OCCASIONAL PAPERS

of the

MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas

NUMBER 37, PAGES 1-27 JULY 9, 1975

STUDIES OF SMALL MAMMAL POPULATIONS AT THREE SITES ON THE NORTHERN GREAT PLAINS

by

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An important North American region, the Great Plains, has been studied by the Grassland Biome of the International Biological Program through a network of study sites ranging from Texas and New Mexico to North Dakota and Montana (French, 1971). The purpose of this study was to compare some of the characteristics of small mammal populations in three generally similar grassland sites in the northern Great Plains. Intrasite and intersite comparisons of grazed versus ungrazed, snap-trapping versus live-trapping, and prebaiting versus nonprebaiting procedures in grid sampling were undertaken. Population density, standing crop biomass, reproduction, and movements were the principal autecological factors analyzed.

Acknowledgements

The senior author gratefully acknowledges support by NSF Grant No. GA 12415. Philip S. Humphrey made thoughtful comments about the manuscript. In the field and laboratory work, we also received help from Alberto Cadena and Peter Lowther. Studies at Cottonwood and Dickinson were supported by a grant to the junior author and J. K. Jones, Jr. from the Grassland Biome section of the International Biological Program, administered through Colorado State University (G. M. Van Dyne, Director).

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Study Areas

The three sites were located as follows: (1) Long Pine Hills, Carter County, Montana, 5½ mi. N, 3½ mi. W Camp Crook, South Dakota; (2) 1 mi. N, 1 mi. W Dickinson, Stark County, North Dakota; and (3) ½ mi. S, 2½ mi. E Cottonwood, Jackson County, South Dakota. Detailed site descriptions may be found in Pefaur (1971), and Hoffmann *et al.* (1971).

Each of the three sites is characterized by a great range of climatic variation; winters are cold and dry, and summers are warm. Although the pattern of temperature is more or less predictable, the pattern of precipitation is not, and periods of drought are not infrequent (Coupland, 1958). Mean monthly temperature and precipitation are presented in the form of hitergraphs (Fig. 1), which are very similar for the three sites in shape and position. A Gaussen-Walter Ombrothermic diagram for each site is shown in Figure 2. At Camp Crook, favorable moisture conditions are present from November to July, but precipitation is below the temperature curve during August and September. This hydric deficiency probably affects the growing season as much as do low temperatures from November to February; favorable growing months extend from April to July. At Dickinson, a favorable precipitation balance is present over the entire year; thus, length of the growing season is governed by low temperatures in the winter months. At Cottonwood, a deficit extends from July to September, making this site the driest of the three studied.

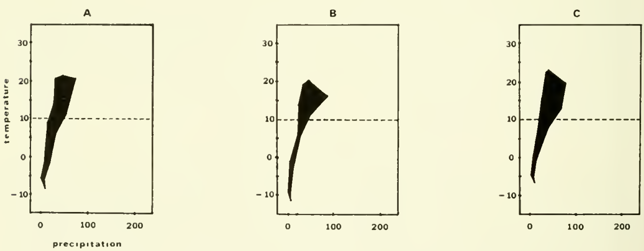

Fig. 1.—Hitergraphs for three localities on the northern Great Plains. A, Camp Cook, South Dakota, includes information from 1896 to 1967; B, Dickinson, North Dakota, includes information from 1892 to 1960; C, Cottonwood, South Dakota, includes information from 1910 to 1967. Temperature is given in °C, precipitation in mm.

Histograms for temperature and precipitation during the summer the study was conducted (Fig. 3) reveal that the total amount of rainfall was below normal in 1970; during the previous summer no month had a hydric deficit at any of the three sites. However,

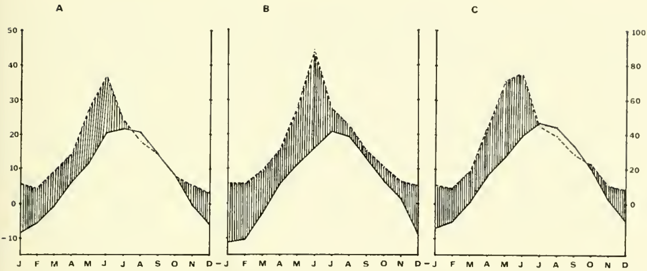

FIG. 2.—Ombrothermic diagrams for (A) Camp Crook, South Dakota, (B) Dickinson, North Dakota, and (C) Cottonwood, South Dakota. Axes to the left show temperature in °C; axes to the right show precipitation in mm; the bottom axis shows the calendar months. Broken lines indicate precipitation curves; solid lines indicate temperature curves. The period covered by each diagram is the same as in Fig. 1.

daily weather changes appeared to have no marked affect on trap captures.

The study site at the Long Pine Hills was on a north–facing slope where the native prairie was neither grazed nor mowed. Sixty–four species of plants were identified at the site and classified as abundant, moderate or incidental (Pefaur, 1971). They formed a *Carex–Bouteloua–Agropyron* community; other communities in the Long Pine Hills include the Bluestem *(Andropogon scoparium)* community (Jonas, 1966).

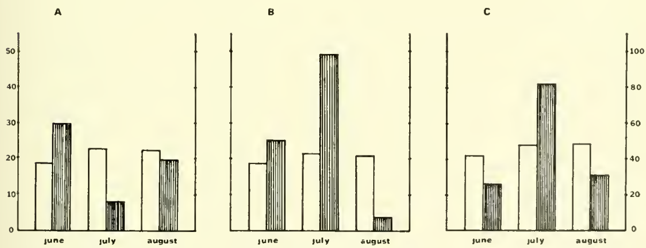

FIG. 3.—Histograms for temperature in °C (left axes) and precipitation in mm (right axes) of (A) Camp Crook, South Dakota, (B) Dickinson, North Dakota, and (C) Cottonwood, South Dakota. Data analyzed include the 1970 summer months only. Empty histograms show temperatures, lined histograms show precipitation.

The Dickinson study site included a small enclosure ungrazed since 1961, though the grassland outside had been grazed or harvested yearly. The grassland vegetation on the site is a Needle and

Thread–Blue grama–Sedge (*Stipa comata–Bouteloua gracilis–Carex* sp.) community (Hanson and Whitman, 1938). An account of the plants occurring at this station has been provided by Whitman (1970).

