megalotis, Spermophilus tridecemlineatus,* and *Onychomys leucogaster*) inhabiting six 1-ha manipulated shortgrass prairie plots and two 1-ha control plots was studied for a 1-year period. The manipulation of the shortgrass prairie has been conducted by application of water, nitrogen, or both. The vegetation biomass and vertical structure have responded differentially to the manipulation, and a gradient of prairie habitats similar to shortgrass (control treatment), midgrass (water and nitrogen treatments), and tallgrass habitat (nitrogen + water treatment) have been formed.

The small mammal species also responded to the habitat modification. Two new species (*M. ochrogaster* and *R. megalotis*), which are not typical to most of the shortgrass prairie habitat types, have invaded the area. The community composition of the small mammal species was different in each of the treatments. *O. leucogaster* was found only in the control and the nitrogen treatments. The greatest numbers of *R. megalotis* and *M. ochrogaster* were found in the nitrogen + water treatment, although a relatively low population density of *M. ochrogaster* was established in the water treatment and few individuals of *R. megalotis* were caught infrequently in both the water and the nitrogen treatments.

The densities of the small mammal species were also different in the four treatments. Abundances of the small mammal species in the different treatments correlated with a measure of the habitat complexity--foliage height diversity (FHD). The three native species showed

negative correlation with FHD, while the two exotic species exhibited positive correlation with FHD.

Species diversity of the small mammals in the different stress plots exhibited high negative correlation with FHD in contrast to that reported for natural habitats. The difference between the relation of species diversity of small mammal species and FHD in man-made and natural habitats was interpreted in terms of colonization rate, the size of the stress plots, the distance between the stress plots and potential source populations, and the short time that has passed since the creation of the treatments (6 years).

Possible explanations suggested to explain the differences between the community structures of the small mammals in the four treatments were interspecific competition between the species, habitat priorities, or both.

Interspecific competition between the small mammals was studied for the food and the habitat dimensions of the ecological niche. The diet of the species was studied by analyzing the fresh pellets by microscopic analysis. Competition indices for food and habitat were calculated. The elements of the food and habitat competition matrices were multiplied and one overall competition matrix for each treatment and sample date was obtained. The competition coefficients between species varied among habitats and dates. These changes were interpreted as an evidence that competition between species probably was not intensive through all the seasons of the year; the species probably competed only in a relatively short period when resources were limited.

The data suggest that *M. ochrogaster* was found primarily in the nitrogen + water treatment because of habitat priority and the native

analysis of niche breadth also suggested that interspecific competition may play an important role in determining community structure. Unfortunately, it was not possible without further experiments to determine the relative importance of interspecific competition and habitat preference, and further experiments are suggested to examine this subject.

Alfalfa pellets and whole oats were spread evenly in a separate 1-ha plot every 10-14 days to determine if food was limiting. None of the small mammal species that inhabited this plot responded to the excess of food because normally most consume seeds only in small amounts. However a new species *Dipodomys ordii* invaded this plot, persisted in it, and had 95% oats in its diet. No individuals of this species were trapped around the plot and it was concluded that the invasion of *D. ordii* to the food plot was a response to the addition of the food. It is probabl that seed availability limits the distribution of *D. ordii* in most habitat types of the shortgrass prairie.

The population dynamics and demographic parameters of *M. ochrogaste* were analyzed. The numbers of the other species were too small for such analyses.

M. ochrogaster invaded the nitrogen + water treatment in 1971 and exhibited a progressive yearly increase in population peak densities. Unlike most populations of microtines that exhibit a typical 2- to 4-year cycle, *M. ochrogaster* in the nitrogen + water treatment plots had only an annual cycle. No correlation was found between the density of *M. ochrogaster* and the amount of the major food types taken by this species nor the total herbage biomass, suggesting that it was not food limited. The five demographic parameters (reproduction, mortality, sex ratio, body weight, and population growth rates) of this population do

not differ from literature pattern of change for these parameters in "normal" cyclic populations of the same species.

It was suggested that the similarity in demographic parameters between cyclic and noncyclic populations of microtines point to the importance of the degree of isolation of the populations. Continuous populations of microtines show normal cycle; fenced (isolated) populations do not show the cycle and the populations attain high densities; and semi-isolated populations show "normal" densities and only an annual cycle.

The current theories in the literature on the importance of dispersal and the results of this work were utilized to construct a population dynamics model in which reproduction and mortality were assumed to be time-dependent constants. Emigration rates were determined from the relative inter- and intraspecific competition suffered by a given species at a given habitat and time. Immigration was assumed to be dependent on the size of the habitat, its distance, and habitat priority index.

The model simulated with good agreement the community compositions observed in the field study and the species changes in density. Only in one treatment, the nitrogen + water treatment, did the model results greatly differ from the observed densities. However, although the actual densities in this treatment were not simulated with good agreement with the observed data, the general trends of the population dynamics were similar.

The model is not sensitive to small changes in competition, mortality, and threshold density before emigration can occur. The model showed high sensitivity to small changes in the slope of the line that

describes the relation between competition and emigration and to smal changes in the density of the species in the environment.

Environmental runs in which dispersal was prevented resulted in significant changes in the community compositions and the persistence *P. maniculatus* in all four treatments. When the habitat priority ind of all species was set equal for all habitats, the differential habit utilization exhibited by all the species was partly removed because a species were found in all four habitats. The model results support t current theories on the importance of dispersal in determining specie distribution and abundance.

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Appendix I.

Mean percent density of major (≥5%) types of animal and plant matter in the feces of *Peromyscus maniculatus*. (Numbers in parentheses represent sample size on the ESA plots. More than one fecal sample may have been taken from the same individual during the sampling period.)

Treatment	Period													
	May 1975		June 1975		July 1975		Aug. 1975		Sept. 1975		Dec. 1975		March 1976	
	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)
Control	Arte frig	8	Coleop.	46	Seed	57	Seed	18	Unid inse	62	Orthop.	91	Arte frig	38
	Sals kali	5	Lepidop.	21	Coleop.	21	Coleop.	41	Coleop.	32			Erig dive	14
	Unid inse	42	Araneida	19	Hymenop.	57	Diptera	32					Coleop.	11
	Orthop.	35	Hymenop.	12									Hymenop.	7
													Lepidop.	15
	(1)		(2)		(4)		(7)		(1)		(10)		(13)	

Mean percent density of major (≥5%) types of animal and plant matter in the feces of *Microtus ochrogaster*. (Numbers in parentheses represent sample size on the ESA plots. More than one fecal sample may have been taken from the same individual during the sampling period.)

Treatment	Period													
	May 1975		June 1975		July 1975		Aug. 1975		Sept. 1975		Dec. 1975		March 1976	
	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)
Water	--	--	Agro smit	38	Care eleo	34	Care eleo	17	Seed	44	Seed	40	--	--
			Care eleo	31	Stip coma	8	Bout grac	16	Arte frig	34	Erig dive	25		
			Bout grac	10	Arte frig	8	Spor cryp	10			Arte frig	20		
			Hymenop.	6	Atri cane	5	Arte frig	8						
					Agro smit	5	Sals kali	6						
					Unid inse	12	Unid inse	36						
			(5)		(8)		(12)		(3)		(3)			
Nitrogen + water	Arte frig	73	Care eleo	32	Care eleo	29	Seed	13	Seed	55	Seed	36	Arte frig	89
	Care eleo	16	Arte frig	30	Bout grac	23	Care eleo	27	Arte frig	19	Arte frig	31		
			Bout grac	15	Spha cocc	13	Bout grac	11	Care eleo	17	Care eleo	21		
			Coleop.	12	Arte frig	7	Arte frig	5						
					Atri cane	7	Unid inse	11						
					Coleop.	6	Coleop.	9						
							Hymenop.	8						
	(2)		(20)		(17)		(12)		(13)		(18)		(17)	

Appendix I. (Cont.)

Mean percent density of major (≥5%) types of animal and plant matter in the feces of *Onychomys leucogaster*. (Numbers in parentheses represent sample size on the ESA plots. More than one fecal sample may have been taken from the same individual during the sampling period.)

Treatment	Period													
	May 1975		June 1975		July 1975		Aug. 1975		Sept. 1975		Dec. 1975		March 1976	
	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)
Control	--	--	Orthop.	52	Coleop.	91	Coleop.	84	Coleop.	94	Unid inse	67	--	--
			Coleop.	26			Hymenop.	9			Coleop.	13		
				(9)		(3)		(2)		(1)	Araneida	9		
												(1)		
Nitrogen	--	--	Orthop.	66	Coleop.	50	Coleop.	84	Coleop.	32	--	--	--	--
			Hymenop.	13	Orthop.	49	Orthop.	6	Hymenop.	31				
			Coleop.	10					Orthop.	30				
				(2)		(2)		(11)		(3)				

Mean percent density of major (≥5%) types of animal and plant matter in the feces of *Spermophilus tridecemlineatus*. (Numbers in parentheses represent sample size on the ESA plots. More than one fecal sample may have been taken from the same individual during the sampling period.)

Treatment	Period													
	May 1975		June 1975		July 1975		Aug. 1975		Sept. 1975		Dec. 1975		March 1976	
	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)	Animal and Plant Matter	Mean Density (%)
Control	Arte frig	14	Arte frig	7	Seed	27	Orthop.	56	Coleop.	47	Koch scop	10	Arte frig	47
	Coleop.	33	Lepidop.	66	Coleop.	35	Hymenop.	29	Hymenop.	18	Unid inse	83	Town gran	21
	Orthop.	27	Hymenop.	12	Hymenop.	23	Coleop.	5	Orthop.	14	Coleop.	5	Hymenop.	7
	Hymenop.	9			Orthop.	9	Diptera	5	Hemip.	12				
		(6)		(2)		(15)		(10)	Araneida	7		(1)		(5)
										(1)				
Nitrogen	Arte frig	18	Arte frig	15	Seed	78	Orthop.	53	Koch scop	6	--	--	Seed	30
	Bout grac	6	Coleop.	39	Coleop.	10	Hymenop.	23	Coleop.	38			Arte frig	34
	Coleop.	31	Lepidop.	36			Coleop.	17	Orthop.	34			Town gran	7
	Orthop.	18											Coleop.	10
	Lepidop.	13											Hymenop.	5
		(6)		(2)		(9)		(16)		(4)				(5)
Water	Coleop.	48	Orthop.	35	Coleop.	71	Coleop.	40	Seed	20	--	--	Seed	21
	Orthop.	18	Araneida	35	Hymenop.	15	Hymenop.	33	Orthop.	24			Arte frig	23
	Hymenop.	16	Coleop.	7	Orthop.	6	Orthop.	18	Coleop.	24			Town gran	19
									Hymenop.	16			Orthop.	11
		(9)		(1)		(10)		(10)		(1)			Hymenop.	11
														(5)
Nitrogen + water	Hymenop.	33	Arte frig	16	--	--	--	--	--	--	--	--	--	--
	Coleop.	29	Coleop.	69										
	Orthop.	24	Hymenop.	5										

Appendix I. (Cont.)

List of code names used for animal and plant matter found in the diet of the small mammal species

Plant:	Species
Agro smit	*Agropyron smithii*
Arte frig	*Artemisia frigida*
Atri cane	*Atriplex canescens*
Bout grac	*Bouteloua gracilis*
Care eleo	*Carex eleocharis*
Erig dive	*Erigeron divergens*
Koch scop	*Kochia scoparia*
Sals kali	*Salsola kali*
Spha cocc	*Sphaeralcea coccinea*
Spor cryp	*Sporobolus cryptandrus*
Town gran	*Townsendia grandiflora*

Arthropods:	Order
Coleop	Coleoptera
Hemip	Hemiptera
Homop	Homoptera
Hymeno	Hymenoptera
Lepido	Lepidoptera
Orthop	Orthoptera
Unid inse	Unidentified insects

Appendix II.

Examples of Calculations Used in the Text

Suppose that two species appear in two environments (A and B) in the following frequencies

	Environment	
Species	A	B
1	0.66	0.34
2	0.00	1.00

1. Calculation of species diversity:

$$H'' = -\Sigma P_i \ln P_i^{*}$$

for species 1

$$H'' = (-1) \times (0.66 \cdot \ln 0.66 + 0.34 \cdot \ln 0.34) = 0.63$$

for species 2

$$H'' = (-1) \times (0.00 \cdot \ln 0.00 + 1.00 \cdot \ln 1.00) = 0.00$$

2. Calculation of niche breadth:

$$\ln B = -\Sigma P_i \ln P_i = H''$$

for species 1

$$\ln B = 0.63$$

$$B = 1.87$$

for species 2

$$\ln B = 0$$

$$B = 1$$

*See method section for symbols.

