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Short-Term Effects of Shrew Predation Upon Invertebrate Prey Sets in Prairie Ecosystems

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SYNOPSIS: During August of 1971, the effects of different densities of shrews (*Sorex cinereus*) upon the density and species composition of invertebrate prey sets on two prairies in northwestern Iowa were studied. Invertebrates were sampled using pitfall traps set on areas containing known shrew densities. In general, different levels of shrew predation produced certain differences in the prey sets. Increased shrew density was associated with the following

prey set characteristics:

- 1) decreased numerical densities, but not the total biomass of prey sets;
- 2) decreased species dominance of prey sets; and
- 3) increased species diversity of the largest prey size subsets of the total prey set.

These observed effects of shrew predation are short-term effects which are typical of keystone predators.

INDEX DESCRIPTORS: Shrews, Invertebrates, Prairies, Predation, Keystone Predators.

The role of predation in the organization and functioning of communities has been demonstrated using natural situations and experimental techniques (Brooks and Dodson, 1965; Dodson, 1970; Paine, 1966; Hall, Cooper and Werner, 1970; Hurlbert, Zedler, and Fairbanks, 1972). Mechanisms by which predation might act to regulate the density of prey populations have been proposed by Holling (1959, 1965). Theoretical arguments based upon these models and the experimental data suggest that perturbation of a predator-prey system will result in a predictable series of events before an equilibrium is reattained.

During the early summer of 1971 a decline in the population densities of the prairie vole, *Microtus ochrogaster*, and one of its principal predators, the short-tailed shrew, *Blarina brevicauda*, was noticed on prairies and grasslands in the vicinity of Lakeside Laboratory in northwestern Iowa. After an interval of about one month, increases in populations of the meadow jumping mouse, *Zapus hudsonicus*, and the masked shrew, *Sorex cinereus*, occurred. At this time an unreplicated pilot study was initiated to study the effects upon the invertebrate prey of this interruption and subsequent renewal of shrew predation. Analysis of these preliminary data suggests that predation by *S. cinereus* has a number of primary effects upon the invertebrates in prairie ecosystems.

MATERIALS AND METHODS

A. Study Areas

Two prairie ecosystems in northwestern Iowa on or close to the Iowa Lakeside Laboratory were used in this study. These were Cayler Prairie, a relatively undisturbed and mature prairie, and the Lakeside Grasslands, a tract of less mature prairie. The vegetational patterns on both areas have

been studied, and so a relatively good history of both areas was available (Aikman and Thorne, 1956; Anderson, 1936, 1946; Rudman and Pohl, 1951). Two quadrats, measuring 25 by 50 feet (0.03 acres), were set up on each grassland ecosystem. In both ecosystems, one quadrat was located on the top of a hill, and the other was on the hill slope between upland prairie and a low swale. The abbreviations for each quadrat to be used in the rest of this paper are as follows:

- CPu—upland quadrat on Cayler Prairie,
- CPs—slope quadrat on Cayler Prairie,
- LGu—upland quadrat on the Lakeside Laboratory Grasslands,
- LGs—slope quadrat on the Lakeside Laboratory Grasslands.

The vegetation types present on both areas were tall grass prairies. Xeric upland species associations were present on the hilltops in both areas. More mesic prairie species associations were present on the slopes. The plant species diversity was higher on Cayler Prairie than on the Lakeside Grasslands (Platt, unpublished data). In both ecosystems the standing crop biomass of plants and the amount of duff (litter) was greater on the slopes than on the upland regions (Platt, unpublished data). The primary production and amounts of litter on the various quadrats were less different between ecosystems than between the slopes and upland regions on each prairie (e.g., LGu resembled CPu more than LGs). From these conditions potential associations of community complexity (plant species diversity) and productivity (plant production) were made with invertebrate prey set characteristics.

B. Methods of Estimating the Relative Densities of *Sorex cinereus* on the Study Quadrats

Fifty live traps were used on each quadrat. Live trapping was conducted in June and was renewed late in July. Trapping was conducted about one week prior to the installation of the pitfall traps and during the three week period of the investigation. Shrews were also collected in the pitfall traps. The total number of shrews captured by both methods was used as an estimate for the density on each quadrat.