At Cottonwood the study site lies in the central portion of the mixed prairie; grazing is a common feature. Under good conditions the vegetation is dominated by midgrasses, especially *Agropyron smithii* and *Stipa viridula,* with an understory of shortgrasses, especially *Bouteloua gracilis* and *Buchloe dactyloides.* Several forbs are conspicuous during the early part of the year. Shrubs are of minor importance except in the wetter drainageways where *Symphoricarpos occidentalis* and *Rosa* sp. may be important. Lewis *et al.* (1956) provide an account of the plants found at this site.

Methods

Trapping Procedures

At the three study sites a sampling system was adapted from the Standard Minimum Method (Grodzinski *et al.,* 1966), as modified by French (1971) for use in the I.B.P. Grassland Biome Study in the United States. The trapping grid consisted of twelve by twelve stations, with two traps in each station, and with a 15 m interval between stations. Each grid occupied an area of approximately 2.72 ha, and with a border strip width of 7.5 m, sampled 3.24 ha. Traps were baited with dry oatmeal, set at 1700-1800 hrs, and checked at 2300 hrs; the following morning at 0600-0700, they were checked, and sprung until the next evening. Snap–trap captures were removed at each trap check; if at 2300, the traps were left unset. Any trap found sprung and empty was recorded, and the trap was reset if at 2300 hours. Two grids were established; one was a "snap–trap" grid using Animal Trap Company Museum Special snap traps, while the other was a "live–trap" grid with aluminum Sherman live traps. Both were run concurrently (Table 1). In the Long Pine Hills, a second snap–trap grid was established. Both snap– and live–trapping grids at Cottonwood and Dickinson were first prebaited (baited but not set to catch) for five days, and then operated for ten days. The field trap procedure at the Long Pine Hills was to some extent more complex than in the other two localities. Snap–trapping Grid I had no prebaiting period and was trapped all 15 days, while snap–trapping Grid II had a five day prebaiting period, as at the other two sites. Grid III was first live–trapped with a prebaiting period as at Cottonwood and Dickinson; subsequently it was also snap–trapped for 15 days, as was Grid I (Table 1). Because intra–individual variation in probability of capture may be a function of trap location, traps were shifted at the end of the fifth day of capture (tenth day for snap trap grids I and II) from the original

TABLE 1.—ACTIVITY SCHEDULE FOR LIVE- AND SNAP-TRAPPING AT THREE SITES ON THE NORTHERN GREAT PLAINS

	LIVE-TRAPPING					SNAP-TRAPPING						
	Long Pines Hills	Dickinson		Cottonwood		Long Pines Hills			Dickinson		Cottonwood	
	III July	June	August	June	August	I July	II July	III July-August	June	August	June	August
Prebaiting	5-10	9-14	26-31 (July)	8-13	7-12	—	5-10	(Live Trapping)	9-14	26-31 (July)	7-12	7-12
Trapping	11-21	15-25	1-11	14-24	13-23	6-21	11-21	21-5	15-25	1-11	13-23	13-23
Shifting Traps	16	20	6	19	18	16	16	31	20	6	18	18

position to a point one–half the diagonal distance between stations, to the center of the squares made by neighboring stations.

Grid III of the Long Pine Hills site differed from the others in that it was set up with eleven by thirteen stations in order to maximize homogeneity of the area sampled. The live–trap grid used in Dickinson was smaller than the normal grid because of the area available and consisted of nine rows and a varying number of columns. Two rows had eight columns, two had seven, two had six, two had five, and one had four columns; this grid sampled 1.1 ha, including a boundary strip.

Grid separation was 500 m or more between live-trap and snap-trap grids at all sites. In the Long Pine site, the prebaited snap-trap grid was separted from the non-prebaited grid by 50 m.

At autopsy all animals were weighed and measured, testes measured to the nearest millimeter; molt state, condition of mammary glands, epididymis and seminal vesicles were noted. Reproductive classification of the I.B.P. Grassland Biome (French, 1971) were used for females. In addition, ectoparasites and cheek pouch samples were saved.

On the live-trapping grid small mammals captured were marked by a clean cut toe clip and the code number of each was recorded on an IBP data sheet. Four toes were used on each foot for clipping, following the IBP Grassland Biome system. When an unmarked animal was found dead in the trap this was recorded, but no toe-clip number was assigned. Natural amputation occurring before marking was noted and regular toe clipping was performed.

To calculate biomass density it was necessary first to estimate population density. In this study, six methods were employed; Lincoln-Petersen Index (Adams, 1951); Modified Lincoln Index; Craig-Eberhardt method (Eberhardt, 1969); Edwards and Eberhardt (1967) method; Jolly (1965) method, and Zippin (1956) regression method. The best estimate for the snap-trapped population size was thought to be indicated by the regression method of Zippin (1956); for the live–trapped population the Craig-Eberhardt method (Eberhardt, 1969) was used (Hoffmann, *et al.,* 1971). Mean body weight then was multiplied by the estimated population size and divided by the area of the grid. In Cottonwood, since the Zippin population estimate was unrealistic, the actual number of small mammals caught was used as the best estimate of population size. Biomass and biomass density for each sex were calculated in the same way, except that the number per sex was estimated from the ratio of females to males in the total population. For example, at the Dickinson snap-trap grid in June, the total population estimate was thirty-four, and the estimated proportion was fourteen females to twenty males.

For certain individuals of some species it was possible to record the spatial distribution and relationships with other individuals on the grids. To calculate species diversity two formulas were employed, the well-known formula of Shannon and Weaver (1963), and that given by Margalef (1968).

Comparisons for statistically significant differences among the capture procedures, *i.e.*, removal trapping with prebaiting and non-prebaiting procedures, and live trapping procedure, were devised for every locality under study through the UNIVAR Computer Program (Power, 1970). The characteristics tested were (a) number of individuals caught/number of species caught ratio, (b) diversity indices derived from the Shannon-Weaver formulas, and (c) diversity indices derived from the Margalef formula. UNIVAR also was used to test differences between sexes within localities and between species from different localities with respect to total length and total weight.

Results

General

Ninety-four individuals belonging to ten species of small rodents and one insectivore were captured in the Long Pine Hills snap trap grids. All except *Perognathus hispidus* had previously been recorded from eastern Montana (Hoffmann and Pattie, 1968; Hoffmann *et al.*, 1969; Pefaur and Hoffmann, 1971). Other mammals seen in or near the grids were *Erethizon dorsatum, Odocoileus hemionus* and *Odocoileus virginianus.* Thirteen individuals of three species of rodents were taken in the live-trapping grid (Tables 2, 3). The minimum nightly live-trap catch was three individuals on three occasions (Fig. 4), with a total of forty-eight captures and recaptures.