Appendix II. (Cont.)

3. Calculation of competition indices:

$$\alpha_{ij} = \sum_h P_{ih} \cdot P_{jh} / \sum_h P_{ih}^2$$

$$\alpha_{21} = (0.66 \cdot 1.00 + 0.34 \cdot 0.00)/(1^2) = 0.66$$

$$\alpha_{12} = (0.66 \cdot 1.00 + 0.34 \cdot 0.00)/(0.66^2 + 0.34^2) = 1.18$$

The resultant competition mainly is

$$\begin{bmatrix} 1.00 & 0.66 \\ 1.18 & 1.00 \end{bmatrix}$$

4. Calculating average competition $\bar{a}$:

$$\bar{a} = (1.18 + 0.66)/2 = 0.92$$

5. Example of competition matrices multiplication (by elements):

$$\begin{bmatrix} 1.00 & 0.50 \\ 0.70 & 1.00 \end{bmatrix} \cdot \begin{bmatrix} 1.00 & 0.90 \\ 0.10 & 1.00 \end{bmatrix} = \begin{bmatrix} 1.00 & 0.45 \\ 0.70 & 1.00 \end{bmatrix}$$

6. Calculating similarity index. Suppose that two species appear in two environments (A and B) in the following densities:

	Environment	
Species	A	B
1	2	6
2	0	5

$$SI = 2 \sum_{i=1}^{n} w_i / \sum_{i=1}^{n} (a_i + b_i)$$

$$SI = 2 \cdot (0 + 5)/(2 + 0 + 6 + 5) = 0.77$$

Appendix III.

Mean density (number/0.5 m^2) and standard error of insects trapped on the four treatments (C = control treatment; N = nitrogen treatment; W = water treatment; NW = nitrogen + water treatment. Sample size was 10 for all dates and treatments.

Order	June 1975				August 1975			
	C	N	W	NW	C	N	W	NW
Araneida	3.3 ± 0.77	3.9 ± 2.08	2.7 ± 0.74	8.2 ± 0.92	3.3 ± 0.64	2.4 ± 0.85	5.8 ± 3.49	2.1 ± 0.69
Coleoptera	2.9 ± 0.57	5.2 ± 0.77	8.4 ± 1.28	7.5 ± 1.42	4.1 ± 0.61	5.0 ± 0.69	6.6 ± 2.01	12.1 ± 4.63
Diptera	2.4 ± 0.53	2.9 ± 0.84	2.5 ± 0.67	1.0 ± 0.41	8.7 ± 0.72	10.6 ± 2.54	5.5 ± 1.55	3.6 ± 1.55
Hemiptera	1.0 ± 0.21	1.1 ± 0.29	1.9 ± 0.47	3.8 ± 2.02	1.4 ± 0.39	2.8 ± 0.68	1.5 ± 0.61	1.6 ± 0.48
Homoptera	2.9 ± 0.56	7.2 ± 1.30	6.3 ± 1.40	1.4 ± 0.37	31.0 ± 4.85	91.9 ± 9.95	22.4 ± 6.88	25.5 ± 8.80
Hymenoptera	43.0 ± 13.08	16.0 ± 2.84	15.5 ± 5.05	1.6 ± 0.66	46.8 ± 6.88	73.9 ± 11.56	20.2 ± 6.30	4.3 ± 0.82
Lepidoptera	0.4 ± 0.19	0.5 ± 0.23	0.1 ± 0.10	--	0.1 ± 0.10	0.1 ± 0.10	0.1 ± 0.10	0.4 ± 0.32
Orthoptera	0.6 ± 0.22	0.3 ± 0.22	0.9 ± 0.42	0.2 ± 0.14	0.5 ± 0.17	1.2 ± 0.34	1.5 ± 0.54	1.1 ± 0.37

Order	September 1975				December 1975			
	C	N	W	NW	C	N	W	NW
Araneida	1.3 ± 0.44	1.8 ± 0.37	3.6 ± 0.91	16.0 ± 4.06	0.2 ± 0.12	0.4 ± 0.28	1.1 ± 0.37	7.3 ± 2.01
Coleoptera	5.3 ± 0.92	5.2 ± 1.23	34.7 ± 5.68	35.4 ± 9.63	2.4 ± 0.84	1.8 ± 2.20	3.1 ± 0.62	9.4 ± 2.45
Diptera	6.8 ± 1.22	4.8 ± 0.95	12.4 ± 2.15	6.7 ± 1.99	0.4 ± 0.23	0.4 ± 0.32	1.2 ± 0.45	0.8 ± 0.34
Hemiptera	0.4 ± 0.24	0.5 ± 0.14	4.7 ± 0.98	4.6 ± 1.54	7.2 ± 6.85	--	0.6 ± 0.36	0.4 ± 0.17
Homoptera	6.5 ± 1.80	7.2 ± 2.90	26.0 ± 5.55	23.4 ± 5.15	10.3 ± 4.23	3.3 ± 1.90	15.5 ± 4.69	9.2 ± 2.66
Hymenoptera	30.5 ± 9.84	27.5 ± 6.98	49.6 ± 23.49	9.0 ± 3.27	3.1 ± 1.31	1.1 ± 1.00	2.3 ± 0.70	2.1 ± 0.66
Lepidoptera	0.6 ± 0.19	2.2 ± 0.73	2.3 ± 0.59	1.4 ± 0.40	0.6 ± 0.19	0.1 ± 0.10	0.1 ± 0.10	0.1 ± 0.10
Orthoptera	0.5 ± 0.23	0.8 ± 0.25	8.2 ± 2.39	5.4 ± 1.50	--	--	--	--

Appendix IV. Statistical Analyses

Analysis of variance for weights of *M. ochrogaster*.

Source	df	SS	MS	F	p	Q
Replicate	1	1.22	1.22	1.11	0.311	
Month	6	78.65	13.10	11.88	0.001	2.56
linear	1	0.56	0.56	0.51	0.488	
quadratic	1	10.14	10.14	9.19	0.009	
cubic	1	43.66	43.66	39.57	0.001	
quartic	1	0.13	0.13	0.12	0.730	
quintic	1	13.01	13.01	11.79	0.004	
sextic	1	11.13	11.13	10.09	0.007	
Sex	1	0.68	0.68	0.62	0.445	
Month * Sex	6	41.62	6.93	6.29	0.003	4.24, 3.62, 2.27
Error 1 = reps	13	14.34	1.10	0.62	0.838	
Error 2 = quadrats	520	925.47	1.78			
Total	547					

Analysis of variance between weights of *M. ochrogaster* on the water only and the nitrogen + water treatments.

Source	df	SS	MS	F	p	Q
Treatment	1	75.51	75.51	28.82	0.001	
Sex	1	0.22	0.22	0.08	0.772	
T * S	1	0.57	0.57	0.22	0.639	
Residual	658	1724.33	2.62			
Total	661					

Appendix IV. (Cont.)

Analysis of variance between weight of males *M. ochrogaster* in breeding and nonbreeding conditions.

Source	df	SS	MS	F	p	Q
Breeding condition	1	13.12	12.12	9.92	0.020	
Month	5	24.53	4.91	3.71	0.003	3.28
linear	1	11.11	11.11	8.41	0.004	
quadratic	1	0.64	0.64	0.48	0.486	
cubic	1	0.06	0.06	0.04	0.837	
quartic	1	9.85	9.85	7.45	0.007	
quintic	1	2.86	2.86	2.17	0.142	
B * M	5	5.16	1.03	0.78	0.564	
Residual	208	274.89	1.32			
Total	219					

Analysis of variance for survival rates during increasing, peak, and decreasing population of *M. ochrogaster*.

Source	df	SS	MS	F	p	Q
Sex	1	0.002	0.002	0.147	0.709	
Month	2	0.142	0.071	4.411	0.042	0.22
S * M	2	0.003	0.002	0.118	0.889	
Residual	10	0.161	0.016			
Total	15					

Appendix IV. (Cont.)

Analysis of variance for mean number of individuals caught/hr assuming activity at all hours.

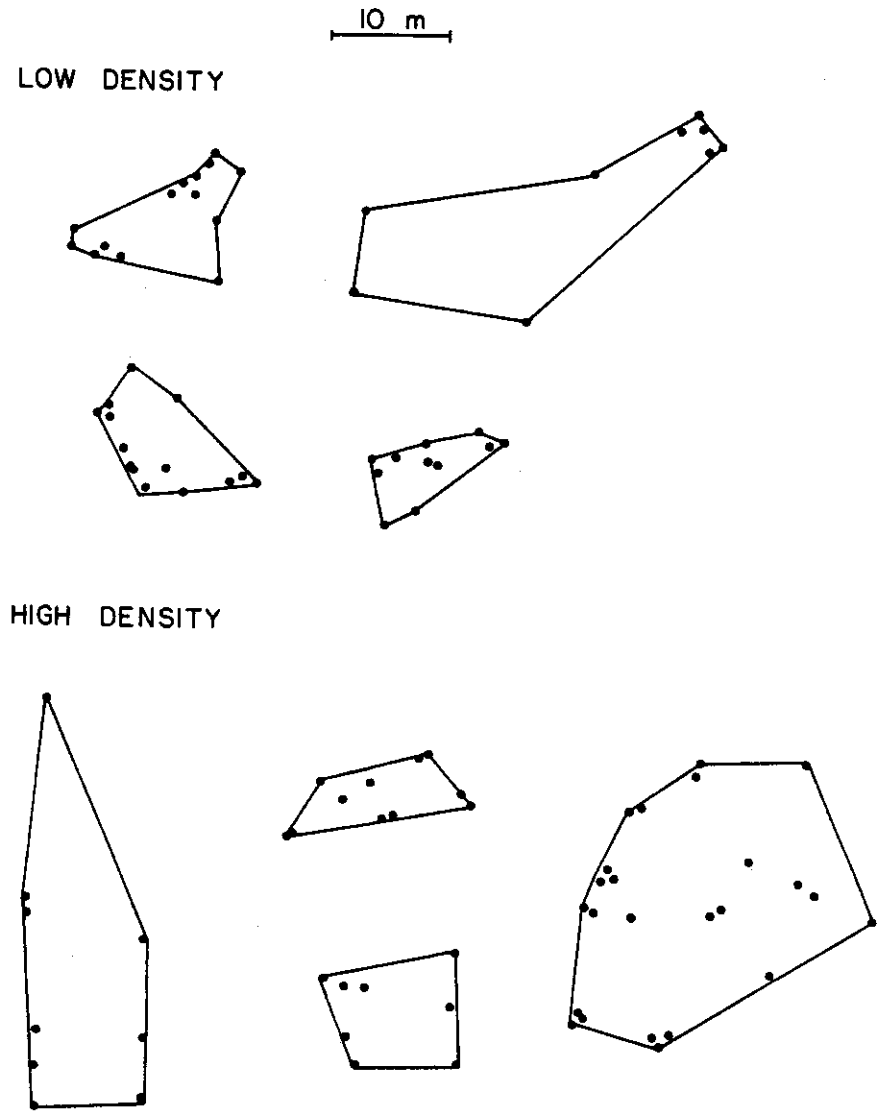
Source	df	SS	MS	F	p	Q
Month	1	0.54	0.54	3.77	0.072	
Time of day	2	0.36	0.18	1.27	0.311	
M * T	2	0.27	0.13	0.94	0.413	
Residual	14	2.00	0.14			
Total	19					

Analysis of variance for mean number of individuals caught/hr assuming active only during the daylight hours.

Source	df	SS	MS	F	p	Q
Month	1	5.41	5.41	5.00	0.042	
Time of day	2	22.01	11.01	10.16	0.002	1.57
M * T	2	7.00	3.50	3.23	0.070	2.79, 2.22, 1.82
Residual	14	15.16	1.08			
Total	19					

Appendix V.

Home ranges determined by radiotelemetry equipment. Each point represents one location reading.



Appendix VI.