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C. Methods of Collection and Analysis of Invertebrate Prey Sets

Invertebrate species assemblages were collected using pitfall traps on each quadrat. Eight empty number ten cans were used as pitfall traps on each quadrat; these were buried so that the open end was just below the ground surface. The traps were spaced about 10 feet apart. During a three week period at the beginning of August, 1971, traps were examined daily and invertebrates in each trap were collected. On days that heavy rains occurred, samples contained very few invertebrates; these samples were not included in the data analyses. The number of individuals and the number of species of invertebrates collected per day did not decline over the three week period of pitfall trapping. Consequently, it was inferred that invertebrate populations in the vicinity of the traps were not depleted during the period of collection. All invertebrates over three millimeters in body length were assumed to be potential prey for shrews. Thus ants, collembolans, mites, and other small invertebrates were excluded from the data analysis. Invertebrates collected were sorted to families using taxonomic keys (Jaques, 1947; Kaston, 1952). Individuals in the same family were grouped on the basis of obvious morphological characteristics. These groups were considered as "species." Forty-one different "species" were collected over the three week period of study. The number of individuals and the "species" collected in each pitfall trap on each quadrat were recorded for each collection date. Samples of each "species" collected were dried and weighed; the body length also was measured. The mean dry weights of "species" were used to divide prey sets roughly equally among six weight classes for data analyses: (I) 0.1-2.0 mg; (II) 2.1-5.0 mg; (III) 5.1-20.0 mg; (IV) 20.1-50.0 mg; (V) 50.1-100.0 mg; and (VI) 100.1-400.0 mg. Prey sets also were divided into herbivore-detritivore and carnivore trophic components. The herbivore-detritivore component included herbivorous insects feeding upon live vegetation, pollen-nectar feeding insects, detritivorous invertebrates, and scavenging insects such as silphid beetles. Although these invertebrates utilized a wide variety of resources, they were grouped together since they represented primary consumers. The majority of the invertebrates in the herbivore-detritivore component of the prey sets were detritivores (crickets, isopods, millipedes, beetles). Herbivorous insects, such as weevils, leafhoppers, Lepidoptera larvae, grasshoppers, and katydids were collected less often in the pitfall traps. Pollen-nectar feeding species such as bees or adult Lepidoptera were taken only rarely. The carnivore component included predatory and parasitic invertebrates. Those commonly taken included two "species" of lycosid spiders, two "species" of carabid beetles, and a phalangid, all of which were litter or ground surface dwelling forms. Predaceous and parasitic Hymenoptera, predaceous beetle larvae, predaceous Hemipterans, and centipedes were collected less often.

Data analyses of prey sets obtained were made by pooling all invertebrates taken in pitfall traps on each quadrat. For some analyses, dates of collection were treated as replicates; other analyses were made using the total collection of invertebrates from each quadrat taken during the study. As indicated by observations and stomach contents, shrews were taking prey on the surface of the ground, rather than in the soil. This was found to be similar to the foraging behavior reported by Platt (1972). Thus invertebrate collections were assumed to be similar to ones that would be encountered by a shrew while foraging.

Three methods were used to estimate relative prey densities. First, the numerical prey density was calculated as the number of prey items collected per quadrat per day or per quadrat during the entire period of study. Second, the biomass of prey collected on each quadrat was obtained from the numerical prey densities and mean prey weights. For size selective predators (Platt, 1972), correlations between predator and prey densities might not be detected by numerical density by the body lengths of the prey "species," body length of the invertebrate "species" was used as an index to the relative size of prey items. By weighting the numerical density by the body lengths of the prey "species," the third parameter, which we called the prey size density (psd), was obtained.

Graphical analyses of dominance-diversity relationships using methods developed by Whittaker (1965) were used to determine if differences existed between the composition of prey sets on the four study quadrats. The concentration of dominance (C) in prey sets, measured using the index developed by Simpson (1949), was calculated as: $C = \sum f_i^2$, where f_i is the frequency of occurrence of the i th "species." The contribution of the i th "species" (C_i) to the total dominance (C), calculated as $C_i = \log_{10} (C_i/C) (100)$, was used to illustrate graphically differences in the dominance relationships of prey sets.