Sixty-one individuals belonging to seven rodent species were snap-trapped, and forty-one more individuals of five species were live-trapped at Dickinson during two sampling periods in June and August (Tables 2, 3). Other mammals collected in the area included *Sorex cinereus, Lepus townsendii, Lagurus curtatus, Mus musculus, Vulpes vulpes, Mustela frenata,* and *Mephitis mephitis* (Genoways and Jones, 1972). In June, *Spermophilus tridecemlineatus, Perognathus fasciatus, Peromyscus maniculatus, Onchomys leucogaster,* and *Microtus pennsylvanicus* were captured in live trapping, while in August only the first three were taken. Rate of captures per day for both periods is shown in Figure 4.

At Cottonwood, the number of species and individuals captured was low. Seventeen specimens of five rodent species were caught in two snap-trapping periods; sixteen individuals of four species were live-trapped (Tables 2, 3). Other mammals taken close to the grid site were *Sorex cinereus, Lepus townsendii, Cynomys ludovicianus, Reithrodontomys megalotis, Ondatra zibethicus, Mus musculus,*

TABLE 2.—QUANTITATIVE AND QUALITATIVE COMPOSITION OF SMALL MAMMALS CAUGHT IN LIVE-TRAP GRIDS AT THREE DIFFERENT LOCALITIES OF THE NORTHERN GREAT PLAINS

SPECIES	DICKINSON			LONG PINES	COTTONWOOD			ALL SITES
	June	August	Total		June	August	Total	
Spermophilus tridecemlineatus	6	7	13	—	—	1	1	14
Thomomys talpoides	—	—	—	1	—	—	—	1
Perognathus fasciatus	2	1	3	4	—	—	—	7
Peromyscus leucopus	—	—	—	—	1	—	1	1
Peromyscus maniculatus	7	8	15	8	2	7	9	32
Onychomys leucogaster	1	—	1	—	—	—	—	1
Microtus ochrogaster	—	—	—	—	2	3	5	5
Microtus pennsylvanicus	9*	—	9	—	—	—	—	9
Total Individuals	25	16	41	13	5	11	16	70
Total Species	5	3	5	3	3	3	4	8

* Six more individuals found dead in traps were not used in following analysis.

TABLE 3.—QUANTITATIVE AND QUALITATIVE COMPOSITION OF THE SNAP-TRAPPED SMALL MAMMALS AT THREE LOCALITIES ON THE NORTHERN GREAT PLAINS

SPECIES	LONG PINES HILLS								DICKINSON						COTTONWOOD						TOTAL THREE SITES
	Grid I		Grid II		Grid III		Total		June		August		Total		June		August		Total		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
Sorex merriami	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Spermophilus tridecemlineatus	3	6	5	3	—	—	8	9	2	1	5	1	7	2	1	—	—	—	1	—	27
Thomomys talpoides	2	5	—	1	1	3	3	9	—	—	—	1	—	1	1	—	—	—	1	—	14
Perognathus fasciatus	4	4	1	3	4	6	9	13	1	3	—	2	1	5	—	—	—	—	—	—	28
Perognathus hispidus	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Reithrodontomys megalotis	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Reithrodontomys montanus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	1	1	2
Peromyscus leucopus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	1	1	2
Peromyscus maniculatus	5	3	4	2	12	2	21	7	14	6	11	4	25	10	4	2	2	3	6	6	74
Onychomys leucogaster	—	—	—	—	—	—	—	—	—	1	1	—	1	1	—	—	—	—	—	—	2
Microtus ochrogaster	1	—	—	—	1	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	3
Microtus pennsylvanicus	1	1	1	—	1	1	3	2	1	1	4	1	5	2	—	—	—	—	—	—	12
Mus musculus	—	—	—	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	2
Zapus hudsonius	1	—	—	—	1	—	2	—	—	—	1	—	1	—	—	—	—	—	—	—	3
Total, by sex	18	19	11	10	22	14	51	43	18	12	22	9	40	21	8	4	2	3	10	7	
Grand Total	37		21		36		94		30		31		61		12		5		17		172

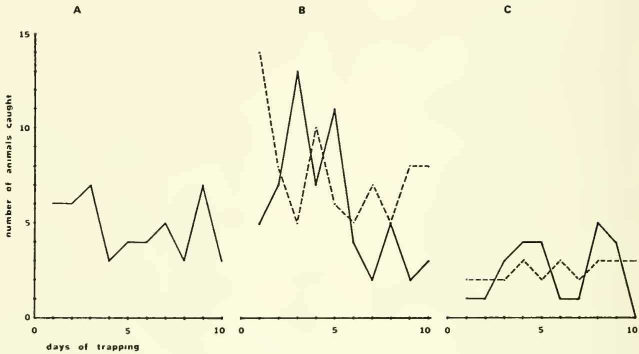

FIG. 4.—Frequency of live-trapping captures at (A) Long Pines Hills, (B) Dickinson, and (C) Cottonwood. For Dickinson and Cottonwood, broken lines show the June captures and the solid line shows the August captures.

Erethizon dorsatum, Vulpes vulpes, Procyon lotor, Mephitis mephitis, Mustela frenata, Taxidea taxus, and *Odocoileus hemionus.* In June, three species taken: *Peromyscus leucopus, Peromyscus maniculatus* and *Microtus ochrogaster;* and in August *Spermophilus tridecemlineatus, Peromyscus maniculatus* and *Microtus ochrogaster.* During June the daily capture rate was rather low and constant, but during August the rate fluctuated between zero and five (Fig. 4).

More detailed accounts of individual species may be found in Genoways and Jones (1972), Pefaur and Hoffmann (1971), Hoffmann *et al.* (1971), Hoffmann and Birney (1972), Lampe *et al.* (1974), and Pefaur and Hoffmann (1975).