List of variable code names used in the simulation model.

```
C     ********************************************************************************
C
C     SPECIES NAME
C     MIOC - M. OCHROGASTER
C     ONLE - O. LEUCOGASTER
C     PEMA - P. MANICULATUS
C     REME - R. MEGALOTIS
C     SPTR - S. TRILECEMLINEATUS
C     -------------------------
C     AMOC - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND ONLE IN CONTROL TREAT.
C     AMON - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND ONLE IN NITROGEN TREAT.
C     AMONW- MAX. COMPETITION POSSIBLE BETWEEN MIOC AND ONLE IN NITROGEN+ WATER
C     AMOW - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND ONLE IN WATER TREAT.
C     AMPC - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND PEMA IN CONTROL TREAT.
C     AMPN - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND PEMA IN NITROGEN TREAT.
C     AMPNW- MAX. COMPETITION POSSIBLE BETWEEN MIOC AND PEMA IN NITROGEN+WATER
C     AMPW - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND PEMA IN WATER TREAT.
C     AMRC - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND REME IN CONTROL TREAT.
C     AMRN - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND REME IN NITROGEN TREAT.
C     AMRNW- MAX. COMPETITION POSSIBLE BETWEEN MIOC AND REME IN NITROGEN + WATER
C     AMRW - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND REME IN WATER TREAT.
C     AMSC - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND SPTR IN CONTROL TREAT.
C     AMSN - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND SPTR IN NITROGEN TREAT.
C     AMSNW- MAX. COMPETITION POSSIBLE BETWEEN MIOC AND SPTR IN NITROGEN +WATER
C     AMSW - MAX. COMPETITION POSSIBLE BETWEEN MIOC AND SPTR IN WATER TREAT.
C     AOMC - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND MIOC IN CONTROL TREAT.
C     AOMN - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND MIOC IN NITROGEN TREAT.
C     AOMNW- MAX. COMPETITION POSSIBLE BETWEEN ONLE AND MIOC IN NITROGEN + WATER
C     AOMW - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND MIOC IN WATER TREAT.
C     AOPC - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND PEMA IN CONTROL TREAT.
C     AOPN - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND PEMA IN NITROGEN TREAT.
C     AOPNW- MAX. COMPETITION POSSIBLE BETWEEN ONLE AND PEMA IN NITROGEN + WATER
C     AOPW - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND PEMA IN WATER TREAT.
C     AORC - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND REME IN CONTROL TREAT.
C     AORN - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND REME IN NITROGEN TREAT.
C     AORNW- MAX. COMPETITION POSSIBLE BETWEEN ONLE AND REME IN NITROGEN + WATER
C     AORW - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND REME IN WATER TREAT.
C     AOSC - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND SPTR IN CONTROL TREAT.
C     AOSN - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND SPTR IN NITROGEN TREAT.
C     AOSNW- MAX. COMPETITION POSSIBLE BETWEEN ONLE AND SPTR IN NITROGEN + WATER
C     AOSW - MAX. COMPETITION POSSIBLE BETWEEN ONLE AND SPTR IN WATER TREAT.
C     APMC - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND MIOC IN CONTROL TREAT.
C     APMN - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND MIOC IN NITROGEN TREAT.
C     APMNW- MAX. COMPETITION POSSIBLE BETWEEN PEMA AND MIOC IN NITROGEN + WATER
C     APMW - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND MIOC IN WATER TREAT.
C     APOC - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND ONLE IN CONTROL TREAT.
C     APON - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND ONLE IN NITROGEN TREAT.
C     APONW- MAX. COMPETITION POSSIBLE BETWEEN PEMA AND ONLE IN NITROGEN + WATER
C     APOW - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND ONLE IN WATER TREAT.
C     APRC - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND REME IN CONTROL TREAT.
C     APRN - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND REME IN NITROGEN TREAT.
C     APRNW- MAX. COMPETITION POSSIBLE BETWEEN PEMA AND REME IN NITROGEN + WATER
C     APRW - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND REME IN WATER TREAT.
C     APSC - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND SPTR IN CONTROL TREAT.
C     APSN - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND SPTR IN NITROGEN TREAT.
C     APSNW- MAX. COMPETITION POSSIBLE BETWEEN PEMA AND SPTR IN NITROGEN + WATER
C     APSW - MAX. COMPETITION POSSIBLE BETWEEN PEMA AND SPTR IN WATER TREAT.
C     ARMC - MAX. COMPETITION POSSIBLE BETWEEN REME AND MIOC IN CONTROL TREAT.
C     ARMN - MAX. COMPETITION POSSIBLE BETWEEN REME AND MIOC IN NITROGEN TREAT.
C     ARMNW- MAX. COMPETITION POSSIBLE BETWEEN REME AND MIOC IN NITROGEN + WATER
C     ARMW - MAX. COMPETITION POSSIBLE BETWEEN REME AND MIOC IN WATER TREAT.
C     AROC - MAX. COMPETITION POSSIBLE BETWEEN REME AND ONLE IN CONTROL TREAT.
C     ARON - MAX. COMPETITION POSSIBLE BETWEEN REME AND ONLE IN NITROGEN TREAT.
C     ARONW- MAX. COMPETITION POSSIBLE BETWEEN REME AND ONLE IN NITROGEN + WATER
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Appendix VI. (Cont.)

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C     AROW - MAX. COMPETITION POSSIBLE BETWEEN REME AND ONLE IN WATER TREAT.
C     ARPC - MAX. COMPETITION POSSIBLE BETWEEN REME AND PEMA IN CONTROL TREAT.
C     ARPN - MAX. COMPETITION POSSIBLE BETWEEN REME AND PEMA IN NITROGEN TREAT.
C     ARPNW- MAX. COMPETITION POSSIBLE BETWEEN REME AND PEMA IN NITROGEN + WATER
C     APPW - MAX. COMPETITION POSSIBLE BETWEEN REME AND PEMA IN WATER TREAT.
C     ARSC - MAX. COMPETITION POSSIBLE BETWEEN REME AND SPTR IN CONTROL TREAT.
C     ARSN - MAX. COMPETITION POSSIBLE BETWEEN REME AND SPTR IN NITROGEN TREAT.
C     ARSNW- MAX. COMPETITION POSSIBLE BETWEEN REME AND SPTR IN NITROGEN + WATER
C     ARSW - MAX. COMPETITION POSSIBLE BETWEEN REME AND SPTR IN WATER TREAT.
C     ASMC - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND MIOC IN CONTROL TREAT.
C     ASMN - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND MIOC IN NITROGEN TREAT.
C     ASMNW- MAX. COMPETITION POSSIBLE BETWEEN SPTR AND MIOC IN NITROGEN + WATER
C     ASMW - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND MIOC IN WATER TREAT.
C     ASOC - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND ONLE IN CONTROL TREAT.
C     ASON - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND ONLE IN NITROGEN TREAT.
C     ASONW- MAX. COMPETITION POSSIBLE BETWEEN SPTR AND ONLE IN NITROGEN + WATER
C     ASOW - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND ONLE IN WATER TREAT.
C     ASPC - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND PEMA IN CONTROL TREAT.
C     ASPN - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND PEMA IN NITROGEN TREAT.
C     ASPNW- MAX. COMPETITION POSSIBLE BETWEEN SPTR AND PEMA IN NITROGEN + WATER
C     ASPW - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND PEMA IN WATER TREAT.
C     ASRC - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND REME IN CONTROL TREAT.
C     ASRN - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND REME IN NITROGEN TREAT.
C     ASRNW- MAX. COMPETITION POSSIBLE BETWEEN SPTR AND REME IN NITROGEN + WATER
C     ASRW - MAX. COMPETITION POSSIBLE BETWEEN SPTR AND REME IN WATER TREAT.
C     ENMI(I) - MEAN DENSITY OF MIOC IN THE ENVIRONMENT
C     ENON(I) - MEAN DENSITY OF ONLE IN THE ENVIRONMENT
C     ENPE(I) - MEAN DENSITY OF PEMA IN THE ENVIRONMENT
C     ENRE(I) - MEAN DENSITY OF REME IN THE ENVIRONMENT
C     ENSP(I) - MEAN DENSITY OF SPTR IN THE ENVIRONMENT
C     GPE(I,J,K) - A THREE DIMENSION SPACE THAT ACCUMULATES THE FLOWS.  FOR PEMA
C        I STANDS FOR VARIABLE TYPE.1 - REP. 2 - MORTALITY 3 - EMIG. 4 - IMMIG.
C        J STANDS FOR HABITAT 1 - CONTROL 2 - NITROGEN 3 - WATER 4 - NITOGEN +
C        WATER. K STANDS FOR TIME
C     GMI(I,J,K) - THE SAME AS ABOVE FOR MIOC
C     GRE(I,J,K) - THE SAME AS ABOVE FOR REME
C     GSP(I,J,K) - THE SAME AS ABOVE FOR SPTR
C     GON(I,J,K) - THE SAME AS ABOVE FOR ONLE
C     HA(I,J) - AREA OF HABITATS
C     HD(I,J) - MEAN DISTANCE BETWEEN HABITATS
C     HI(I,J) - WEIGTENED PRIORITY INDEX FOR SPECIES I ON HABITAT J CALCULATED
C        AS (5*HP+ 2*HA + HD)/8.
C     HP(I,J) - HABITAT PRIORITY INDEX FOR SPECIES I ON HABITAT J
C     IMIC - THRESHOLD DENSITY FOR EMIGRATION OF MIOC ON CONTROL TREAT.
C     IMIN - THRESHOLD DENSITY FOR EMIGRATION OF MIOC ON NITROGEN TREAT.
C     IMINW- THRESHOLD DENSITY FOR EMIGRATION OF MIOC ON NITROGEN + WATER TREAT.
C     IMIW - THRESHOLD DENSITY FOR EMIGRATION OF MIOC ON WATER TREAT.
C     IONC - THRESHOLD DENSITY FOR EMIGRATION OF ONLE ON CONTROL TREAT.
C     IONN - THRESHOLD DENSITY FOR EMIGRATION OF ONLE ON NITROGEN TREAT.
C     IONNW- THRESHOLD DENSITY FOR EMIGRATION OF ONLE ON NITROGEN + WATER TREAT.
C     IONW - THRESHOLD DENSITY FOR EMIGRATION OF ONLE ON WATER TREAT.
C     IPEC - THRESHOLD DENSITY FOR EMIGRATION OF PEMA ON CONTROL TREAT.
C     IPEN - THRESHOLD DENSITY FOR EMIGRATION OF PEMA ON NITROGEN TREAT.
C     IPENW- THRESHOLD DENSITY FOR EMIGRATION OF PEMA ON NITROGEN + WATER TREAT.
C     IPEW - THRESHOLD DENSITY FOR EMIGRATION OF PEMA ON WATER TREAT.
C     IREC - THRESHOLD DENSITY FOR EMIGRATION OF REME ON CONTROL TREAT.
C     IRENW- THRESHOLD DENSITY FOR EMIGRATION OF REME ON NITROGEN + WATER TREAT.
C     IREN - THRESHOLD DENSITY FOR EMIGRATION OF REME ON NITROGEN TREAT.
C     IREW - THRESHOLD DENSITY FOR EMIGRATION OF REME ON WATER TREAT.
C     ISPC - THRESHOLD DENSITY FOR EMIGRATION OF SPTR ON CONTROL TREAT.
C     ISPN - THRESHOLD DENSITY FOR EMIGRATION OF SPTR ON NITROGEN TREAT.
C     ISPNW- THRESHOLD DENSITY FOR EMIGRATION OF SPTR ON NITROGEN + WATER TREAT.
C     ISPW - THRESHOLD DENSITY FOR EMIGRATION OF SPTR ON WATER TREAT.
C     LMIOC(I) - LITTER SIZE OF MIOC , ALL HABITATS
C     LONLE(I) - LITTER SIZE OF ONLE , ALL HABITATS
C     LPEMA(I) - LITTER SIZE OF PEMA , ALL HABITATS
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Appendix VI. (Cont.)

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C     LREME(I) - LITTER SIZE OF REME , ALL HABITATS
C     LSPTR(I) - LITTER SIZE OF SPTR , ALL HABITATS
C     MIONC(I) - COMPETITION INDECES BETWEEN MIOC AND ONLE IN CONTROL TREAT.
C     MIONN(I) - COMPETITION INDECES BETWEEN MIOC AND ONLE IN NITROGEN TREAT.
C     MIONNW(I)- COMPETITION INDECES BETWEEN MIOC AND ONLE IN NITROGEN+WATER TR.
C     MIONW(I) - COMPETITION INDECES BETWEEN MIOC AND ONLE IN WATER TREAT.
C     MIPEC(I) - COMPETITION INDECES BETWEEN MIOC AND PEMA IN CONTROL TREAT.
C     MIPEN(I) - COMPETITION INDECES BETWEEN MIOC AND PEMA IN NITROGEN TREAT.
C     MIPENW(I)- COMPETITION INDECES BETWEEN MIOC AND PEMA IN NITROGEN+WATER TR.
C     MIPEW(I) - COMPETITION INDECES BETWEEN MIOC AND PEMA IN WATER TREAT.
C     MIREC(I) - COMPETITION INDECES BETWEEN MIOC AND REME IN CONTROL TREAT.
C     MIREN(I) - COMPETITION INDECES BETWEEN MIOC AND REME IN NITROGEN TREAT.
C     MIRENW(I)- COMPETITION INDECES BETWEEN MIOC AND REME IN NITROGEN+WATER TR.
C     MIREW(I) - COMPETITION INDECES BETWEEN MIOC AND REME IN WATER TREAT.
C     MISPC(I) - COMPETITION INDECES BETWEEN MIOC AND SPTR IN CONTROL TREAT.
C     MISPN(I) - COMPETITION INDECES BETWEEN MIOC AND SPTR IN NITROGEN TREAT.
C     MISPNW(I)- COMPETITION INDECES BETWEEN MIOC AND SPTR IN NITROGEN+WATER TR.
C     MISPW(I) - COMPETITION INDECES BETWEEN MIOC AND SPTR IN WATER TREAT.
C     MMIOC(I) - MORTALITY RATE OF MIOC - ALL HABITATS
C     MONLE(I) - MORTALITY RATE OF ONLE - ALL HABITATS
C     MPEMA(I) - MORTALITY RATE OF PEMA - ALL HABITATS
C     MREME(I) - MORTALITY RATE OF REME - ALL HABITATS
C     MSPTR(I) - MORTALITY RATE OF SPTR - ALL HABITATS
C     ONMIC(I) - COMPETITION INDECES BETWEEN ONLE AND MIOC IN CONTROL TREAT.
C     ONMIN(I) - COMPETITION INDECES BETWEEN ONLE AND MIOC IN NITROGEN TREAT.
C     ONMINW(I)- COMPETITION INDECES BETWEEN ONLE AND MIOC IN NITROGEN+WATER TR.
C     ONMIW(I) - COMPETITION INDECES BETWEEN ONLE AND MIOC IN WATER TREAT.
C     ONPEC(I) - COMPETITION INDECES BETWEEN ONLE AND PEMA IN CONTROL TREAT.
C     ONPEN(I) - COMPETITION INDECES BETWEEN ONLE AND PEMA IN NITROGEN TREAT.
C     ONPENW(I)- COMPETITION INDECES BETWEEN ONLE AND PEMA IN NITROGEN+WATER TR.
C     ONPEW(I) - COMPETITION INDECES BETWEEN ONLE AND PEMA IN WATER TREAT.
C     ONREC(I) - COMPETITION INDECES BETWEEN ONLE AND REME IN CONTROL TREAT.
C     ONREN(I) - COMPETITION INDECES BETWEEN ONLE AND REME IN NITROGEN TREAT.
C     ONRENW(I)- COMPETITION INDECES BETWEEN ONLE AND REME IN NITROGEN+WATER TR.
C     ONREW(I) - COMPETITION INDECES BETWEEN ONLE AND REME IN WATER TREAT.
C     ONSPC(I) - COMPETITION INDECES BETWEEN ONLE AND SPTR IN CONTROL TREAT.
C     ONSPN(I) - COMPETITION INDECES BETWEEN ONLE AND SPTR IN NITROGEN TREAT.
C     ONSPNW(I)- COMPETITION INDECES BETWEEN ONLE AND SPTR IN NITROGEN+WATER TR.
C     ONSPW(I) - COMPETITION INDECES BETWEEN ONLE AND SPTR IN WATER TREAT.
C     PAMIO(I) - PROPORTION OF ADULTS IN POP., MIOC
C     PAONL(I) - PROPORTION OF ADULTS IN POP., ONLE
C     PAPEM(I) - PROPORTION OF ADULTS IN POP., PEMA
C     PAREM(I) - PROPORTION OF ADULTS IN POP., REME
C     PASPT(I) - PROPORTION OF ADULTS IN POP., SPTR
C     PCM - PROPORTION OF MORTALITY DUE TO COLD WEATHER
C     PEMIC(I) - COMPETITION INDECES BETWEEN PEMA AND MIOC IN CONTROL TREAT.
C     PEMIN(I) - COMPETITION INDECES BETWEEN PEMA AND MIOC IN NITROGEN TREAT.
C     PEMINW(I)- COMPETITION INDECES BETWEEN PEMA AND MIOC IN NITROGEN+WATER TR.
C     PEMIW(I) - COMPETITION INDECES BETWEEN PEMA AND MIOC IN WATER TREAT.
C     PEONC(I) - COMPETITION INDECES BETWEEN PEMA AND ONLE IN CONTROL TREAT.
C     PEONNW(I)- COMPETITION INDECES BETWEEN PEMA AND ONLE IN NITROGEN+WATER TR.
C     PEONN(I) - COMPETITION INDECES BETWEEN PEMA AND ONLE IN NITROGEN TREAT.
C     PEONW(I) - COMPETITION INDECES BETWEEN PEMA AND ONLE IN WATER TREAT.
C     PEREC(I) - COMPETITION INDECES BETWEEN PEMA AND REME IN CONTROL TREAT.
C     PEREN(I) - COMPETITION INDECES BETWEEN PEMA AND REME IN NITROGEN TREAT.
C     PERENW(I)- COMPETITION INDECES BETWEEN PEMA AND REME IN NITROGEN+WATER TR.
C     PEREW(I) - COMPETITION INDECES BETWEEN PEMA AND REME IN WATER TREAT.
C     PESPC(I) - COMPETITION INDECES BETWEEN PEMA AND SPTR IN CONTROL TREAT.
C     PESPN(I) - COMPETITION INDECES BETWEEN PEMA AND SPTR IN NITROGEN TREAT.
C     PESPNW(I)- COMPETITION INDECES BETWEEN PEMA AND SPTR IN NITROGEN+WATER TR.
C     PESPW(I) - COMPETITION INDECES BETWEEN PEMA AND SPTR IN WATER TREAT.
C     REONC(I) - COMPETITION INDECES BETWEENREMEC AND ONLE IN CONTROL TREAT.
C     REONN(I) - COMPETITION INDECES BETWEENREMEC AND ONLE IN NITROGEN TREAT.
C     REONNW(I)- COMPETITION INDECES BETWEENREMEC AND ONLE IN NITROGEN+WATER TR.
C     REONW(I) - COMPETITION INDECES BETWEENREMEC AND ONLE IN WATER TREAT.
C     REPEC(I) - COMPETITION INDECES BETWEENREMEC AND PEMA IN CONTROL TREAT.
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Appendix VI. (Cont.)

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C     REPEN(I) - COMPETITION INDECES BETWEENREMEC AND PEMA IN NITROGEN TREAT.
C     REPENW(I)- COMPETITION INDECES BETWEENREMEC AND PEMA IN NITROGEN+WATER TR.
C     REPEW(I) - COMPETITION INDECES BETWEENREMEC AND PEMA IN WATER TREAT.
C     REMIC(I) - COMPETITION INDECES BETWEENREMEC AND MIOC IN CONTROL TREAT.
C     REMIN(I) - COMPETITION INDECES BETWEENREMEC AND MIOC IN NITROGEN TREAT.
C     REMINW(I)- COMPETITION INDECES BETWEENREMEC AND MIOC IN NITROGEN+WATER TR.
C     REMIW(I) - COMPETITION INDECES BETWEENREMEC AND MIOC IN WATER TREAT.
C     RESPC(I) - COMPETITION INDECES BETWEENREMEC AND SPTR IN CONTROL TREAT.
C     RESPN(I) - COMPETITION INDECES BETWEENREMEC AND SPTR IN NITROGEN TREAT.
C     RESPNW(I)- COMPETITION INDECES BETWEENREMEC AND SPTR IN NITROGEN+WATER TR.
C     RESPW(I) - COMPETITION INDECES BETWEENREMEC AND SPTR IN WATER TREAT.
C     RMIOC(I) - PROP. OF FEMALES MIOC IN REPRODUCTION , ALL HABITATS
C     RONLE(I) - PROP. OF FEMALES ONLE IN REPRODUCTION, ALL HABITATS
C     RPEMA(I) - PROP. OF FEMALES PEMA IN REPRODUCTION , ALL HABITATS
C     RREME(I) - PROP. OF FEMALES REME IN REPRODUCTION , ALL HABITATS
C     RSPTR(I) - PROP. OF FEMALES SPTR IN REPRODUCTION, ALL HABITATS
C     SLM - SLOP OF THE LINE THAT DETERMINES WHAT PROP. OF MIOC BECOMES EMIGRANT
C     SLO - SLOP OF THE LINE THAT DETERMINES WHAT PROP. OF ONLE BECOMES EMIGRANT
C     SLP - SLOP OF THE LINE THAT DETERMINES WHAT PROP. OF PEMA BECOMES EMIGRANT
C     SLR - SLOP OF THE LINE THAT DETERMINES WHAT PROP. OF REME BECOMES EMIGRANT
C     SLS - SLOP OF THE LINE THAT DETERMINES WHAT PROP. OF SPTR BECOMES EMIGRANT
C     SMIOC(I) - SEX RATIO OF MIOC, ALL HABITATS
C     SONLE(I) - SEX RATIO OF ONLE, ALL HABITATS
C     SPEMA(I) - SEX RATIO OF PEMA, ALL HABITATS
C     SREME(I) - SEX RATIO OF REME, ALL HABITATS
C     SSPTR(I) - SEX RATIO OF SPTR, ALL HABITATS
C     SPMIC(I) - COMPETITION INDECES BETWEEN SPTR AND MIOC IN CONTROL TREAT.
C     SPMIN(I) - COMPETITION INDECES BETWEEN SPTR AND MIOC IN NITROGEN TREAT.
C     SPMINW(I)- COMPETITION INDECES BETWEEN SPTR AND MIOC IN NITROGEN+WATER TR.
C     SPMIW(I) - COMPETITION INDECES BETWEEN SPTR AND MIOC IN WATER TREAT.
C     SPONC(I) - COMPETITION INDECES BETWEEN SPTR AND ONLE IN CONTROL TREAT.
C     SPONN(I) - COMPETITION INDECES BETWEEN SPTR AND ONLE IN NITROGEN TREAT.
C     SPONNW(I)- COMPETITION INDECES BETWEEN SPTR AND ONLE IN NITROGEN+WATER TR.
C     SPONW(I) - COMPETITION INDECES BETWEEN SPTR AND ONLE IN WATER TREAT.
C     SPPEC(I) - COMPETITION INDECES BETWEEN SPTR AND PEMA IN CONTROL TREAT.
C     SPPEN(I) - COMPETITION INDECES BETWEEN SPTR AND PEMA IN NITROGEN TREAT.
C     SPPENW(I)- COMPETITION INDECES BETWEEN SPTR AND PEMA IN NITROGEN+WATER TR.
C     SPPEW(I) - COMPETITION INDECES BETWEEN SPTR AND PEMA IN WATER TREAT.
C     SPREC(I) - COMPETITION INDECES BETWEEN SPTR AND REME IN CONTROL TREAT.
C     SPREN(I) - COMPETITION INDECES BETWEEN SPTR AND REME IN NITROGEN TREAT.
C     SPRENW(I)- COMPETITION INDECES BETWEEN SPTR AND REME IN NITROGEN+WATER TR.
C     SPREW(I) - COMPETITION INDECES BETWEEN SPTR AND REME IN WATER TREAT.
C     TAVER(I) - AVERAGE TEMP.
C     TMAX(I) - MAX. MEAN TEMP.
C     X(  1) - SOURCE FOR REP.  OF PEMA IN CONTROL TREAT.
C     X(2) - SOURCE FOR PEMA EMIGRANTS IN THE ENVIRONMENT AROUND THE ESA
C     X(  3) - NO. OF PEMA IN CONTROL TREAT.
C     X(  4) - SINK FOR MORTALITY OF PEMA IN CONTROL TREAT.
C     X(5) - SINK FOR MORTALITY OF PEMA EMIGRANTS
C     X(  6) - SOURCE FOR REPRODUCTION OF MIOC IN CONTROL TREAT.
C     X(7) - SOURCE FOR MIOC EMIGRANTS FROM THE ENVIRONMENT AROUND ESA
C     X(  8) - NO. OF MIOC ON CONTROL TREAT.
C     X(  9) - SINK FOR MIOC MORTALITY IN CONTROL TREAT.
C     X(10) - SINK FOR MORTALITY OF MIOC EMIGRANTS
C     X( 11) - SOURCE FOR REPRODUCTION OF REME IN CONTROL TREAT.
C     X( 12) - SOURCE FOR EMIGRANTS REME FROM THE ENVIRONMENT AROUND THE ESA
C     X( 13) - NO. OF REME IN CONTROL TREAT.
C     X( 14) - SINK FOR MORTALITY OF REME IN CONTROL TREAT.
C     X(15) - SINK FOR MORTALITY OF REME EMIGRANTS
C     X( 16) - SOURCE FOR REPRODUCTION OF SPTR IN CONTROL TREAT.
C     X(17) - SOURCE FOR EMIGRANTS SPTR FROM THE ENVIRONMENT AROUND ESA
C     X( 18) - NO. OF SPTR IN CONTROL TREAT.
C     X( 19) - SINK FOR MORTALITY OF SPTR IN CONTROL TREAT.
C     X(20) - SINK FOR MORTALITY OF SPTH EMIGRANTS
C             ONLE - O. LEUCOGASTER
C     X( 21) - SOURCE FOR REPRODUCTION OF ONLE IN CONTROL TREAT.
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Appendix VI. (Cont.)

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C     X(22) - SOURCE FOR EMIGRANTS UNLE FROM THE ENVIRONMENT AROUND ESA
C     X( 23) - NO. OF ONLE IN CONTROL TREAT.
C     X( 24) - SINK FOR MORTALITY OF ONLE IN CONTROL TREAT.
C     X(25) - SINK FOR MORTALITY OF ONLE EMIGRANTS
C     X( 30) - HYBERNATING SPTR IN CONTROL TREAT.
C     X(40) - DUMMY VARIABLE IN WHICH EMIGRANTS OF PEMA ARE STORED BEFORE
C        TURNING INTO IMMIGRANTS
C     X(50) - DUMMY VARIABLE IN WHICH EMIGRANTS OF MIOC ARE STORED BEFORE
C        TURNING INTO IMMIGRANTS.
C     X(60) - DUMMY VARIABLE IN WHICH EMIGRANTS OF REME ARE STORED BEFORE
C        TURNNING INTO IMMIGRANTS
C     X(70) - DUMMY VARIABLE IN WHICH EMIGRANTS OF SPTR ARE STORED BEFORE
C        TURNNING IMMIGRANTS
C     X(80) - DUMMY VARIABLE IN WHICH EMIGRANTS OF ONLE ARE STORED BEFORE
C        TURNNING INTO IMMIGRANTS
C     X(101) - SOURCE FOR REP.  OF PEMA IN NITROGEN TREAT.
C     X(103) - NO. OF PEMA IN NITROGEN TREAT.
C     X(104) - SINK FOR MORTALITY OF PEMA IN NITROGEN TREAT.
C     X(106) - SOURCE FOR REPRODUCTION OF MIOC IN NITROGEN TREAT.
C     X(108) - NO. OF MIOC ON NITROGEN TREAT.
C     X(109) - SINK FOR MIOC MORTALITY IN NITROGEN TREAT.
C     X(111) - SOURCE FOR REPRODUCTION OF REME IN NITROGEN TREAT.
C     X(113) - NO. OF REME IN NITROGEN TREAT.
C     X(114) - SINK FOR MORTALITY OF REME IN NITROGEN TREAT.
C     X(116) - SOURCE FOR REPRODUCTION OF SPTR IN NITROGEN TREAT.
C     X(118) - NO. OF SPTR IN NITROGEN TREAT.
C     X(119) - SINK FOR MORTALITY OF SPTR IN NITROGEN TREAT.
C     X(121) - SOURCE FOR REPRODUCTION OF ONLE IN NITROGEN TREAT.
C     X(123) - NO. OF ONLE IN NITROGEN TREAT.
C     X(124) - SINK FOR MORTALITY OF ONLE IN NITROGEN TREAT.
C     X(130) - HYBERNATING SPTR IN NITROGEN TREAT.
C     X(201) - SOURCE FOR REP.  OF PEMA IN WATER TREAT.
C     X(203) - NO. OF PEMA IN WATER TREAT.
C     X(204) - SINK FOR MORTALITY OF PEMA IN WATER TREAT.
C     X(206) - SOURCE FOR REPRODUCTION OF MIOC IN WATER TREAT.
C     X(208) - NO. OF MIOC ON WATER TREAT.
C     X(209) - SINK FOR MIOC MORTALITY IN WATER TREAT.
C     X(211) - SOURCE FOR REPRODUCTION OF REME IN WATER TREAT.
C     X(213) - NO. OF REME IN WATER TREAT.
C     X(214) - SINK FOR MORTALITY OF REME IN WATER TREAT.
C     X(216) - SOURCE FOR REPRODUCTION OF SPTR IN WATER TREAT.
C     X(218) - NO. OF SPTR IN WATER TREAT.
C     X(219) - SINK FOR MORTALITY OF SPTR IN WATER TREAT.
C     X(221) - SOURCE FOR REPRODUCTION OF ONLE IN WATER TREAT.
C     X(223) - NO. OF ONLE IN WATER TREAT.
C     X(224) - SINK FOR MORTALITY OF ONLE IN WATER TREAT.
C     X(230) - HYBERNATING SPTR IN WATER TREAT.
C     X(301) - SOURCE FOR REP.  OF PEMA IN NITROGEN + WATER TREAT.
C     X(303) - NO. OF PEMA IN NITROGEN + WATER TREAT.
C     X(304) - SINK FOR MORTALITY OF PEMA IN NITROGEN + WATER TREAT.
C     X(306) - SOURCE FOR REPRODUCTION OF MIOC IN NITROGEN + WATER TREAT.
C     X(308) - NO. OF MIOC ON NITROGEN + WATER TREAT.
C     X(309) - SINK FOR MIOC MORTALITY IN NITROGEN + WATER TREAT.
C     X(311) - SOURCE FOR REPRODUCTION OF REME IN NITROGEN + WATER TREAT.
C     X(313) - NO. OF REME IN NITROGEN + WATER TREAT.
C     X(314) - SINK FOR MORTALITY OF REME IN NITROGEN + WATER TREAT.
C     X(316) - SOURCE FOR REPRODUCTION OF SPTR IN NITROGEN + WATER TREAT.
C     X(318) - NO. OF SPTR IN NITROGEN + WATER TREAT.
C     X(319) - SINK FOR MORTALITY OF SPTR IN NITROGEN + WATER TREAT.
C     X(321) - SOURCE FOR REPRODUCTION OF ONLE IN NITROGEN + WATER TREAT.
C     X(323) - NO. OF ONLE IN NITROGEN + WATER TREAT.
C     X(324) - SINK FOR MORTALITY OF ONLE IN NITROGEN + WATER TREAT.
C     X(330) - HYBERNATING SPTR IN NITROGEN + WATER TREAT.
C     X(503) - SINK FOR PEMA INDIVIDUALS THAT LEAVE THE ESA
C     X(508) - SINK FOR MIOC INDIVIDUALS THAT LEAVE THE ESA
C     X(513) - SINK FOR REME INDIVIDUALS THAT LEAVE THE ESA
C     X(518) - SINK FOR SPTR THAT LEAVE THE ESA
C     X(523) - SINK FOR ONLE THAT LEAVE THE ESA
C     Y - DUMMY VARIABLE THAT ESTIMATE THE MAX. COMPETITION POSSIBLE
C
C     ************************************************************************
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Appendix VII.

Values of variables used in the simulation model. For variable name see Appendix II (C = control treatment; N = nitrogen treatment; W = water treatment; NW = nitrogen + water treatment; E = environment outside the study area; ALL = all habitats).

Species	Habitat	Variable	Time in weeks (starting in May)																										
			2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52
P. maniculatus	ALL	RPEMA	0.29	0.29	0.19	0.19	0.28	0.28	0.28	0.28	0.16	0.16	0.03	0.03	0.05	0.05	0.05	0.05	0.00	0.00	0.00	0.00	0.07	0.07	0.18	0.18	0.25	0.25
	ALL	SPEMA	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38	0.38
	ALL	LPEMA	4.70	4.70	4.90	4.90	5.10	5.10	5.20	5.20	4.00	4.00	6.00	6.00	4.50	4.50	0.00	0.00	0.00	0.00	0.00	0.00	3.70	3.70	4.00	4.00	4.10	4.10
	ALL	PAPEM	0.80	0.80	0.80	0.80	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.80	0.80	0.80	0.80	0.80	0.80	0.80
	ALL	MPEMA	0.35	0.35	0.35	0.35	0.35	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
	ALL	AMAX	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62
	ALL	SLP	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	C	IPEL	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00
	N	IPEN	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
	W	IPEW	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
	NW	IPENW	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	HI	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
	N	HI	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
	W	HI	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.18
	NW	HI	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
	E	HI	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37
M. ochrogaster	ALL	RMIOC	0.50	0.50	0.41	0.41	0.19	0.19	0.23	0.23	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.01	0.01	0.01	0.01	0.25	0.25	0.05	0.05	0.15	0.15
	ALL	SMIOC	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	ALL	LMIOC	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90	2.90
	ALL	PAMIO	0.65	0.65	0.60	0.60	0.80	0.80	0.82	0.82	0.75	0.75	0.63	0.63	0.63	0.63	0.57	0.57	0.55	0.55	0.94	0.94	0.95	0.95	0.94	0.94	0.90	0.90
	ALL	MMIOC	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20
	ALL	AMAX	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62
	ALL	SLP	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	C	IMIC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	N	IMIN	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	W	IMIW	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00
	NW	IMINW	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	C	HI	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
	N	HI	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
	W	HI	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
	NW	HI	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62	0.62
	E	HI	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20
R. megalotis	ALL	RREME	0.03	0.03	0.07	0.07	0.04	0.04	0.06	0.06	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.00	0.00	0.09	0.09	0.03	0.03	0.19	0.19
	ALL	SREME	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	ALL	LREME	4.00	4.00	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80	3.80
	ALL	PAREM	0.60	0.60	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.60	0.60
	ALL	MREME	0.03	0.03	0.03	0.03	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
	ALL	AMAX	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62
	ALL	SLR	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	C	IREC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	N	IREN	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	W	IREW	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	NW	IRENW	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
	C	HI	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
	N	HI	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20

Appendix VII. (Cont.)

Species	Habitat	Variable	Time in weeks (starting in May)																									
			2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52
S. trideem-lineatus	ALL	RSPTR	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	ALL	SSPTR	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60	0.60
	ALL	LSPTR	8.50	8.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	ALL	PASPT	1.00	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	ALL	MSPTR	0.30	0.30	0.10	0.10	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
	ALL	AMAX	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62
	ALL	SLS	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	C	ISPC	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
	N	ISPN	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00	4.00
	W	ISPW	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00
	NW	ISPNW	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
	C	HI	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
	N	HI	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
	W	HI	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
	NW	HI	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
	E	HI	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37
O. leucogaster	ALL	RONLE	0.12	0.12	0.29	0.29	0.08	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.35	0.35
	ALL	SONLE	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47
	ALL	LONLE	4.00	4.00	3.90	3.90	4.00	4.00	4.80	4.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	4.00	4.00	5.30	5.30
	ALL	PAONL	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70	0.70
	ALL	MONLE	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09
	ALL	AMAX	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62	1.62
	ALL	SLO	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	C	IONC	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
	N	IONN	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	W	IONW	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	NW	IONNW	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	C	HI	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26
	N	HI	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
	W	HI	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
	NW	HI	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
	E	HI	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40

APPENDIX VIII.

The code of the simulation model

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      STORAGE,AMPC,AMRC,AMSC,AMOC,ARPC,ARMC,ARSC,AROC,ASPC,ASMC,ASRC,ASOC
      STORAGE,AOPC,AOMC,AORC,AOSC,APMN,APRN,APSN,APON,AMPN,AMRN,AMSN,AMON
      STORAGE,APMW,APRW,APSW,APOW,AMPW,AMRW,AMSW,AMOW,ARPW,ARMW,ARSW,AROW
      STORAGE,APMNW,APRNW,APSNW,APONW,AMPNW,AMRNW,AMSNW,AMONW,ARPNW,ARMNW
      STORAGE,ARPN,ARSN,ARON,ARMN,ASPN,ASMN,ASRN,ASON,AOPN,AOMN,AORN,AOSN
      STORAGE,ARSNW,ARONW,ASPNW,ASMNW,ASRNW,ASONW,AOPNW,AOMNW,AORNW,AOSNW
      STORAGE,ASPW,ASMW,ASRW,ASOW,AOPW,AOMW,AORW,AOSW,APMC,APRC,APSC,APOC
      STORAGE,ENON(26),ENPE(26),ENSP(26),ENMI(26),ENRE(26)
      STORAGE,GPE(4,4,26),GMI(4,4,26),GRE(4,4,26),GSP(4,4,26) ,GON(4,4,26)
      STORAGE,HA(5,5),HP(5,5),HO(5,5),HI(5,5),TOT(5),TOT1(5),TOT2(5),TOT4(5)
      REAL,IMIC,IPEC,IREC,ISPC,IONC,IMIN,IPEN,IREN,ISPN,IONN
      REAL,IMIW,IPEW,IREW,ISPW,IONW,IMINW,IPENW,IRENW,ISPNW,IONNW
      REAL,     LPEMA(26),LMIOC(26),LREME(26),LSPTR(26),LONLE(26)
      REAL,     MHPEN,MHPC,MHPN,MHPW,MHPNW
      REAL,     MIPEC(26),MIREC(26),MISPC(26),MIONC(26)
      REAL,     MIPEN(26),MIREN(26),MISPN(26),MIONN(26)
      REAL,     MIPEW(26),MIREW(26),MISPW(26),MIONW(26)
      REAL,     MIPNW(26),MIRNW(26),MISNW(26),MION1(26)
      REAL, MPEMA(26),MMIOC(26),MREME(26),MSPTR(26),MONLE(26)
      STORAGE,OHPN,OHPW,OHPNW,OHPC,OHPEN
      STORAGE,ONMIC(26),ONPEC(26),ONREC(26),ONSPC(26)
      STORAGE,ONMIN(26),ONPEN(26),ONREN(26),ONSPN(26)
      STORAGE,ONMIW(26),ONPEW(26),ONREW(26),ONSPW(26)
      STORAGE,ONMNW(26),ONPNW(26),ONRNW(26),ONSNW(26)
      STORAGE,P1,P2,P3,P4
      STORAGE, PAMI1(26)
      STORAGE, PAPEM(26),PAMIO(26),PAREM(26),PASPT(26),PAONL(26)
      STORAGE, PCM
      STORAGE,PEMIC(26),PEREC(26),PESPC(26),PEONC(26)
      STORAGE,PEMIN(26),PEREN(26),PESPN(26),PEONN(26)
      STORAGE,PEMIW(26),PEREW(26),PESPW(26),PEONW(26)
      STORAGE,PEMNW(26),PERNW(26),PESNW(26),PEON1(26)
      STORAGE,PHPN,PHPW,PHPNW,PHPC,PHPEN
      STORAGE,REMIC(26),REPEC(26),RESPC(26),REONC(26)
      STORAGE,REMIN(26),REPEN(26),RESPN(26),REONN(26)
      STORAGE,RMIO1(26),RREMI(26),RONL1(26),RSPT1(26)
      STORAGE,REMIW(26),REPEW(26),RESPW(26),REONW(26)
      STORAGE,REMNW(26),REPNW(26),RESNW(26),REON1(26)
      STORAGE,RHPN,RHPW,RHPNW,RHPC,RHPEN
      STORAGE,SAV1,SAV2,SAV3,SAV4
      STORAGE,SHPN,SHPW,SHPNW,SHPC,SHPEN
      STORAGE,SLO,SLP,SLM,SLR,SLS
      STORAGE, SPEMA(26),SMIOC(26),SREME(26),SSPTR(26),SONLE(26)
      STORAGE, RPEMA(26),RMIOC(26),RREME(26),RSPTR(26),RONLE(26)
      STORAGE,SPMIC(26),SPPEC(26),SPREC(26),SPONC(26)
      STORAGE,SPMIN(26),SPPEN(26),SPREN(26),SPONN(26)
      STORAGE,SPMIW(26),SPPEW(26),SPREW(26),SPONW(26)
      STORAGE,SPMNW(26),SPPNW(26),SPRNW(26),SPON1(26)
      STORAGE,SUM1(4,4),SUM2(4,4),SUM3(4,4),SUM4(4,4),SUM5(4,4)
      STORAGE, SUM6(4,4)
      STORAGE, TAVER(26)
      STORAGE, TMAX(26)
      STORAGE,Y
C     THIS PART CALCULATES THE HABITAT PRIORITY INDEX
      SUBROUTINE START
      DO 99 I=1,4
      DO 99 J=1,4
      SUM1(I,J)=0.
      SUM2(I,J)=0.
      SUM3(I,J)=0.
      SUM4(I,J)=0.
      SUM5(I,J)=0.
      SUM6(I,J)=0.
   99 CONTINUE
      DO 6 I=1,5
```