Quantitative measurements of prey set diversity were made using the number of "species" and number of individuals per "species" collected. Species diversity parameters were used in the analysis of daily collections, and to characterize total prey sets, trophic components, and weight classes. Species richness (d), from Margalef (1958), the species diversity (H'), using the Shannon-Wiener information theory formula (Lloyd, Zar, and Karr, 1968), and equitability (e) from Pielou (1966) were calculated. The formulas used are given below:

$$d = (S-1)/\log_2 N$$

$$H' = -\sum p_i \log_2 p_i \text{ and}$$

$$e = H'/H_{\max}$$

In these formulas S is the number of "species" in a sample, N is the total number of individuals in a sample, p_i is the proportion of N that is represented by the number of individuals (N_i) in the i th "species" ($p_i = n_i/N$), and $H_{\max} = -\log_2 S$ is the maximum diversity of a sample containing S "species."

RESULTS

A. Relative Densities of *Sorex cinereus* on the Study Quadrats

The total number of *Sorex* collected on the four quadrats while data on invertebrate prey sets were being collected are presented in Table I. *S. cinereus* populations contained a number of resident breeding adults. Since all quadrats con-

TABLE I. RELATIVE DENSITIES OF *SOREX CINEREUS*
Quadrat

Quadrat	Shrews Trapped During Invertebrate Data Collection	
	<i>Blarina</i>	<i>Sorex</i>
LGu	0	10
LGs	0	7
CPu	0	6
CPs	0	2

tained a large number of traps, the shrews trapped during the time period of invertebrate data collection probably included most of the resident and nomadic shrews that entered each quadrat. During the study, *B. brevicauda* populations remaining on both ecosystems were confined to swales and low wet areas.

TABLE 2. NUMERICAL INVERTEBRATE PREY DENSITIES

Quadrat	LGu	LGs	CPu	CPs
Number of <i>Sorex</i> captured	10	7	6	2
Number of prey collected per day (\pm S.E.)	9.5 \pm 1.4	11.5 \pm 1.5	13.3 \pm 1.3	15.9 \pm 1.8
Total number of prey collected	104	127	146	175
Total number of herbivorous and detritivorous prey collected	51	66	68	88
Total number of carnivorous prey collected	53	61	78	87

1. Numerical Prey Density

The numerical densities of prey on the different quadrats are presented in Table 2. The total number of prey organisms collected from each quadrat varied inversely with the shrew density. Likewise the number of invertebrates collected per day of sampling decreased with increasing shrew densities. An analysis of variance was made on the number of prey captured per day on each quadrat. The daily collections from a given quadrat were not significantly different

from each other ($P < .10$). The numerical prey densities on the LGu and CPs quadrats were different from the other two quadrats and from each other ($P > .05$). The LGs and CPu quadrats were not significantly different from each other in terms of the number of prey collected per day ($P < .10$). Similar results occurred for the numbers of invertebrates in the herbivore-detritivore and carnivore trophic levels (Table 2). However, the trends for decreasing prey density with increasing shrew density were not observed for the numbers of individuals in the different weight classes.

2. Prey Biomass

The data for the total invertebrate biomass are presented in Table 3. Total prey biomass was greater on the slopes than on the upland areas and was associated with community productivity. The biomass of the six weight classes comprising the invertebrate fauna is presented as a function of the shrew density in Figure 1. The biomass of the weight classes showed little association with shrew density.

3. Prey Size Density

The results (Figure 2) indicated that the psd of both trophic levels and for the total invertebrate fauna were inversely correlated with the shrew density. However, the mean prey sizes expressed in terms of body length were not very different at any shrew density. Apparently, the association between psd and shrew density was primarily a function of the great differences between the numerical prey densities on the different quadrats. However, other factors were involved. Although the numerical prey densities of each trophic level on the quadrats were very similar (Table 2), the psd for the two trophic levels were quite different (Figure 2). In general, the herbivores and detritivores on all four quadrats were larger than the invertebrate carnivores and therefore they contributed more to the total psd than did the carnivores.