Trapping Results

Sequence of Snap-trap Captures—Daily capture sequence was fairly irregular on all three Long Pine grids (Fig. 5a). On the nonprebaited Grid I captures ranged from zero to seven individuals per day, with the majority of captures on the second, third, and fifth days. Sixty-two percent of the total captures were attained by the fifth trapping day; no more than four individuals per day were subsequently captured, even when traps were shifted on the tenth day. However, a truncated regression would show a steeper line for the first ten days of captures than for the last five days. On Grid II, which was prebaited, the situation was different—by the third trapping day 57% of the total captures were achieved. The three first days recorded the greatest captures, and subsequently no more than three individuals were caught per day; a tendency for the daily trapping captures to decrease was noted on the first

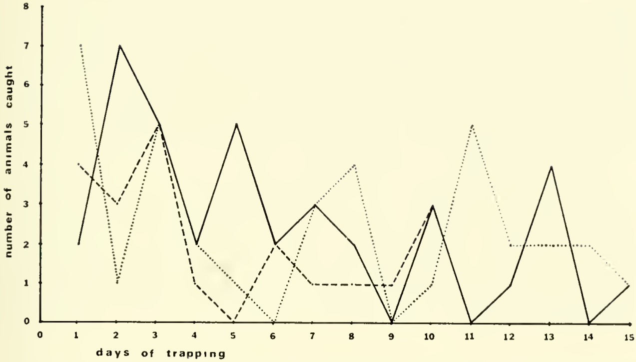

FIG. 5a.—Frequency of snap-trapping captures in Grids I (non-prebaited; solid line); II (prebaited; broken line); and III (following live-trapping; dotted line) at Long Pine Hills, Montana.

five days, instead of a tendency to increase during the last five days of trapping following the shifting of traps. Grid III was unique in that it was run after a period of live-trapping; this may be considered a form of prebaiting since bait was available and there was no removal of animals. Daily captures in this grid ranged from zero to seven individuals, with the highest catches on the first, third, and eighth days of trapping; however, by the fifth day of trapping only 44% of the total captures had been made. Another large catch was achieved on the eleventh day of trapping following the shifting of the traps.

At Dickinson (Fig. 5b), two periods of snap-trapping, both with five days of prebaiting followed by ten days of snap-trapping, were completed (cf. Long Pine Grid II). The range for the June cap-

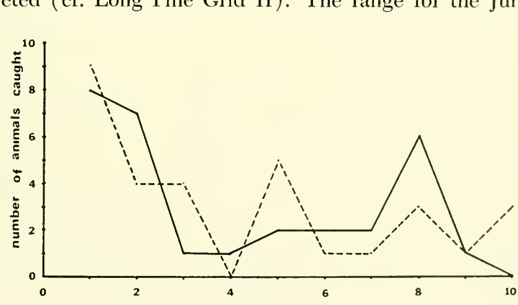

FIG. 5b.—Frequency of snap-trapping captures in June (solid line) and August (broken line) at Dickinson, North Dakota.

tures was from one to eight with the largest capture of rodents on the first, second, and eighth day of trapping. For the August captures, the range was from zero to nine and with the largest captures on the first and fifth day of trapping. In both June and August the largest catches occurred on the first night of trapping. Shifting of the traps to the center of the squares had a less apparent effect on the June grid than on the August one.

Daily variation in the snap-trap catch in June at Cottonwood varied from zero to three individuals per day (Fig. 5c); maximum catch was reached on the ninth day of trapping. For August captures, the range was between zero and one individual; all the captured rodents were caught every other day during the ten-day trapping period. Shifting traps did not affect the rate of trapability at this site.

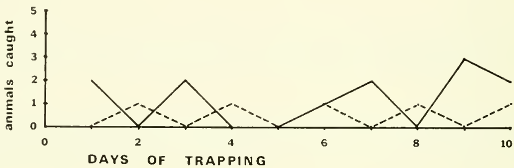

FIG. 5c.—Frequency of snap-trapping captures in June (solid line) and August (broken line) at Cottonwood, South Dakota.

Rate of Removal—Considering the total cumulative catch as 100%, the daily cumulative percent of individuals captured on successive days of trapping was calculated in order to express the rate of removal for the community or for the species.

The community rate of removal at the three sites is shown for the first 10 trapping days in Figure 6. The cumulative percent of captures followed a similar trend in both Long Pine and Dickinson, where about a 65% of removal was attained by the fifth day of trapping. No strong difference was found between any of the grids at Long Pine. At Dickinson, no seasonal differences were recorded by the rate of catches obtained. At Cottonwood, the rate of removal was somewhat slower, as by the fifth day only 50% of the rodents was removed from the area in August, the same percentage being attained on the sixth day in the June catches.

Daily cumulative capture curves for the four most commonly snap-trapped species at Long Pine (Fig. 7) show that all four species had rather uniform probability of capture during the period, with irregularity only in *Thomomys*, for which the system of trapping used (traps on ground surface) was not suitable. For Grid I the capture percentage for the four species is fairly uniform; the four species achieved 100% on the twelfth or thirteenth day of trapping. On Grid II five days were spent in prebaiting in order

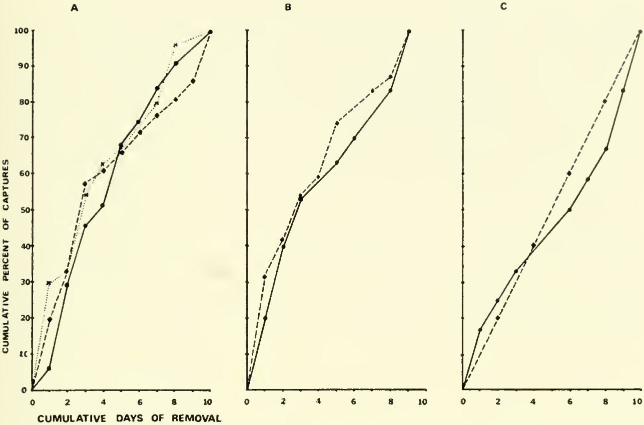

FIG. 6.—Rate of removal for snap-trapped small mammals at (A) Long Pines, (B) Dickinson, and (C) Cottonwood. In (A), solid line shows the removal for Grid I, broken line for Grid II, and dotted line for Grid III; at Grid I and III, the removal period was fifteen days; however, to make them comparable with Grid II, only the first ten days of data are taken into account. In (B) and (C), solid lines show data for June captures and broken lines show data for August captures.

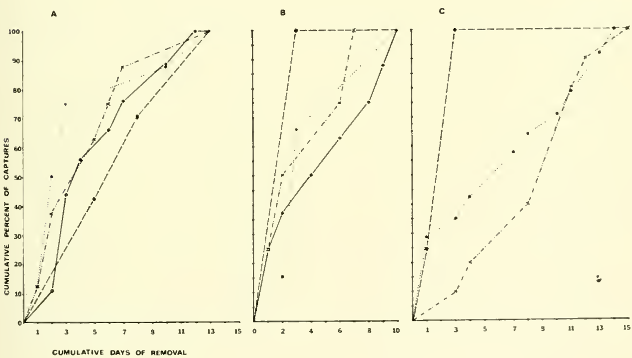

FIG. 7.—Rate of removal for the most commonly snap-trapped species in (A) Grid I, (B) Grid II, and (C) Grid III at Long Pine Hills, Montana. Key:

——————— *Spermophilus tridecemlineatus*
- - - - - - - *Thomomys talpoides*
—.....—.....—..... *Perognathus fasciatus*
.... *Peromyscus maniculatus*

to increase initial probability of capture (cf. Sealander *et al.*, 1958; Trojan and Wojciechowska, 1967) and as a result, the first trap night obtained 25% of the total of both *Spermophilus* and *Perognathus*, the second trapping added 15% of *Peromyscus;* the trapped population of *Perognathus* was removed by the seventh day of trapping. At Grid III, *Perognathus* and *Peromyscus* were continuously captured throughout the trapping period, reaching 100% on the fifteenth and fourteenth days respectively; no *Spermophilus* were trapped.