Appendix VIII. (Cont.)

```
      TOT(I)=0.
      TOT1(I)=0.
      TOT2(I)=0.
      TOT4(I)=0.
6     CONTINUE
      DO 1 I=1,5
      DO 1 J=1,5
      TOT (I)=TOT (I)+HP(I,J)
      TOT1(I)=TOT1(I)+HA(I,J)
      TOT2(I)=TOT2(I)+HD(I,J)
1     CONTINUE
      DO 2 I=1,5
      DO 2 J=1,5
      HP(I,J)=HP(I,J)/TOT(I)
      HA(I,J)=HA(I,J)/TOT1(I)
      HD(I,J)=HD(I,J)/TOT2(I)
2     CONTINUE
      DO 3 I=1,5
      DO 3 J=1,5
      HI(I,J)=(5.*HP(I,J)+2.*HA(I,J)+HD(I,J))/8.
 3    CONTINUE
      DO 4 I=1,5
      DO 4 J=1,5
      TOT4(I)=TOT4(I)+HI(I,J)
4     CONTINUE
      DO 5 I=1,5
      DO 5 J=1,5
      HI(I,J)=HI(I,J)/TOT4(I)
5     CONTINUE
      DO 9 I=1,5
9     PRINT 10,(HI(I,J),J=1,5)
10    FORMAT(3X,*HI*,5(3X,F6.4))
      DO 11 I=1,5
11    PRINT 12,(HP(I,J),J=1,5),(HA(I,J),J=1,5),(HD(I,J),J=1,5)
12    FORMAT(3X,*HP*,5(3X,F6.4)/3X,*HA*,5(3X,F6.4)/3X,*DD*,5(3X,F6.4))
      DO 20 K=1,26
      DO 20 I=1,4
      DO 20 J=1,4
      GPE(I,J,K)=0.
      GMI(I,J,K)=0.
      GRE(I,J,K)=0.
      GSP(I,J,K)=0.
      GON(I,J,K)=0.
20    CONTINUE
      RETURN
      END
C     THIS PART SIMULATES THE POPULATION DYNAMICS IN THE CONTROL TREATMENT
(2-40).
      I=TIME
      FLOW=0.
      Y=ENMI(I)*AMPC+ENRE(I)*ARPC+ENSP(I)*ASPC+ENON(I)*AOPC+ENPE(I)
      IF(ENPE(I).GT.IPEC)
     1FLOW= (ENMI(I)*MIPEC(I)+ENRE(I)*REPEC(I)+ENSP(I)*SPPEC(I)
     1 +ENON(I)*ONPEC(I)+ENPE(I))/Y*SLP*ENPE(I)*8.
(1-3).
      FLOW=X(3)*PAPEM(I)*SPEMA(I)*RPEMA(I)*LPEMA(I)
      GPE(1,1,I)=GPE(1,1,I)+FLOW
(40-3).
      FLOW=X(40)*HI(1,1) *P2
      GPE(4,1,I)=GPE(4,1,I)+FLOW
(3-4).
      IF(TAVER(I).GT.4.3)FLOW=X(  3)*MPEMA(I)
      IF(TAVFR(I).LE.4.2)FLOW=X(3)*(MPEMA(I)+MPEMA(I)*PCM)
      GPE(2,1,I)=GPE(2,1,I)+FLOW
(3-40).
      FLOW=0.
```