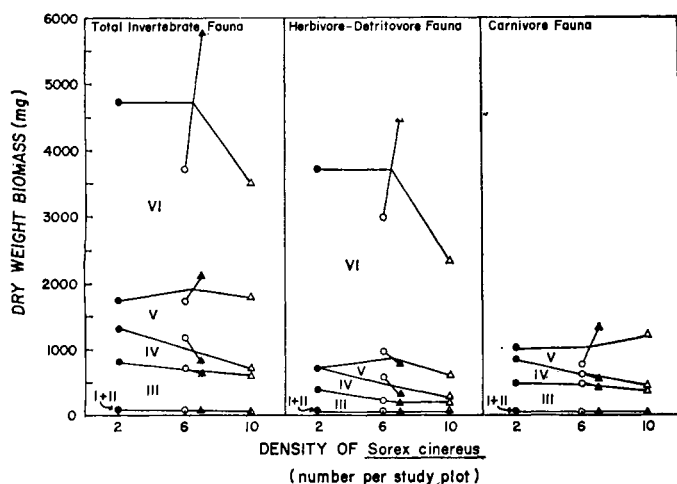


Figure 1. A comparison of invertebrate prey biomass with shrew predation levels, as indicated by relative shrew densities. Roman numerals represent weight classes of invertebrates. See text for discussion of the weight classes used. Solid symbols represent Cayler Prairie and open symbols the Lakeside Grasslands quadrats. Upland quadrats are represented by triangles and slopes quadrats are represented by circles.

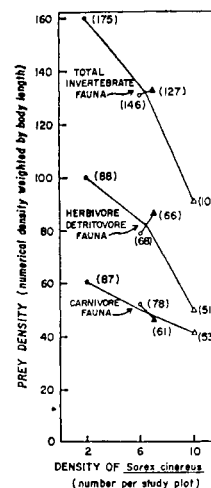


Figure 2. A comparison of invertebrate prey size density with shrew densities on the four quadrats. Solid symbols represent Cayler Prairie and open symbols the Lakeside Grasslands quadrats. Upland quadrats are represented by triangles and slopes quadrats are represented by circles.

TABLE 3. DRY WEIGHT BIOMASS OF INVERTEBRATE PREY

Quadrat	LGu	LGs	CPu	CPs
Number of <i>Sorex</i> captured	10	7	6	2
Total biomass of invertebrate prey (mg)	3510	5780	3760	4130
Biomass of herbivorous and detritivorous prey (mg)	2320	4460	2980	3120
Biomass of carnivorous prey (mg)	1190	1320	780	1010

B. Species Dominance in Prey Sets

1. Dominance Indices

The dominance values of the total prey set biomass on each quadrat and dominance values for the herbivore-detritivore components were inversely related to shrew density (Table 4). The dominance indices for the carnivores were higher for the LG quadrats than for the CP quadrats. Since the herbivore-detritivore component comprised a greater proportion of the total biomass than did the carnivores, the trends of the herbivore-detritivore component are reflected in the dominance indices for the total invertebrate fauna on each quadrat (Table 4).

TABLE 4. COMPOSITION OF PREY SETS: DOMINANCE INDICES FOR PREY SET BIOMASS

Quadrat	LGu	LGs	CPu	CPs
Number of <i>Sorex</i> captured	10	7	6	2
Dominance index to total prey biomass	0.23	0.33	0.33	0.42
Dominance index to herbivorous + detritivorous prey biomass	0.41	0.51	0.49	0.66
Dominance index to carnivorous prey biomass	0.44	0.44	0.28	0.21

2. Dominance-Diversity Relationships

The dominance-diversity curves for all "species" in the prey sets on the four quadrats are presented in Figure 3. The dominance-diversity curves illustrate the contributions of the different "species" to the dominance index. The dominant "species" (a large cricket) comprised 74% of the total dominance on LGu, 89% on LGs, 92% on CPu, and 96% on CPs. The importance of this "species" declined as the shrew density increased. There was a slight but persistent tendency for subdominants to increase in importance as the shrew density increased (Figure 3). The number of "species" with intermediate importance values was about the same on all four quadrats.