Thomomys talpoides captures were of young, transient individuals, and illustrate well the irregularity of removal obtained with snap-traps for a species with subterranean rather than surface movements. Additionally, since traps were closed between 0700 and 1700, diurnal *Spermophilus* were exposed to traps only during early morning and evening, thus reducing relative probability of capture.

Removal by trapping at Dickinson gave irregular results (Fig. 8). When traps were run in June only *Spermophilus, Perognathus,* and *Peromyscus* were caught in the first two days of trapping, and

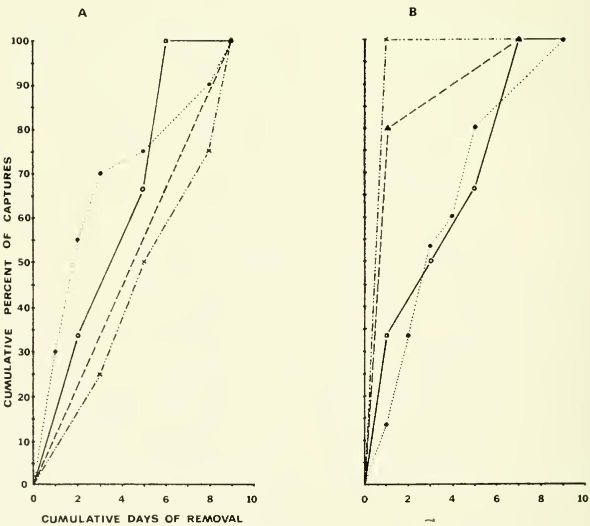

FIG. 8.—Rate of removal for the most commonly snap-trapped species in (A) the June grid and (B) the August grid at Dickinson, North Dakota. Key:

——————— *Spermophilus tridecemlineatus*
—‥—‥—‥ *Perognathus fasciatus*
………………… *Peromyscus maniculatus*
- - - - - - - *Microtus pennsylvanicus*

they were very even in the daily percentage obtained; *Microtus pennsylvanicus* appeared as an invader—both individuals of this species were taken on the fourteenth day. In August, all trapped *Perognathus* were captured on the first trapping night; two other species, *Spermophilus* and *Microtus*, reached 100% on the seventh night, and *Peromyscus* on the ninth; 80% of *Microtus* were caught in the first night in contrast to the June sample. The rate of captures of both *Perognathus* and *Microtus* was somewhat slower in June as compared with the faster rate of removal in August.

Snap-trap captures were neither abundant nor varied at Cottonwood in either period. Only *Perognathus maniculatus* was captured enough times to warrant a cumulative capture curve (Fig. 9). The rate of removal for this species in June had a sigmoid shape, which might have been influenced by the shifting of traps exposing more individuals to capture; the rate of removal in August was constant for the whole period.

Movement Patterns

Spermophilus tridecemlineatus—Two or more recaptures at different stations recorded movements of individual thirteen-lined ground squirrels. At Dickinson, greatest distances between points of capture were 118.8, 94.6, 61.1, and 54.2 m; at Cottonwood, the only record was 35.3 m.

Perognathus fasciatus—Movements of some *Perognathus fasci-*

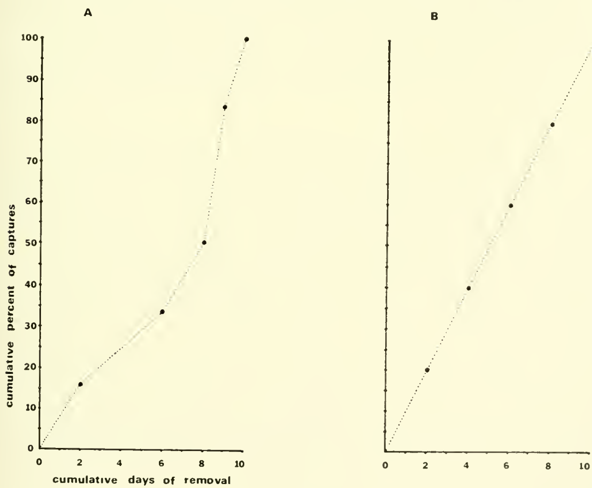

FIG. 9.—Rate of removal for *Peromyscus maniculatus* caught in (A) the June grid and (B) the August grid at Cottonwood, South Dakota.

atus were recorded on the live-trapping grid at the Long Pine Hills. Two animals were recaptured at the same station, another was captured at two different stations, and a fourth pocket mouse was recaptured four times at different stations. Greatest distances observed between points of capture for the latter two individuals were 26.5 m, and 65.7 m, respectively.

Peromyscus maniculatus—*Peromyscus maniculatus* has a large home range (Stickel, 1968). Captures and recaptures from the Long Pine Hills grid are in agreement, for the "greatest distance between points of captures" recorded range from 15 to 177.6 m.

Recaptures at Dickinson showed "greatest distance" ranging from 15 to 78.5 m in the June captures, and from 15 to 90.0 m in the August captures. Two deer mice marked in June were recaptured again in August; for one of them the "greatest distance" remained the same (78.5 m), but for the other it reached 120 m. Also, a *P. maniculatus* marked in the live-trap grid was recaptured in the snap-trap grid, although the grids were separated about 500 m. "Greatest distance" found in deer mice captured at Cottonwood had values from 15 to 186.9 m.

Microtus ochrogaster—No snap-trapped animals were taken in Dickinson or Cottonwood, but at the latter site there were six live-trapped specimens having greatest distance between point of captures of 15.0, 23.0, and 35.3 m.

Microtus pennsylvanicus—Movements of individuals *M. pennsylvanicus* seem to range widely. At Dickinson in June, one of the live-trapped marked mice was released and later recaptured in the snap-trap grid, about 50 m away. Recaptures on the live-trapping grid showed "greatest distances" of 131.5, 103.5, 65.7, and 53.0 m.