Appendix VIII. (Cont.)

```
      Y=X(8)*AMPC+X(13)*ARPC+X(18)*ASPC+X(23)*AOPC+X(3)
      IF(X(3),GT,IPEC)
     1FLOW=(X( 8)*MIPEC(I)+X(13)*REPEC(I)+X(18)*SPPEC(I) +X(23)*ONPEC(I)
     1+X(3))/Y*SLP*X(3)
      GPE(3,1,I)=GPE(3,1,I)+FLOW
(7-50).
      FLOW=0.
      Y=ENPE(I)*APMC+ENRE(I)*ARMC+ENSP(I)*ASMC+ENON(I)*AOMC+ENMI(I)
      IF(ENMI(I),GT,IMIC)
     1FLOW= (ENPE(I)*PEMIC(I)+ENRE(I)*REMIC(I)+ENSP(I)*SPMIC(I)+ENON(I)*
     1ONMIC(I)+ENMI(I))/Y*SLM*ENMI(I)*8.
(6-8).
      FLOW=X(8)*PAMII(I)*SMIOC(I)*RMIOI(I)*LMIOC(I)
      GMI(1,1,I)=GMI(1,1,I)+FLOW
(8-9).
      IF(TAVER(I),GT,4.3)FLOW=X(  8)*MMIOC(I)
      IF(TAVER(I),LE,4.2)FLOW=X(  8)*( MMIOC(I)+MMIOC(I)*PCM)
      GMI(2,1,I)=GMI(2,1,I)+FLOW
(8-50).
      FLOW=0.
      Y=X(3)*APMC+X(13)*ARMC+X(18)*ASMC+X(23)*AOMC+X(8)
      IF(X(8),GT,IMIC)
     1FLOW=(X(3)*PEMIC(I)+X(13)*REMIC(I)+SPMIC(I)*X(18)+X(23)*ONMIC(I)+
     1X(8))/Y*SLM*X(8)
      GMI(3,1,I)=GMI(3,1,I)+FLOW
(50-8).
      FLOW=X(50)*HI(2,1)*P2
      GMI(4,1,I)=GMI(4,1,I)+FLOW
(11-13).
      FLOW=X(13)*PAREM(I)*SREME(I)*RREMI(I)*LREME(I)
      GRE(1,1,I)=GRE(1,1,I)+FLOW
(12-60).
      FLOW=0.
      Y=ENPE(I)*APRC+ENMI(I)*AMRC+ENSP(I)*ASRC+ENON(I)*AORC+ENRE(I)
      IF(ENRE(I),GT,IREC)
     1FLOW= (ENPE(I)*PEREC(I)+ENMI(I)*MIREC(I)+ENSP(I)*SPREC(I)+ENON(I)*
     1ONREC(I)+ENRE(I))/Y*SLR*ENRE(I)*8.
(13-14).
      IF(TAVER(I),GT,4.3)FLOW=X( 13)*MREME(I)
      IF(TAVER(I),LE,4.2)FLOW=X( 13)*( MREME(I)+MREME(I)*PCM)
      GRE(2,1,I)=GRE(2,1,I)+FLOW
(13-60).
      FLOW=0.
      Y=X(3)*APRC+X(8)*AMRC+X(18)*ASRC+X(23)*AORC+X(13)
      IF(X(13),GT,IREC)
     1FLOW=(X(3)*PEREC(I)+X(8)*MIREC(I)+X(18)*SPREC(I)+X(23)*ONREC(I)+
     1X(13))/Y*SLR*X(13)
      GRE(3,1,I)=GRE(3,1,I)+FLOW
(60-13).
      FLOW=X(60)*HI(3,1)*P2
      GRE(4,1,I)=GRE(4,1,I)+FLOW
(30-18).
      FLOW=0.
      IF(I,GE,10,AND,I,LT,25,AND,TMAX(I),GT,8.5)FLOW=X(30)*.05
      SAV1=FLOW
(17-70).
      FLOW=0.
      Y=ENMI(I)*AMSC+ENRE(I)*ARSC+ENPE(I)*APSC+ENON(I)*AOSC+ENSP(I)
      IF(ENSP(I),GT,ISPC)
     1FLOW= (ENMI(I)*MISPC(I)+ENRE(I)*RESPC(I)+ENPE(I)*PESPC(I)+ENON(I)*
     1ONSPC(I)+ENSP(I))/Y*SLS*ENSP(I)*8.
(30-19).
      FLOW=X(30)*MSPTR(I)
(18-30).
      FLOW=SAV1
(16-18).
```