The dominance-diversity curves for the herbivore-detritivore fauna (Figure 4) were similar to the dominance-diversity curves for all invertebrate "species" (Figure 3). The dominant "species" contributed 94% of the total herbivore-detritivore dominance on LGu, 96% on both LGs and CPu, and 98% on CPs. On LGu, LGs, and CPu, there were one or two subdominants contributing 3-4% of the dominance,

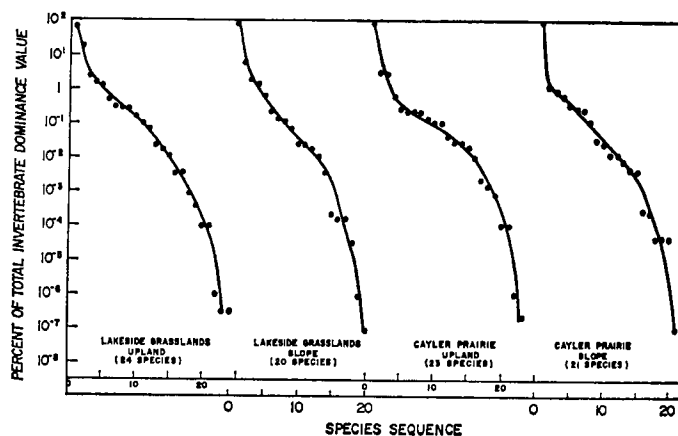


Figure 3. Dominance-diversity curves for the contributions of all invertebrate "species" to the dominance index. Quadrats are arranged in order of decreasing shrew density.

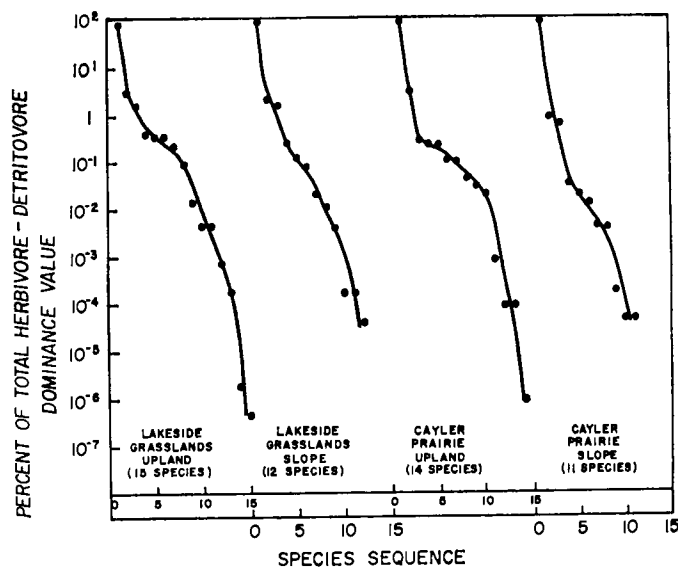


Figure 4. Dominance-diversity curves for the contributions of individual "species" of invertebrate herbivores and detritivore dominance index. Quadrats are arranged in order of decreasing shrew density.

while on CPs there was no subdominant contributing more than 1% of the dominance. The dominance-diversity curves for the carnivores are presented in Figure 5. On all quadrats more than one "species" contributed greater than 1% of the total dominance index. Furthermore, on CPs, four "species" contributed more than 10% of the total dominance. Therefore increases in the importance of invertebrate carnivores were associated with decreased shrew density.

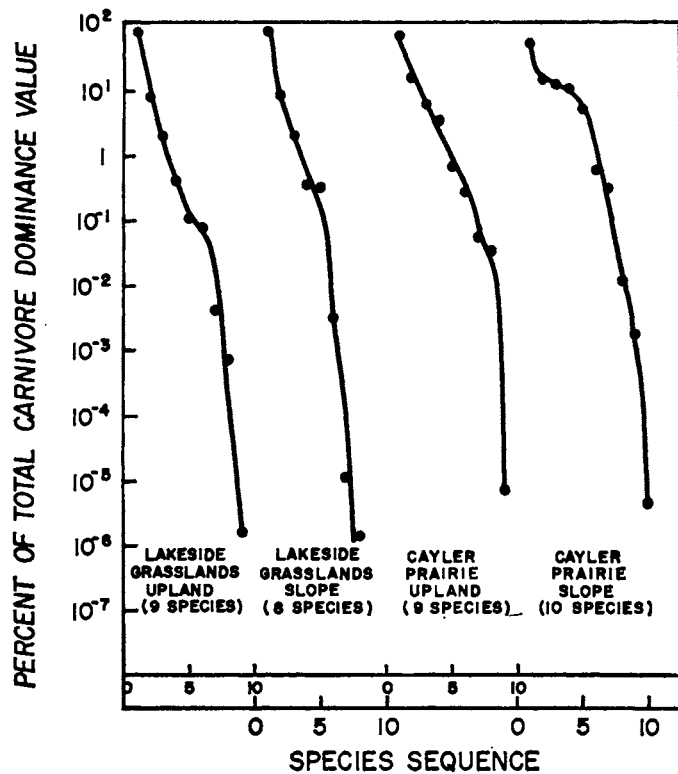


Figure 5. Dominance-diversity curves for the invertebrate carnivores. Quadrats are arranged in order of decreasing shrew density.