Density Estimates

At the three sites, five methods for estimating population size from livetrapping captures were used (see METHODS). Table 4 shows the population density estimates based on those methods. The data did not permit calculation of an estimate by the Edwards and Eberhardt method at Cottonwood in June, nor could the Jolly method be used for any locality other than Dickinson because the data did not fulfill their requirements. In general, all methods gave fairly concordant results, with the exception of the Edwards and Eberhardt estimate for the Long Pine Hills. In a similar study, French (1971) concluded that the Jolly stochastic procedure provided the more accurate estimate of a small mammal population, all members of which were believed to have been previously marked. However, when assumptions of the Jolly method are not met, the Craig-Eberhardt method appears to give the most satisfactory results (Hoffmann, *et al.*, 1971).

At Dickinson, the live-trapping grid was not only smaller than the standard IBP live-trap grid used at the other sites, but also, at

TABLE 4.—INITIAL TOTAL POPULATION ESTIMATE FOR CAPTURE-RECAPTURE AND REMOVAL PROCEDURES, CALCULATED THROUGH DIFFERENT METHODS IN THREE PLACES OF THE NORTHERN GREAT PLAINS

Site and Grid		Live-Trapping Estimate: Edwards & Eberhardt	Craig & Eberhardt*	Lincoln	Modified Lincoln	Jolly	Snap-Trapping Estimate Zippin
Long Pines	I						44
	II						23
	III	41	16	14	18	—	47
Dickinson	June	32	34	27	37	26	47
	August	26	21	16	26	—	36
Cottonwood	June	—	6	6	9	—	−12**
	August	20	19	16	25	—	72**

* Considered best live-trapping estimate.
** Actual numbers caught used as best estimate; see Table 3.

the end of the August trapping period, a long-tailed weasel *(Mustela frenata)* raided the traps on the grid for several nights killing and eating the trapped mice. It is thus not possible to say that the population actually declined in size there from June to August. On the other hand, at Cottonwood, the total number of small mammals and all population estimates increased from June to August.

Population densities on the snap-trapping grids were estimated by the Zippin method (Table 4). The catches at Cottonwood failed to fulfill the requirements for the Zippin method, resulting in a negative number for June and a meaningless figure of seventy-two animals for August.

Since the Long Pines Grid III was first live-trapped and then snap–trapped, it was also possible to estimate the population size by the Lincoln Index method. Live-trapped animals were used as the sample period, and snap-trapped animals as recaptures. Applying the Lincoln Index, the result was seventy-two, and with Modified Lincoln Index, 154; these values are much higher than estimates obtained by any other method.

Biomass

Mean body weight, species biomass, and biomass density for all the species combined (except *Thomomys;* see above) were calculated. Species biomass was obtained by multiplying the best estimate of initial species population times the actual mean body weight by species for the three studied sites separately. The procedure used previously by Hoffmann *et al.* (1971) of adjusting individual weights by subtracting stomach and reproductive tract weight (in pregnant females) from the total body weight to obtain an adjusted species biomass was not used here.

Live-trap grid biomass density reached 62.69 g/ha in Montana, 2,316.92 and 975.14 in North Dakota (for June and August respectively) and 40.78 and 186.03 g/ha in the spring and summer captures at South Dakota. Snap-trap grid biomass density was 289.85, 222.59, and 207.35 g/ha for grids I-III in Long Pines; 273.75 and 335.39 in Dickinson; and 102.83 and 25.64 g/ha in Cottonwood. The higher biomass density for the Dickinson live–trapped grids was a result of the high number of thirteen-lined squirrels captured.

Significant biomass contributions at the study sites was apportioned among five species (Table 5). The most important of them was *Spermophilus tridecemlineatus,* with a high contribution in grams per hectare in live–trapping at Dickinson, and in snap-trapping at both Long Pine and Dickinson. Because of its higher density, *Peromyscus maniculatus* was the second most important biomass contributor to all three sites; on the live-trapping grids, the largest biomass was achieved at Dickinson in both June and August; on the snap-trapping grids the highest biomass density was attained at Dickinson. Relatively large biomass density was contributed by *Perognathus fasciatus;* these pocket mice had higher biomass density in the Dickinson live–trapping grids than at Long Pine, but on snap-trapping grids the contribution was larger in Long Pine. *Microtus ochrogaster* made biomass contributions only on the live-trapping grids at Cottonwood, and on snap-trapping Grids I and III of Long Pine. The standing crop biomass was highly influenced by the contribution that *Microtus pennsylvanicus* provided in the June live–trapping grid at Dickinson; somewhat smaller numbers were obtained in the snap-trapping grids of both Long Pine and Dickinson.

Species Diversity

Species diversity on the study areas was measured by H', of the Shannon–Weaver formula, $H' = -\sum_{i=1}^{S} p_i \log_2 p_i$ (Shannon and Weaver, 1963; Lloyd *et al.*, 1968), and by $D' = (S-1)/\log_e N$, a formula presented by Margalef (1968). Species richness (Lloyd and Ghelardi, 1964), one of the components of the first formula, is also presented. In Margalef's formula, species richness S, is very important because of its position in the numerator of the proportion, $(S-1)/\log_e N$.

Species diversity calculated from live-trapping and snap-trapping grids is shown in Tables 6 and 7. Density for the live-trapped small animals at all sites combined reached H'=2.26 and D'=1.62, and for the snap-trapped H'=2.55 and D'=2.52. For live-trapping at individual sites, the highest H' value was reached at Dickinson

TABLE 5.—BIOMASS DENSITY CONTRIBUTION BY SOME SPECIES CAUGHT AT THREE SITES ON THE NORTHERN GREAT PLAINS

SPECIES	LIVE-TRAPPED BIOMASS DENSITY					SNAP-TRAPPED BIOMASS DENSITY						
	Long Pines	Dickinson		Cottonwood		Long Pines			Dickinson		Cottonwood	
	III	June	August	June	August	I	II	III	June	August	June	August
S. tridecemlineatus	—	1927.21	841.19	—	56.23	174.10	154.80	—	123.00	182.10	56.23	—
P. fasciatus	19.64	30.61	7.65	—	—	29.31	12.30	38.99	14.34	5.19	—	—
P. maniculatus	43.05	145.65	126.30	10.61	62.62	50.86	34.24	88.79	117.05	87.97	31.25	25.64
M. ochrogaster	—	—	—	24.96	67.18	10.12	—	39.81	—	—	—	—
M. pennsylvanicus	—	197.55	—	—	—	18.21	11.01	25.42	13.96	47.58	—	—
Other Species	—	15.90	—	5.21	—	7.25	10.24	14.34	5.40	8.11	15.35	—
Total	62.69	2316.92	975.14	40.78	186.03	289.85	222.59	207.35	273.75	335.39	102.83	25.64