Appendix VIII. (Cont.)

```
      FLOW=X(18)*PASPT(I)*SSPTR(I)*HSPTR(I)*LSPTR(I)
      GSP(1,1,I)=GSP(1,1,I)+FLOW
(18-19).
      IF(TAVER(I).GT.4.3)FLOW=X( 18)*MSPTR(I)
      IF(TAVER(I).LE.4.2)FLOW=X( 18)*( MSPTR(I)+MSPTH(I)*PCM)
      GSP(2,1,I)=GSP(2,1,I)+FLOW
(18-70).
      FLOW=0.
      Y=X(3)*APSC+X(8)*AMSC+X(13)*AHSC+X(23)*AOSC+X(18)
      IF(X(18).GT.ISPC)
     1FLOW=(X(3)*PESPC(I)+X(8)*MISPC(I)+X(13)*RESPC(I)+X(23)*ONSPC(I)+
     1X(18))/Y*SLS*X(18)
      GSP(3,1,I)=GSP(3,1,I)+FLOW
(70-18).
      FLOW=X(70)*HI(4,1)*P2
      GSP(4,1,I)=GSP(4,1,I)+FLOW
(21-23).
      FLOW=X(23)*PAONL(I)*SONLE(I)*HONLE(I)*LONLE(I)
      GON(1,1,I)=GON(1,1,I)+FLOW
(22-80).
      FLOW=0.
      Y=ENPE(I)*APOC+ENMI(I)*AMOC+ENRE(I)*AROC+ENSP(I)*ASOC+ENON(I)
      IF(ENON(I).GT.IONC)
     1FLOW= (ENPE(I)*PEONC(I)+MIONC(I)*ENMI(I)+ENRE(I)*REONC(I)+ENSP(I)*
     1*SPONC(I)+ENON(I))/Y*SLO*ENON(I)*8.
(23-24).
      IF(TAVER(I).GT.4.3)FLOW=X( 23)*MONLE(I)
      IF(TAVER(I).LE.4.2)FLOW=X( 23)*( MONLE(I)+MONLE(I)*PCM)
      GON(2,1,I)=GON(2,1,I)+FLOW
(23-80).
      FLOW=0.
      Y=X(3)*APOC+X(8)*AMOC+X(13)*AHOC+X(18)*ASOC+X(23)
      IF(X(23).GT.IONC)
     1FLOW=(X(3)*PEONC(I)+X(8)*MIONC(I)+X(13)*REONC(I)+X(18)*SPONC(I)+
     1X(23))/Y*SLO*X(23)
      GON(3,1,I)=GON(3,1,I)+FLOW
(80-23).
      FLOW=X(80)*HI(5,1)*P2
      GON(4,1,I)=GON(4,1,I)+FLOW
C     THIS PART SIMULATES THE POPULATION DYNAMICS IN THE NITROGEN TREATMENT
(101-103).
      FLOW=X(103)*PAPEM(I)*SPEMA(I)*RPEMA(I)*LPEMA(I)
      GPE(1,2,I)=GPE(1,2,I)+FLOW
(40-103).
      FLOW=X(40)*HI(1,2)*P2
      GPE(4,2,I)=GPE(4,2,I)+FLOW
(103-104).
      IF(TAVER(I).GT.4.3)FLOW=X(103)*MPEMA(I)
      IF(TAVER(I).LE.4.2)FLOW=X(103)*(MPEMA(I)+MPEMA(I)*PCM)
      GPE(2,2,I)=GPE(2,2,I)+FLOW
(103-40).
      Y=X(108)*AMPN+X(113)*ARPN+X(118)*ASPN+X(123)*AOPN+X(103)
      FLOW=0.
      IF(X(103).GT.IPEN)
     1FLOW=(X(108)*MIPEN(I)+X(113)*REPEN(I)+X(118)*SPPEN(I)+X(123)*ONPEN
     1(I)+X(103))/Y*SLP*X(103)
      GPE(3,2,I)=GPE(3,2,I)+FLOW
(108-50).
      Y=X(103)*APMN+X(113)*ARMN+X(118)*ASMN+X(123)*AOMN+X(108)
      FLOW=0.
      IF(X(108).GT.IMIN)
     1FLOW=(X(103)*PEMIN(I)+X(113)*REMIN(I)+SPMIN(I)*X(118)+X(123)*ONMIN
     2(I)+X(108))/Y*SLM*X(108)
      GMI(3,2,I)=GMI(3,2,I)+FLOW
(50-108).
      FLOW=X(50)*HI(2,2) *P2
```