TABLE 5. SPECIES DIVERSITY PARAMETERS FOR TOTAL INVERTEBRATE ASSEMBLAGES, USING DATES OF COLLECTION FOR REPLICATION (N = 11)

Quadrat	Number of <i>Sorex</i> Captured	$d \pm S.E.$	$H' \pm S.E.$	$e \pm S.E.$
LGu	10	1.64 ± 0.06	2.40 ± 0.09	0.94 ± 0.01
LGs	7	1.53 ± 0.09	2.42 ± 0.11	0.93 ± 0.01
CPu	6	1.54 ± 0.15	2.34 ± 0.16	0.87 ± 0.02
CPs	2	1.47 ± 0.11	2.43 ± 0.12	0.89 ± 0.02

C. The Species Diversity of Prey Sets

1. Species Diversity of Invertebrate Assemblages Using Dates of Collection for Replication

The means and standard errors of the species richness (d), species diversity (H') and equitability (e) are presented in Table 5. The species richness showed a positive association with shrew density. The mean number of "species" collected per day varied from 6.1 to 5.7 and was not different on any of the quadrats. However, the number of individuals collected per day (Table 2) decreased with increasing shrew density. Thus the increase in the species richness with increasing shrew density results from a decrease in the density of prey items rather than any change

in the number of "species" present. The equitability, calculated for each date of collection, was higher on LG than on CP. This was attributed to the larger number of small carnivores (lycosid spiders) collected on CP than on LG. The species diversity (H') for daily collections was not significantly different on any of the quadrats. Small sample sizes affected the values obtained each day, and thus the daily H' fluctuated widely.

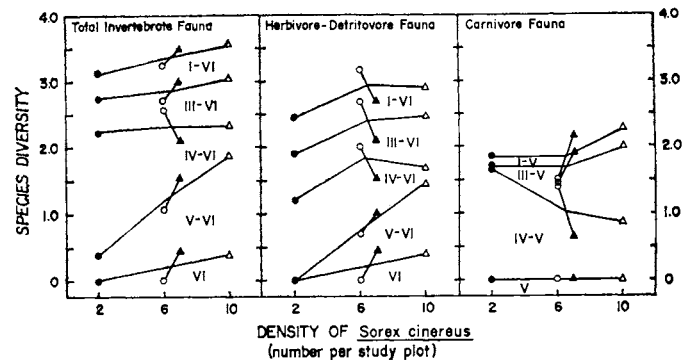


Figure 6. Invertebrate prey species diversity (H') is presented as a function of shrew densities. See text for discussion of the use of weight classes I-VI. Solid symbols represent Cayler Prairie quadrats and open symbols Lakeside Grasslands quadrats. Upland quadrats are represented by triangles and slopes quadrats are represented by circles.

2. Species Diversity of Total Invertebrate Assemblages

The species diversity (H') of the weight classes comprising the total invertebrate fauna is presented in Figure 6. Species diversity indices were obtained by adding successively the contributions of the different weight classes to the largest (weight class VI). For the herbivore-detritivore faunal component, the species diversity of weight classes V and VI combined was positively associated with the shrew density. Compensatory increases in the species diversity of weight class V may have occurred when the dominance of weight class VI was reduced by increased shrew predation. Among other weight classes, the high carnivore diversity on LG and the high herbivore-detritivore diversity on both uplands resulted in a higher diversity on LGu and a lower diversity on CPs. Thus there was an apparent positive association of total species diversity with shrew density.