TABLE 6.—LIVE-TRAPPED SMALL MAMMAL DIVERSITY IN THREE DIFFERENT LOCALITIES IN MONTANA, NORTH DAKOTA, AND SOUTH DAKOTA

	DIVERSITY		SPECIES
SITES	Shannon & Weaver, H'	Margalef D'	RICHNESS
Long Pine Hills	1.238	0.779	3
Dickinson *in toto*	1.936	1.038	5
June Grid	1.865	1.164	5
August Grid	1.271	0.721	3
Cottonwood *in toto*	1.491	1.082	4
June Grid	1.521	1.242	3
August Grid	1.240	0.834	3
Diversity, All Sites	2.258	1.616	8

(1.94) and the highest value for D' was attained at Cottonwood (1.08). For individual grids, the highest H' value, as well as D' were found at the June grids at Dickinson and Cottonwood respectively.

Species richness and apportioning of individuals within species was somewhat different in the snap-trapping grids at the three study sites, leading to differences in both $H'$and D' values for the removal procedure. This was the most marked at the Long Pine, where eleven species and ninety-four individuals were snap-trapped but only three species and thirteen individuals were taken in live traps. However, diversity value for all grids combined was more similar when measured with the Shannon-Weaver formula, whereas diversity as calculated by the Margalef formula was much lower

TABLE 7.—SNAP-TRAPPED SMALL MAMMALS DIVERSITY IN THREE DIFFERENT LOCALITIES IN MONTANA, NORTH DAKOTA, AND SOUTH DAKOTA

	DIVERSITY		SPECIES
SITES	Shannon & Weaver, H'	Margalef D'	RICHNESS
Long Pine Hills *in toto*	2.643	2.185	11
Grid I	2.555	1.938	8
Grid II	2.129	1.642	6
Grid III	2.433	2.183	9
Dickinson *in toto*	1.910	1.459	7
June Grid	1.533	1.176	5
August Grid	2.124	1.747	7
Cottonwood *in toto*	1.613	1.411	5
June Grid	1.959	1.609	5
August Grid	0.000	0.000	1
Diversity, All Sites	2.549	2.517	14

for the live-trapped samples. This is explained principally by the nature of the two formulas; Margalef's does not consider the intra-sample distribution of animals, but rather only the total distribution of N.

Snap-trapped small mammal diversity was highest for both H' and D' on the Long Pine grids, individually as well as *in toto*. Moderately high values for H' and D' were also attained on the August grid at Dickinson. At the Cottonwood site, species diversity based on snap-trapping was higher than that of live-trapping despite the fact that the August snap-trapping had species richness of one and the diversity was zero.

To test whether the differences in the index "number of individuals/number of species," H' values, and D' values among the three study sites were statistically significant, an analysis of variance was computed. No statistical differences were found within the three sites themselves, nor between grazed versus ungrazed treatment, nor between live-trapping versus snap-trapping procedures. However, the number of variables used was small (three), thus giving F (test of F hypothesis) a high value.

Discussion

Simultaneous studies of small mammal populations comparing different aspects of the environment and different capture procedures are few, yet they provide a considerable amount of useful information about the ecology of species and communities. The present study compared several variables affecting mammal populations in relation to their structure and dynamics.

Grazing

A comparison of the catches obtained for two ungrazed habitats with a grazed one shows ungrazed habitats support more rodents. At the ungrazed Long Pine Hills and Dickinson sites, ninety-four individuals of eleven species, and sixty-one individuals of seven species were respectively snap-trapped, whereas only seventeen individuals of five species were snap-trapped at the grazed Cottonwood site. These differences in population density and species richness in turn modify species diversity. Taking only the H' values, the mean snap-trapped diversity for ungrazed stands revealed 2.15 bits per individual, as compared with only 1.78 bits for the grazed stand. Mean live-trapped diversity for ungrazed stands was 1.46 bits per individual, while for the grazed stand the diversity was 1.38 bits. The mean diversity for snap-trapping at the three localities was 2.05 bits, and the mean for all live-trapping grids was 1.43. All these figures are similar to the diversity of 1.9 bits shown by grassland birds (Tramer, 1969), and they are what might be expected for northerly, homogeneous habitats such as the northern Great Plains (see Table 7).

Because the latitudes of the three sites differ only slightly, a major gradient of increasing diversity from north to south should not be expected (Fischer, 1960; Pianka, 1966 and 1971; Hermosilla *et al.,* 1966). In an earlier report Hoffmann *et al.* (1971) commented that small mammals data coming from grassland stations scattered at different latitudes in North America showed no indication of such a trend. The monotony of the grassland habitat may be responsible for this—grasslands have the same general plant life-forms throughout, and small mammals make use of the space only in a two-dimensional way; grasslands thus differ from other biomes in which more diversified habitat permits the development of more ecological niches containing more mammalian species.

Ultimately, small mammals form part of the energy flux expressed as the productivity of the ecosystem; one way in which productivity is expressed is as biomass density. According to this parameter, the mean snap-trapped biomass for ungrazed stands was 323 g/ha, as compared with only 91 g/ha for the grazed stand; the mean live-trapped biomass for ungrazed stands was 958 g/ha whereas in grazed stands it was only 113 g/ha. These figures clearly show the restriction on small mammal productivity that grazing imposes on the grassland ecosystem. In the northern Great Plains, an ungrazed stand supports a larger and more diversified community of small mammals, and thus its productivity is larger, as compared with grazed stands.

Trapping

When comparing live-trapping versus snap-trapping results, one concern is which method obtains the most reliable estimate of population size? French (1971) expressed the opinion that the Jolly (Jolly, 1965) and Hansson (Hansson, 1969) methods give the best population estimates for live–trapping and snap-trapping data, respectively. However, neither method was suitable for the data gathered in this study, and the Craig-Eberhardt (Eberhardt, 1969) and the regression method (Zippin, 1956) were used.

Yang *et al.* (1970) have questioned the effect that snap-trapping has on populations of small mammals, and the reliability of the data as an index of population size. Undoubtedly, such reliability depends on the method used to analyze the data. The regression method used herein for snap–trapping data does not permit assessment of density when the number caught does not decrease in successive captures. This was true for Cottonwood, where two meaningless figures were obtained owing to the distribution of captures on the successive days. When there was an increase in the number of rodents captured during the final days of trapping, Grodzinski *et al.* (1966) calculated the equation of regression only for those first days during which there was a tendency for captures to decrease. This method may be applied for rodent species that have a similar dwelling and behavioral pattern, e.g. "surface" rodents; it cannot be applied safely to underground dwellers (the case of the pocket gophers in the present study), or for some insectivores (Aulak, 1967), despite the fact that individuals may be taken as part of the sample.