Appendix VIII. (Cont.)

```
      GMI(4,2,I)=GMI(4,2,I)+FLOW
(106-108).
      FLOW=X(108)*PAMI1(I)*SMIOC(I)*RMIO1(I)*LMIOC(I)
      GMI(1,2,I)=GMI(1,2,I)+FLOW
(108-109).
      IF(TAVER(I).LE.4.2)FLOW=X(108)*( MMIOC(I)+MMIOC(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(108)*MMIOC(I)
      GMI(2,2,I)=GMI(2,2,I)+FLOW
(113-60).
      FLOW=0.
      Y=X(103)*APRN+X(108)*AMRN+X(118)*ASRN+X(123)*AORN+X(113)
      IF(X(113).GT.IREN)
     1FLOW=(X(103)*PEREN(I)+X(108)*MIREN(I)+X(118)*SPREN(I)+X(123)*
     2ONREN(I)+X(113))/Y*SLR*X(113)
      GRE(4,2,I)=GRE(4,2,I)+FLOW
(60-113).
      FLOW=X(60)*HI(3,2)*P2
      GRE(3,2,I)=GRE(3,2,I)+FLOW
(111-113).
C     FLOW=X(113)*PAREM(I)*SREME(I)*RREMI(I)*LREME(I)
      FLOW=X(113)*PAREM(I)*SREME(I)*RREME(I)*LREME(I)
      GRE(1,2,I)=GRE(1,2,I)+FLOW
(113-114).
      IF(TAVER(I).GT.4.3)FLOW=X(113)*MREME(I)
      IF(TAVER(I).LE.4.2)FLOW=X(113)*( MREME(I)+MREME(I)*PCM)
      GRE(2,2,I)=GRE(2,2,I)+FLOW
(118-70).
      FLOW=0.
      Y=X(103)*APSN+X(108)*AMSN+X(113)*ARSN+X(123)*AOSN+X(118)
      IF(X(118).GT.ISPN)
     1FLOW=(X(103)*PESPN(I)+X(108)*MISPN(I)+X(113)*RESPN(I)+X(123)*ONSPN
     2(I)+X(118))/Y*SLS*X(118)
      GSP(3,2,I)=GSP(3,2,I)+FLOW
(70-118).
      FLOW=X(70)*HI(4,2) *P2
      GSP(4,2,I)=GSP(4,2,I)+FLOW
(130-118).
      FLOW=0.
      IF(I.GE.10.AND.I.LT.25.AND.TMAX(I).GT.8.5) FLOW=X(130)*P1
      SAV2=FLOW
(130-119).
      FLOW=X(130)*MSPTR(I)
(118-130).
      FLOW=SAV2
(116-118).
      FLOW=X(118)*PASPT(I)*SSPTR(I)*RSPTR(I)*LSPTR(I)
      GSP(1,2,I)=GSP(1,2,I)+FLOW
(118-119).
      IF(TAVER(I).LE.4.2)FLOW=X(118)*( MSPTR(I)+MSPTR(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(118)*MSPTR(I)
      GSP(2,2,I)=GSP(2,2,I)+FLOW
(123-80).
      FLOW=0.
      Y=X(103)*APON+X(108)*AMON+X(113)*ARON+X(118)*ASON+X(123)
      IF(X(123).GT.IONN)
     1FLOW=(X(103)*PEONN(I)+X(108)*MIONN(I)+X(113)*REONN(I)+X(118)*SPONN
     2(I)+X(123))/Y*SLO*X(123)
      GON(3,2,I)=GON(3,2,I)+FLOW
(80-123).
      FLOW=X(80)*HI(5,2) *P2
      GON(4,2,I)=GON(4,2,I)+FLOW
(121-123).
      FLOW=X(123)*PAONL(I)*SONLE(I)*RONLE(I)*LONLE(I)
      GON(1,2,I)=GON(1,2,I)+FLOW
(123-124).
      IF(TAVER(I).GT.4.3)FLOW=X(123)*MONLE(I)
```

Appendix VIII. (Cont.)

```
      IF(TAVER(I).LE.4.2)FLOW=X(123)*( MONLE(I)+MONLE(I)*PCM)
      GON(2,2,I)=GON(2,2,I)+FLOW
C     THIS PART SIMULATES THE POPULATION DYNAMICS IN THE WATER TREATMENT
(201-203).
      FLOW=X(203)*PAPEM(I)*SPEMA(I)*RPEMA(I)*LPEMA(I)
      GPE(1,3,I)=GPE(1,3,I)+FLOW
(203-204).
      IF(TAVER(I).LE.4.2)FLOW=X(203)*(MPEMA(I)+MPEMA(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(203)*MPEMA(I)
      GPE(2,3,I)=GPE(2,3,I)+FLOW
(203-40).
      FLOW=0.
      Y=X(208)*AMPW+X(213)*ARPW+X(218)*ASPW+X(223)*AOPW+X(203)
      IF(X(203).GT.IPEW)
     1FLOW=(X(208)*MIPEW(I)+X(213)*REPEW(I)+X(218)*SPPEW(I)+X(223)*ONPEW
     1(I)+X(203))/Y*SLP*X(203)
      GPE(3,3,I)=GPE(3,3,I)+FLOW
(40-203).
      FLOW=X(40)*MI(1,3) *P2
      GPE(4,3,I)=GPE(4,3,I)+FLOW
(208-50).
      FLOW=0.
      Y=X(203)*APMW+X(213)*ARMW+X(218)*ASMW+X(223)*AOMW+X(208)
      IF(X(208).GT.IMIW)
     1FLOW=(X(203)*PEMIW(I)+X(213)*REMIW(I)+SPMIW(I)*X(218)+X(223)*ONMIW
     2(I)+X(208))/Y*SLM*X(208)
      GMI(3,3,I)=GMI(3,3,I)+FLOW
(50-208).
      FLOW=X(50)*MI(2,3) *P2
      GMI(4,3,I)=GMI(4,3,I)+FLOW
(206-208).
      FLOW=X(208)*PAMI(I)*SMIOC(I)*RMIOC(I)*LMIOC(I)
      GMI(1,3,I)=GMI(1,3,I)+FLOW
(208-209).
      IF(TAVER(I).GT.4.3)FLOW=X(208)*MMIOC(I)
      IF(TAVER(I).LE.4.2)FLOW=X(208)*( MMIOC(I)+MMIOC(I)*PCM)
      GMI(2,3,I)=GMI(2,3,I)+FLOW
(213-60).
      FLOW=0.
      Y=X(203)*APRW+X(208)*AMRW+X(218)*ASRW+X(223)*AORW+X(213)
      IF(X(213).GT.IREW)
     1FLOW=(X(203)*PEREW(I)+X(208)*MIREW(I)+X(218)*SPREW(I)+X(223)*
     2ONREW(I)+X(213))/Y*SLR*X(213)
      GRE(3,3,I)=GRE(3,3,I)+FLOW
(60-213).
      FLOW=X(60)*MI(3,3) *P2
      GRE(4,3,I)=GRE(4,3,I)+FLOW
(211-213).
C     FLOW=X(213)*PAREM(I)*SREME(I)*RREM1(I)*LREME(I)
      FLOW=X(213)*PAREM(I)*SREME(I)*RREME(I)*LREME(I)
      GRE(1,3,I)=GRE(1,3,I)+FLOW
(213-214).
      IF(TAVER(I).LE.4.2)FLOW=X(213)*( MREME(I)+MREME(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(213)*MREME(I)
      GRE(2,3,I)=GRE(2,3,I)+FLOW
(218-70).
      FLOW=0.
      Y=X(203)*APSW+X(208)*AMSW+X(213)*ARSW+X(223)*AOSW+X(218)
      IF(X(218).GT.ISPW)
     1FLOW=(X(203)*PESPW(I)+X(208)*MISPW(I)+X(213)*RESPW(I)+X(223)*ONSPW
     2(I)+X(218))/Y*SLS*X(218)
      GSP(3,3,I)=GSP(3,3,I)+FLOW
(70-218).
      FLOW=X(70)*MI(4,3) *P2
      GSP(4,3,I)=GSP(4,3,I)+FLOW
(230-218).
```