DISCUSSION AND CONCLUSIONS

Shrews in general are noted to take a wide variety of prey sizes and to feed upon a wide variety of invertebrates (Hamilton, 1930, 1941; Whitaker and Ferraro, 1963; Rudge, 1968; Platt, 1972; Whitaker and Mumford, 1972). *Sorex* in particular appears to respond to the availability of prey and may exploit seasonally transient members of the litter fauna. Since the species composition of litter fauna changes during the year, it is not unreasonable to expect such a predator to respond to the size of prey it encounters in runways on the surface of the ground. This was indicated in this study by the data on psd. The consequences of prey size selection in

fishes have been well documented (Brooks and Dodson, 1965; Hall, Cooper, and Werner, 1970). Over long-term periods, fish can structure zooplankton communities. A greater diversity of smaller sized organisms occurs when fish are present.

From the association of increased shrew density with increased numerical prey density, decreased prey size density, decreased prey set biomass dominance, and increased species diversity of certain size classes, we tentatively conclude that *S. cinereus* affects the composition of prey sets upon which it feeds. In particular, the masked shrew appears to decrease the density of the dominant, large-sized invertebrate prey species. This decrease in the numerical density of the largest-sized prey resulted in a more equitable distribution of prey individuals among the other "species" present and an increase in the diversity of the larger size classes. We predict that size-selective predation is a short-term response to high densities of certain prey size classes. As the densities of larger prey are decreased by predation, niches are opened to smaller species that may then coexist with the larger and more abundant prey. If the predation rates are maintained over long time periods, a decrease in competition between invertebrate species due to shrew predation should result in further increases in species diversity and increased trophic complexity. A similar hypothesis has been proposed for the maintenance of high diversity in deep sea communities also (Dayton and Hessler, 1972). This phenomenon has been documented for starfish (Paine, 1966, 1971; Dayton, 1971); Paine has described keystone predators as those that reduce competition by preying heavily upon dominant species in the prey set. Thus *S. cinereus* appears to have feeding habits that potentially would enable it to act as a keystone predator in prairie ecosystem litter-detritus food webs.

Keystone predators such as fish and starfish are characterized by indeterminate growth. This permits a facultative response whenever conditions are such that growth is possible. *Sorex*, while not exhibiting the indeterminate growth patterns of the aquatic predators, has a high metabolic rate (Morrison and Pearson, 1946; Morrison, Ryser, and Dawe, 1959). The large food requirements for such a mammal (Morrison, Pierce, and Ryser, 1957), coupled with a high reproductive rate, would facilitate rapid numerical and functional responses to changes in prey density (Platt, 1972). *S. cinereus*, being capable of large intake of prey relative to its body size, should be able to affect prey populations out of proportion to its own population size. This, coupled with the mobility of shrews, makes the ability to alter prey set composition (i.e., a keystone predator) feasible.

The absence of an effect upon the biomass of prey also is not surprising; similar results were noted by Hall, Cooper and Werner (1970) concerning bluegill predation and total pond invertebrate production. Instead only the biomass of the larger size classes of invertebrate prey were correlated with the total fish production. The short time period of the present study precluded any correlation of invertebrate prey and shrew production.

The interactions between *S. cinereus* and other predators is also of interest. The effects of decreasing the dominant largest prey should, if compensatory increases in small prey occur, favor increases in the density of small invertebrate predators. Also, *S. cinereus* populations increased after the *B. brevicauda* populations crashed, and then only in areas where *Blarina* was not present. From unpublished laboratory data

and other studies (Whitaker and Ferraro, 1963; Platt, 1972) it appears that *B. brevicauda* also is prey-size selective. Diet overlaps between the two species of shrews (Whitaker and Mumford, 1972) include many of the medium to large-sized invertebrates. Consequently effects of the two species of shrews upon prey populations might be somewhat similar. When both species of shrews are present in the same ecosystem, it might be expected that they would utilize different areas for foraging. Generally *S. cinereus* is not very numerous unless *B. brevicauda* is scarce; there appears to be some inhibitory effect on the smaller species by the larger. *Blarina*, however, depends upon *Microtus* at least as an alternate prey (Platt, 1972); when vole populations decline, so do those of the short-tailed shrew. At this time the density of *S. cinereus* increases. It seems possible that *Sorex* and *Blarina* may act alternately as a keystone predator over time. This would undoubtedly increase the stability of a system containing populations that exhibit cyclical patterns of population density. If predators higher in the food web normally keep short-tailed shrew populations at densities low enough to enable populations of the smaller masked shrew to coexist, the stability of the system also would be increased.