Anyhow, the reliability of calculations made by means of the regression method depends on the correctness of the assumptions that probability of capture is the same for all individuals, migration is low or absent, changes due to births and deaths are slight, and environmental conditions are similar during the period of capture (Grodzinski *et al.*, 1966; Gentry *et al.*, 1968; Janion *et al.*, 1968). Grodzinski *et al.* (1966) stated that correctness of the premises can be attained by analyzing the difference between the actual number caught and the regression estimate expressed as a percentage; if all the premises are fulfilled, then both figures should coincide, or their differences should not be larger than 10% as a margin of error. These same authors obtained in their study equal or smaller estimated numbers than the total number of rodents caught. Gebczynska (1966), however, found that total community size estimates were always larger than total number removed (except for one species), a situation also found by Gentry *et al.* (1968) as well as in the present study. The reason why the population size estimates were larger than the total number of captures was due to the absence of a steady decrease in the number of daily catches —there were some days where an increase in the number of captured animals occurred, as compared to previous ones. Nevertheless, for the whole period a negative slope of the linear regression was found (with the exceptions of Cottonwood captures). The increases noted might well be the result of immigration into the grids, as well as random factors affecting the daily catch.

In this study there was no way to test which method of estimation of the population on the live-trapping grids was best, as French (1971) did, since he claimed to know the size of the rodent populations he was sampling. Lincoln, Modified Lincoln, and Craig-Eberhardt methods were the only ones available for all samples (see Table 4), and as the Craig-Eberhardt estimates were intermediate, it was arbitrarily chosen as representative.

Close similarity between estimates obtained by the regression and the Craig-Eberhardt methods should not *a priori* be expected, since their theoretical bases are different. Even on those study sites that had one snap-trapping and one live-trapping grid in similar habitat, intra-site values of these two methods cannot be compared directly because of the differences in distribution of small mammals. Live and snap-trapping grids at all the sites were separated by 500 m, a distance large enough to permit the species to have different patterns of density and dispersion. The case of *Spermo-*

philus at Long Pine is illustrative of this situation: the observed as well as the captured populations at Grid I and II were far larger than at Grid III.

Grid III at the Long Pine Hills is remarkable for the information it provides. For the live-trapping captures the Edwards and Eberhardt method gave the highest estimate (41 individuals), and the rest of the methods estimated the population as less than 20; for the subsequent snap-trapping captures the population was estimated by the regression method as 23. If these two treatments are taken as consecutive samples (see above), the Lincoln method estimate of the population is 72 individuals. Thus, three different estimates are obtained on the same grid, using the same data.

Baiting

The aim of prebaiting is to increase the probability of capture, and consequent rate of removal of animals from a given area; a better estimate of population size might then be obtained. This point is unresolved and it has become a focus of discussion among small mammal ecologists, because the estimate might well not be representative of the actual population living in the trapped area, but be significantly influenced by an influx of invaders attracted by the bait. Buchalczyk and Pucek (1968) found that *Microtus oeconomus* captured in prebaited traps were significantly different from those captured in non-prebaited traps. Babinska and Bock (1969) found that rodent captures occurred more quickly when preceded by prebaiting, and that, as a result of prebaiting, more individuals are captured than from non-prebaited areas. Their estimate of numbers by the regression method was found to be equal in prebaited and non-prebaited areas in one experiment, whereas, in another, estimated number of rodents was larger in the non-prebaited areas than in the prebaited ones. Tanaka and Kanamori (1969) found that probability-of-capture estimates obtained with prebaiting were higher than with non-prebaiting in snap-trapping Japanese *Microtus montebelli.*

In this study, the data seem to favor the non-prebaited grid—species richness and number of individuals as well as species diversity were higher. However, a test of the differences between prebaited and non-prebaited treatments showed that they were not significant; the analysis of variance did not distinguish the values, so the differences might be due to chance rather than the actual differentiation in the characteristics compared: number of individuals/number of species, H' value, and D' value.

The percentage of differences between the actual number caught and the regression estimate (Grodzinski *et al.*, 1966; see above) at Long Pine was 16% for the non-prebaited grid, 9% for the prebaited, and 24% following live-trapping; at Dickinson these values were 12% and 14% for both June and August snap-trapped grids; no values were obtained for Cottonwood due to the unrealistic estimates. These percentages force the conclusion that neither prebaited or non-prebaited procedures fulfill the premises of the regression method, and the estimated population sizes cannot be considered reliable. The explanation for the high value (24%) at Grid III in the Long Pine can be found in the extent of the prebaiting period (five days of pre–baiting, plus ten days of live-trapping without removal). This may have resulted in a higher rate of immigration before and during the time the removal captures were going on; every station at that grid played the role of an "oasis" in supplying bait. Tanaka and Kanamori (1969), and Pelikan (1967) have concluded that a long period of prebaiting can cause immigration. Zejda and Holisova (1970) also believed that prebaiting increased the invasion of animals from outside the grid, producing centripetal pressure during the removal period, and probably also during the prebaiting period. They suggested elimination of prebaiting, and, in its stead, increase in the number of trap stations on the Standard Minimum grid, as a way of obtaining a more rapid collection of small mammals, and thus a closer estimate of population size.

Summary and Conclusions

In June-August, 1970, populations of small mammals were compared at three sites in the northern Great Plains (in Carter Co., Montana, Stark Co., North Dakota, and Jackson Co., South Dakota). Live- and snap-trapping procedures were designed to test the effects on captures of prebaiting, rate and sequence of removal, and grazing. Data on movement patterns, population densities, biomass, and species richness and diversity were also analyzed.

In most cases, snap-trapping and live-trapping gave roughly similar population estimates. However, snap-trapping revealed a greater number of species than did live-trapping, 14 versus eight respectively, and all species caught in live-traps were also taken in snap-traps. We conclude that, for the sites studied, snap-trap grids produce better results; they are also cheaper and less time-consuming to use. Since prebaiting did not produce the desired pattern of capture consistently, we also conclude that 10 trapping days without prebaiting are preferable for the sort of time-limited sampling we conducted. Finally, sampling of ungrazed grassland revealed, as expected, higher population densities, and greater species richness and diversity, than did grazed grassland.

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