Appendix VIII. (Cont.)

```
      FLOW=0.
      IF(I.GE.10.AND.I.LT.25.AND.TMAX(I).GT.8.5) FLOW=X(230)*P1
      SAV3=FLOW
(230-219).
      FLOW=X(230)*MSPTR(I)
(218-230).
      FLOW=SAV3
(216-218).
      FLOW=X(218)*PASPT(I)*SSPTR(I)*RSPTR(I)*LSPTR(I)
      GSP(1,3,I)=GSP(1,3,I)+FLOW
(218-219).
      IF(TAVER(I).LE.4.2)FLOW=X(218)*( MSPTR(I)+MSPTR(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(218)*MSPTR(I)
      GSP(2,3,I)=GSP(2,3,I)+FLOW
(223-80).
      FLOW=0.
      Y=X(203)*APOW+X(208)*AMOW+X(213)*AKOW+X(218)*ASOW+X(223)
      IF(X(223).GT.IONW)
     1FLOW=(X(203)*PEONW(I)+X(208)*MIONW(I)+X(213)*REONW(I)+X(218)*SPONW
     2(I)+X(223))/Y*SLO*X(223)
      GON(3,3,I)=GON(3,3,I)+FLOW
(80-223).
      FLOW=X(80)*HI(5,3) *P2
      GON(4,3,I)=GON(4,3,I)+FLOW
(221-223).
C     FLOW=X(223)*PAONL(I)*SONLE(I)*RONL1(I)*LONLE(I)
      FLOW=X(223)*PAONL(I)*SONLE(I)*RONLE(I)*LONLE(I)
      GON(1,3,I)=GON(1,3,I)+FLOW
(223-224).
      IF(TAVER(I).LE.4.2)FLOW=X(223)*( MONLE(I)+MONLE(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(223)*MONLE(I)
      GON(2,3,I)=GON(2,3,I)+FLOW
C     THIS PART SIMULATES THE POPULATION DYNAMICS IN THE NITROGEN + WATER TREAT.
(301-303).
      FLOW=X(303)*PAPEM(I)*SPEMA(I)*RPEMA(I)*LPEMA(I)
      GPE(1,4,I)=GPE(1,4,I)+FLOW
(303-304).
      IF(TAVER(I).LE.4.2)FLOW=X(303)*(MPEMA(I)+MPEMA(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(303)*MPEMA(I)
      GPE(2,4,I)=GPE(2,4,I)+FLOW
(303-40).
      FLOW=0.
      Y=X(308)*AMPNW+X(313)*ARPNW+X(318)*ASPNW+X(323)*AOPNW+X(303)
      IF(X(303).GT.IPENW)
     1FLOW=(X(308)*MIPNW(I)+X(313)*REPNW(I)+X(318)*SPPNW(I)+X(323)*ONPNW
     1(I)+X(303))/Y*SLP*X(303)
      GPE(3,4,I)=GPE(3,4,I)+FLOW
(40-303).
      FLOW=X(40)*HI(1,4) *P2
      GPE(4,4,I)=GPE(4,4,I)+FLOW
(308-50).
      FLOW=0.
      Y=X(303)*APMNW+X(313)*ARMNW+X(318)*ASMNW+X(223)*AOMNW+X(308)
      IF(X(308).GT.IMINW)
     1FLOW=(X(303)*PEMNW(I)+X(313)*REMNW(I)+SPMNW(I)*X(318)+X(323)*ONMNW
     2(I)+X(308))/Y*SLM*X(308)
      GMI(3,4,I)=GMI(3,4,I)+FLOW
(50-308).
      FLOW=X(50)*HI(2,4) *P2
      GMI(4,4,I)=GMI(4,4,I)+FLOW
(306-308).
      FLOW=X(308)*PAMIO(I)*SMIOC(I)*RMIOC(I)*LMIOC(I)
      GMI(1,4,I)=GMI(1,4,I)+FLOW
(308-309).
      IF(TAVER(I).LE.4.2)FLOW=X(308)*( MMIOC(I)+MMIOC(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(308)*MMIOC(I)
```

Appendix VIII. (Cont.)

```
      GMI(2,4,I)=GMI(2,4,I)+FLOW
(313-60).
      FLOW=0.
      Y=X(303)*APRNW+X(308)*AMRNW+X(318)*ASRNW+X(323)*AORNW+X(313)
      IF(X(313).GT.IRENW)
     1FLOW=(X(303)*PERNW(I)+X(308)*MIRNW(I)+X(318)*SPRNW(I)+X(323)*
     2ONRNW(I)+X(313))/Y*SLR*X(313)
      GRE(3,4,I)=GRE(3,4,I)+FLOW
(60-313).
      FLOW=X(60)*HI(3,4) *P2
      GRE(4,4,I)=GRE(4,4,I)+FLOW
(311-313).
      FLOW=X(313)*PAREM(I)*SREME(I)*RREME(I)*LREME(I)
      GRE(1,4,I)=GRE(1,4,I)+FLOW
(313-314).
      IF(TAVER(I).LE.4.2)FLOW=X(313)*( MREME(I)+MREME(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(313)*MREME(I)
      GRE(2,4,I)=GRE(2,4,I)+FLOW
(318-70).
      FLOW=0.
      Y=X(303)*APSNW+X(306)*AMSNW+X(313)*ARSNW+X(323)*AOSNW+X(318)
      IF(X(318).GT.ISPNW)
     1FLOW=(X(303)*PESNW(I)+X(308)*MISNW(I)+X(313)*RESNW(I)+X(323)*ONSNW
     2(I)+X(318))/Y*SLS*X(318)
      GSP(3,4,I)=GSP(3,4,I)+FLOW
(70-318).
      FLOW=X(70)*HI(4,4) *P2
      GSP(4,4,I)=GSP(4,4,I)+FLOW
(330-318).
      FLOW=0.
      IF(I.GE.10.AND.I.LT.25.AND.TMAX(I).GT.8.5) FLOW=X(330)*P1
      SAV4=FLOW
(330-319).
      FLOW=X(330)*MSPTR(I)
(318-330).
      FLOW=SAV4
(316-318).
C     FLOW=X(318)*PASPT(I)*SSPTR(I)*RSPT1(I)*LSPTR(I)
      FLOW=X(318)*PASPT(I)*SSPTR(I)*RSPTR(I)*LSPTR(I)
      GSP(1,4,I)=GSP(1,4,I)+FLOW
(318-319).
      IF(TAVER(I).LE.4.2)FLOW=X(318)*( MSPTR(I)+MSPTR(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(318)*MSPTR(I)
      GSP(2,4,I)=GSP(2,4,I)+FLOW
(323-80).
      FLOW=0.
      Y=X(303)*APONW+X(306)*AMONW+X(313)*ARONW+X(318)*ASONW+X(323)
      IF(X(323).GT.IONNW)
     1FLOW=(X(303)*PEON1(I)+X(308)*MION1(I)+X(313)*REON1(I)+X(318)*SPON1
     2(I)+X(323))/Y*SLO*X(323)
      GON(3,4,I)=GON(3,4,I)+FLOW
(80-323).
      FLOW=X(80)*HI(5,4) *P2
      GON(4,4,I)=GON(4,4,I)+FLOW
(321-323).
      FLOW=X(323)*PAONL(I)*SONLE(I)*RONL1(I)*LONLE(I)
      GON(1,4,I)=GON(1,4,I)+FLOW
(323-324).
      IF(TAVER(I).LE.4.2)FLOW=X(323)*( MONLE(I)+MONLE(I)*PCM)
      IF(TAVER(I).GT.4.3)FLOW=X(323)*MONLE(I)
      GON(2,4,I)=GON(2,4,I)+FLOW
(40-503).
      FLOW=X(40)*HI(1,5) *P2
(50-508).
      FLOW=X(50)*HI(2,5) *P2
(60-513).
```

Appendix VIII. (Cont.)

```
      FLOW=X(60)*HI(3,5) *P2
(70-518).
      FLOW=X(70)*HI(4,5) *P2
(80-523).
      FLOW=X(80)*HI(5,5) *P2
(40-5).
      FLOW=X(40)*P3
(50-10).
      FLOW=X(50)*P3
(60-15).
      FLOW=X(60)*P3
(70-20).
      FLOW=X(70)*P3
(80-25).
      FLOW=X(80)*P3
C     THIS PART ACCUMULATES TOTAL REPRODUCTION, MORTALITY, EMIGRATION, AND
C     IMMIGRATION BY SPECIES AND BY TREATMENT
      SUBROUTINE FINIS
      DO 10 J=1,4
      DO 10 I=1,4
      DO 10 K=1,26
       SUM1(I,J)=GPE(I,J,K)+SUM1(I,J)
      SUM2(I,J)=SUM2(I,J)+GMI(I,J,K)
      SUM3(I,J)=SUM3(I,J)+GRE(I,J,K)
      SUM4(I,J)=SUM4(I,J)+GSP(I,J,K)
      SUM5(I,J)=SUM5(I,J)+GON(I,J,K)
 10   CONTINUE
      DO 1 I=1,4
 1    PRINT 2,(SUM1(I,J),J=1,4)
 2    FORMAT(3X,*GPE*,4(2X,F8.2))
      DO 3 I=1,4
 3    PRINT 4,(SUM2(I,J),J=1,4)
 4    FORMAT(3X,*GMI*,4(2X,F8.2))
      DO 5 I=1,4
 5    PRINT 6,(SUM3(I,J),J=1,4)
 6    FORMAT(3X,*GRE*,4(2X,F8.2))
      DO 7 I=1,4
 7    PRINT 8,(SUM4(I,J),J=1,4)
 8    FORMAT(3X,*GSP*,4(2X,F8.2))
      DO 20 I=1,4
 20   PRINT21,(SUM5(I,J),J=1,4)
 21   FORMAT(3X,*GON*,4(2X,F8.2))
      DO 30 I=1,4
      DO 30 J=1,4
 30   SUM6(I,J)=SUM1(I,J)+SUM2(I,J)+SUM3(I,J)+SUM4(I,J)+SUM5(I,J)
      DO 31 I=1,4
 31   PRINT 32,(SUM6(I,J),J=1,4)
 32   FORMAT(6X,4(2X,F8.2))
      RETURN
      END
      EVENT SPTR8
      X(30)=X(18)
      X(130)=X(118)
      X(230)=X(218)
      X(330)=X(318)
      X(18)=0.
      X(118)=0.
      X(218)=0.
      X(318)=0.
      X(70)=0.
      RETURN
      END
      EVENT SPTR9
      X(18)=X(30)
      X(118)=X(130)
      X(218)=X(230)
```

Appendix VIII. (Cont.)

```
      X(318)=X(330)
      X(30)=0.
      X(130)=0.
      X(230)=0.
      X(330)=0.
      SAV1=0.
      SAV2=0.
      SAV3=0.
      SAV4=0.
      RETURN
      END
&
#
```

Appendix IX.

Modeling Effort and Costs

The model which was described in this section, simple as it was, required a considerable amount of time and cost to develop and run. Approximately five man-work months were invested in literature review, problem conceptualization, coding, and testing at the cost of approximately $1,400.

About one-third of the time was spent in literature review and model conceptualization. The model was coded in 3 to 4 months. Sensitivity analysis and model experiments were done in less than a month.

High proportion (~80%) of the total cost was spent on model development. In this stage the cost per run was $12. After the model was completed, it was compiled and the binary deck was put on permanent file, and thus repeated compilation costs ($7) were avoided. Also, the fact that only main variables were printed in this stage (population densities), reduced the total cost of one model run from $12 to $3.

The cost for sensitivity analysis and model experiments were less than 20% of the total cost, mainly because the cost per model run was decreased and because in this stage I have already gained considerable familiarity with the model.