LITERATURE CITED

- AIKMAN, J. M., and R. F. THORNE. 1956. The Cayler Prairie: An ecologic and taxonomic study of a northwest Iowa prairie. *Proc. Iowa Acad. Sci.* 63:177-200.
- ANDERSON, W. A. 1936. Progress in the regeneration of the prairie at the Iowa Lakeside Laboratory. *Proc. Iowa Acad. Sci.* 43:87-93.
- ANDERSON, W. A. 1946. Development of prairies at Iowa Lakeside Laboratory. *Amer. Midl. Nat.* 36:431-455.
- BROOKS, J. L., and S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* 150:28-35.
- BUCKNER, C. H. 1966. Populations and ecological relationships of shrews in tamarack bogs of southeastern Manitoba. *J. Mammal.* 47:181-194.
- BUCKNER, C. H. 1969. Some aspects of the population ecology of the common shrew, *Sorex araneus*, near Oxford, England. *J. Mammal.* 50:326-332.
- DAYTON, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41:351-389.
- DAYTON, P. K., and R. R. HESSLER. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep Sea Res.* 19:199-208.
- DODSON, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnol. Oceanogr.* 15:131-137.
- HALL, D. J., W. E. COOPER, and E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* 15:839-928.
- HAMILTON, W. J., JR. 1930. The food of the Soricidae. *J. Mammal.* 11:26-39.
- HAMILTON, W. J., JR. 1941. The food of small forest mammals in Eastern United States. *J. Mammal.* 22:250-263.
- HOLLING, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol.* 91:293-320.
- HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Ent. Soc. Canada* 45:1-60.
- HURLBERT, S. H., J. ZEDLER, and D. FAIRBANKS. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. *Science* 175:639-641.

- JAQUES, H. E. 1947. *How to know the insects*. Wm. C. Brown Co., Dubuque.
- KASTON, B. J. 1952. *How to know the spiders*. Wm. C. Brown Co., Dubuque.
- LLOYD, M., J. H. ZAR, and J. R. KARR. 1968. On the calculation of information-theoretical measures of diversity. *Amer. Midl. Natur.* 79:257-272.
- MARGALEF, D. R. 1958. Information theory in ecology. *Gen. Syst.* 3:36-71.
- MICHELSEN, N. C. 1966. Intraspecific and interspecific competition in the shrews *Sorex araneus* L. and *S. minutus* L. *Arch. Neerlandaises Zool.* 17:73-174.
- MORRISON, P. R., and O. P. PEARSON. 1946. The metabolism of a very small mammal. *Science* 104:287-292.
- MORRISON, P. R., M. PIERCE, and F. A. RYSER. 1957. Food consumption and body weight in the masked and short-tailed shrews. *Amer. Midl. Nat.* 57:493-501.
- MORRISON, P. R., F. A. RYSER, and A. R. DAWE. 1959. Studies on the physiology of the masked shrew *Sorex cinereus*. *Physiol. Zool.* 32:256-271.
- PAINÉ, R. T. 1966. Food web complexity and species diversity. *Amer. Nat.* 100:65-75.
- PAINÉ, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* 52:1096-1106.
- PIELOU, E. C. 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13:131-144.
- PLATT, W. J. 1972. An experimental analysis of predator population energetics: the short-tailed shrew in old-field ecosystems. Unpubl. Ph.D. Thesis. Cornell University.
- RUDGE, M. R. 1968. The food of the common shrew *Sorex araneus* L. (Insectivora: *Soricidae*) in Britain. *J. Anim. Ecol.* 37:565-581.
- RUDMAN, S., and R. W. POHL. 1951. Vegetational changes in ungrazed grassland at Iowa Lakeside Laboratory, 1935-1950. *Proc. Iowa Acad. Sci.* 58:189-200.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- WHITAKER, J. O. and M. C. FERRARO. 1963. Summer food of 220 short-tailed shrews from Ithaca, N.Y. *J. Mammal.* 44:419.
- WHITAKER, J. O., and R. E. MUMFORD. 1972. Food and ectoparasites in Indiana shrews. *J. Mammal.* 53:329-335.
- WHITAKER, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147:250-260.